Manual, blowing, and verbal simple reactions to lateralized flashes of light in commissurotomy patients

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Interhemispheric transfer of information was examined in two complete commissurotomy patients with the simple reaction-time paradigm. The patients had to produce a finger, blowing, or verbal response to a light appearing in either the right or the left visual field, and a control subject was tested in exactly the same conditions. The three subjects displayed qualitatively similar patterns of results overall. The finger task yielded a highly significant interaction between visual field and responding hand, and the reaction-time difference between the ipsilateral and contralateral responses was of the order of 30 and 50 msec for each patient, respectively, suggesting that subcortical transfer of information is highly inefficient in the manual task as compared with a callosal route. By contrast, the blowing and the verbal tasks resulted in no visual-field difference, even though the latter require the specialized mechanisms of the left hemisphere for speech production. The results suggest that, before being organized within the left hemisphere, a verbal response may be initiated in subcortical structures to which both hemispheres have equally efficient access.

The simple reaction-time (RT) paradigm has provided one of the most direct means of examining interhemispheric transfer of information. If a light is flashed to either the right or the left of a fixation point, and a subject responds with either the right or the left hand, the RT difference between ipsilateral and contralateral field-hand combination may provide a measure of interhemispheric transmission time (ITT) as a result of the different lengths of the nervous circuits necessary for the production of a response. This logic is based on the anatomical organization of the visual system (contralateral projection of visual field) and of the motor system (contralateral control of finger movement), by virtue of which input reception and response initiation take place within the same cerebral hemisphere in ipsilateral responses and in different hemispheres in contralateral responses. In the first application of this logic, Poffenberger (1912) found that RTs were faster by about 4 msec when the light and the responding hand were on the same side of the body

than when they were on different sides, and this value was taken as a measure of ITT.

The validity of Poffenberger's logic and finding has been repeatedly confirmed in more recent experiments (e.g., Anzola, Bertoloni, Buchtel, & Rizzolatti, 1977; Berlucchi, 1978; Berlucchi, Crea, Di Stefano, & Tassinari, 1977; Jeeves & Dixon, 1970; Rizzolatti, 1977; see Bashore, 1981, for a review). In addition, the anatomical basis of the RT differences was clearly demonstrated by Anzola et al. (1977), who found the same interaction between visual field and responding hand whether the hands were crossed or in their normal uncrossed position, thus ruling out any influence of stimulus-response compatibility in the simple RT task.

By the same logic, it has been assumed that the use of a verbal response, which typically the left hemisphere is equipped to produce, would provide another way of estimating ITT. Since the left anterior cortex controls response production, the RT difference between left (LVF) and right (RVF) visual-field presentations would provide an estimation of the time for information to cross the corpus callosum from the right to the left hemisphere. However, most experiments designed with this objective in mind have not employed simple RT tasks but discrimination or choice RT tasks. As a consequence, the RT difference between LVF and RVF presentations could have resulted not only from ITT, but also from hemispheric differences in the processing of, and decision-

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making on, the information received by each hemisphere. In fact, widely discrepant estimates of ITT have been reported in experiments using vocal RT (Filbey & Gazzaniga, 1969; Kleinman, Carron, Cloninger, & Halvachs, 1976; Moscovitch & Catlin, 1970), and the consensus is now that such discrimination and choice RT tasks are not well suited for this purpose. Indeed, findings of negative transmission time—that is, faster vocal RT to LVF than RVF presentations—have been reported (Amadeo, Roemer, & Shagass, 1977; Bashore, 1981), which, if reliable, necessarily result from hemisphere difference prior to the assumed information transfer. In addition, even when simple verbal RT tasks were used (Milner & Lines, 1982; Tassinari, Morelli, & Berlucchi, 1983), no evidence was found of a consistent advantage to the left hemisphere. Milner and Lines (1982) had to test 24 subjects to find 12 who displayed the expected RVF advantage, and Tassinari et al. (1983) obtained no overall visual field difference.

It thus appears that different neural pathways mediate interhemispheric transfer of information from the light-receiving hemisphere to the response-producing hemisphere in manual and verbal responses, and this has shifted the focus of interest from estimating transmission time to specifying the neural route of this transmission. Although there is good agreement that a manual (finger-key pressing) response is uniquely controlled by the hemisphere contralateral to the responding hand (cf. Brinkman & Kuypers, 1973), and that the left hemisphere subserves the motor speech mechanisms, the question of the form in which, and the pathway through which, the information is received by the responding hemisphere from the light-receiving hemisphere is still a matter of controversy. Milner and Lines (1982) observed variations in transmission speed as a function of stimulus intensity in verbal but not manual tasks. They suggested that a “visual sensory” callosal route was involved in the former, whereas a nonvisual callosal route would subserve interhemispheric transfer in the latter. This interpretation, however, leaves unexplained what underlies the selection of a particular route in the two types of response.

Moscovitch (1983) and Tassinari et al. (1983) disagree with Milner and Lines’s interpretation, each for different reasons. Moscovitch argued that the absence of effects of stimulus energy on RT differences between ipsilateral and contralateral manual responses does not necessarily imply a nonvisual callosal transfer and may result from transmission of a visual “higher order” code that would be free of sensory components. This explanation does not account, however, for the increase in transmission time with reduced intensity in the verbal task. Tassinari et al., on the other hand, while concurring with the idea of a nonvisual callosal transfer in contralateral manual responses, argued that the use of a selected group of subjects in Milner and Lines’s vocal task, whereby half the subjects were discarded because they initially displayed a LVF superiority, could not provide representative information for a valid interpretation of visual-field differ-

ences in the simple verbal RT task. Using a randomly selected group of subjects, Tassinari et al. (1983) found no overall visual-field differences in this RT task, but observed variations across subjects in individual patterns of visual-field performance. They explained their finding by suggesting that the *initiation* of verbal responses is not lateralized, but depends on unified centrencephalic mechanisms to which both hemispheres have equal access, and that only the *organization* of the verbal response is lateralized to the left hemisphere (cf. Penfield & Rasmussen, 1968). This suggestion of a different locus for the initiation of manual and verbal responses in simple RT tasks, and thus of different neural pathways mediating interhemispheric transfer in the two tasks, offers an alternative account of existing results and may explain why the verbal and the manual tasks yield qualitatively different outcomes.

While resolution of this issue must await further experimentation with normal subjects, some information relevant to the problem of interhemispheric transfer may be gathered by testing patients whose main pathways (corpus callosum and anterior commissure) linking the two hemispheres have been severed. Although inferences from performance by commissurotomy patients about normal cerebral functions are not without difficulties (see below), the models of Milner and Lines and of Tassinari et al. make different predictions about the pattern of results in verbal and manual simple RT tasks by “split-brain” patients.

Milner and Lines suggest that the right manual response and the vocal response are both initiated and organized in the left hemisphere, and that, therefore, the advantage of RVF over LVF presentation should be of about the same order in right-finger and verbal responses. Support for this prediction comes from studies with callosal agenesis (e.g., Jeeves, 1969; Milner, 1982; Reynolds & Jeeves, 1977; see Milner & Jeeves, 1979, for a review) that show similar RT advantages in the two types of responses (about 20 msec, Milner, 1982). However, transfer through the anterior commissure, which is sometimes hypertrophied in acallosals, cannot be ruled out, and the atypical organization of cerebral structures in these patients (Chiarello, 1980) makes inferences about normal brain functions highly hazardous. On the other hand, Tassinari et al.’s (1983) model predicts different patterns of results in the verbal and manual tasks: Since a verbal response is assumed to be initiated in centrencephalic areas to which both hemispheres have equal access, section of the forebrain commissures should leave operative such a pathway, and a verbal response should be produced about equally fast to LVF and RVF presentations. In contrast, since a finger response is initiated in the contralateral hemisphere, section of the forebrain commissures precludes a direct transfer from the receiving to the responding hemisphere and should result in large RT difference between ipsilateral and contralateral responses. The experiments reported below were designed to examine these opposite predictions. In addition, a blowing response,

which can be initiated by either hemisphere (Hécaen & Albert, 1978), was included in the design to control for possible hemisphere difference in the processing of light stimuli.

EXPERIMENTS

The experiments consisted of measuring simple RTs of manual, blowing, and verbal response to lateralized flashes of light of two different intensities by two commissurotomed patients. No attempt has previously been made at measuring simple RTs in split-brain subjects, although choice RT, which requires spatial discrimination of the stimulus, has been employed in callosotomized humans from the Van Wagenen series (Smith, 1947) and in commissurotomed baboons (Guiard & Requin, 1978). Although the humans had no difficulty performing the task, possibly because of incomplete section of the commissures, the baboons were unsuccessful in contrast to intact animals.

The use of simple RT tasks with commissurotomed patients raises a series of difficulties which warrant caution for interpretation. First, response latencies are markedly slower in split-brain than in normal subjects, and, consequently, more variable. Indeed, Smith (1947) concluded his investigation of the first series of callosotomized patients by stating that the "radical increase in response time for simple reactions appears to be the *only* psychological function disturbed significantly by surgical section of the cerebral commissures among many different perceptual, motor, intellectual and sidedness activities which have been studied" (p. 375, *italics added*). Second, in normals, research based on the simple RT is concerned with "population" measures in the sense that the mean RT of the group is used for inferences about processes underlying the performance of each subject, even though not all individual results conform to the general pattern. For example, in each of Milner and Lines's (1982) manual RT tasks, at least 3 out of 12 subjects had RT differences between ipsilateral and contralateral responses opposite to that of the group. Although such an averaging procedure may be necessary to refer to the population, it cannot be used with split-brain patients who must be considered as individual cases because of their idiosyncrasies and different etiologies of epileptic seizures. This increases the risk of unrepresentative performance and wrong conclusions. Third, these patients are still under anticonvulsive medication and have lowered attention span and capacity, which precludes use of the large number of trials typical of research based on the simple RT in normal subjects. In order to control for the shorter procedure used in the present experiments, a normal right-handed adult was also tested under exactly the same conditions as the patients. Fourth, not only had the brains of these patients been abnormal since at least infancy, but much reorganization may also have taken place after the commissurotomy, and one must therefore be cautious in making inferences about the normal brain. None-

theless, the patients have presumably intact subcortical pathways and sectioned forebrain commissures, which provides the opportunity to examine specific predictions regarding interhemispheric transfer, depending on the response modality.

Method

The subjects were a woman (N.G., 51 years old) and a man (L.B., 32 years old) who had undergone complete forebrain commissurotomy 21 and 19 years earlier, respectively, for the relief of intractable epilepsy. They are both right-handed with speech production mechanisms represented in the left hemisphere. Details of the medical and surgical histories of these patients have been repeatedly reported (see Bogen & Vogel, 1975). A right-handed male (S.Y., 34 years old) participated as a control subject.

The experiments were conducted in a dimly lit room (1.2 cd/m² ambient luminance). The stimuli were rear-projected on a screen located 57 cm in front of the subject, whose head was held in a fixed position by a chinrest, so that the eyes were exactly at the level of a central fixation point. Three Kodak projectors, equipped with electronic shutters, were used for stimulus presentation. The stimuli were generated using opaque slides, each containing a round transparent hole that let the light of the projector through, resulting in a 10-msec 5-mm-diam flash that appeared 4 cm to the right or left of the fixation point. There was no spreading of light beyond 1 cm of stimulus position and therefore no spreading of light into the other visual field. Two projectors were used for lateral presentation; each was used for right-field presentation on half the trials and for left-field presentation on the other half. The light stimuli could appear at two different intensity levels, 25 or 4 cd/m², on a 1.5-cd/m² background. Reduction in stimulus intensity was achieved by placing a .80 (16%) neutral density filter on appropriate shutters. The third projector was used to send, as a warning signal at the beginning of each trial, a 100-msec flash of dim light (2 cd/m²) right on to the central fixation point. The interval between the warning signal and the onset of the stimulus varied randomly from 1 to 3 sec. Because the opening of the shutter made noise and it was important to prevent the subject from responding to the light stimulus on the basis of an auditory cue, the subject's ears were obstructed with ear wax and white noise was delivered via headphones worn by the subject, so that any external sound was completely masked.

In the manual task, the subject responded by pressing a Morse key with the index finger of one hand, while the other hand lay on the table at least 20 cm away from the midline and legs were apart to avoid any possible cross-cuing. The Morse key was located in the midsagittal plane and was at the same location for right- and left-hand responses. The subject responded by pressing the key with the index finger while the hand and the forearm remained immobile. In the blowing and the verbal tasks, a microphone, located 8 cm in front of and 4 cm below the subject's mouth, was used. The subject responded either by blowing or by pronouncing the word "cat." The use of such a verbal response was intended to provide a sharp voice onset to trigger the voice key. In addition, the complex motor organization involved in the production of stop-consonants is typically subserved by the speech mechanism of the left hemisphere (Leocurs & Lhermitte, 1980), thus making the production of a verbal response by the right hemisphere most unlikely.

An electronic circuit, closed at stimulus onset, was opened when the subject pressed the Morse key, or at the first blow of air or first sound emitted by the subject, which stopped a millisecond counter. The subject was instructed to fixate the central dot, from the warning signal to response production, and to respond as quickly as possible. A single session consisted of 50 trials, preceded by 15 practice trials, and there were eight such sessions: four manual sessions (each hand at two intensity levels), two blowing sessions, and two verbal sessions (at two intensity levels). The order of in-

tensity levels was counterbalanced within subject. Each subject was run on the manual task first, mainly because performance would be evaluated in terms of interaction between field and hand and would thus be less sensitive to practice effects. L.B. performed the verbal task before the blowing task, and N.G. was tested in the reversed order, as was S.Y. Type of response and intensity levels were blocked within session; visual-field presentation was mixed and occurred in a random order.

Responses exceeding 3 SDs above the mean were discarded, and an upper limit of 600 msec was set. This resulted in the elimination of 2.8% of the data for L.B., 3.8% for N.G., and none for S.Y. Both means and medians for each session were calculated and showed the same trend, and the analyses were conducted on means. Comparisons were carried out within subjects by deriving a *t* value for differences in mean RTs, with correction for unequal variances, using the adjustment suggested by Cochran and Cox (1957), when necessary.

Results

Figure 1 shows the means of each subject, averaged over intensity levels, of RTs to stimuli in the left and right visual fields for manual responses (as a function of hand) and for blowing and verbal responses. Because of different basic response latencies across subjects, different scales were used in plotting the results. Figure 1 reveals qualitatively similar patterns of results, but widely dis-

Figure 1. Reaction times (in milliseconds), averaged over intensity levels, to a light appearing in the left (LVF) or right (RVF) visual field as a function of response modality, for each of the three subjects (S.Y., the control subject, and N.G. and L.B., the commissurotomized patients). Different scales are used in plotting reaction times for each subject.

Table 1
Mean Reaction Time (in minutes) and Standard Error (SE) for Subject S.Y. in the Three Tasks, as a Function of Stimulus Intensity, Visual Field, and Responding Hand, and Estimates of Transfer Time

Hand	High Luminance				Low Luminance			
	LVF		RVF		LVF		RVF	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Manual								
Left	249.3	6.38	251.8	5.32	266.4	7.75	280.6	7.03
Right	240.7	5.45	236.4	4.40	260.0	4.70	258.5	5.15
Blowing								
	232.6	6.05	231.7	6.24	262.9	9.33	261.5	6.39
Verbal								
	235.9	4.61	239.4	5.52	265.9	6.07	271.6	7.96
Estimates of Transfer Time								
High Luminance			Low Luminance			Mean		
Manual—Ipsilateral minus Contralateral								
3.40			7.92			5.66		
Blowing—LVF minus RVF								
0.92			1.4			1.16		
Verbal—LVF minus RVF								
-3.56			-6.16			-4.86		

Note—LVF=left visual field; RVF=right visual field.

crepant latencies, across subjects. All three subjects showed the expected interaction of visual field by hand, confirming that ipsilateral responses are made faster than contralateral responses. By contrast, the blowing task yielded about equal performance in the two visual fields, and the verbal task failed to produce a RVF superiority that would be expected if the response was initiated in the left hemisphere. These results will be examined in more detail by considering separately those of the control subject and those of the patients.

Control subject. S.Y.'s response latencies and standard errors are presented in Table 1 for each task as a function of visual field and intensity level, along with "estimates of transfer time" representing RT differences between ipsilateral and contralateral responses in the manual task and between LVF and RVF in the two other tasks. Overall, these results are typical of RTs obtained in previous studies (Milner & Lines, 1982; Tassinari et al., 1983), even though they were based on considerably fewer trials and only a single subject. The procedure used in these experiments was thus sensitive enough to yield relevant information about performance in the simple RT task.

As is apparent in Table 1, intensity affected reaction times and S.Y. responded faster to high- than to low-intensity light by 26.14 msec. This increase was significant [$t(199) = 7.08, p < .01$], and of about the same magnitude in the three tasks, a result similar to that obtained by Milner and Lines (1982). In the manual task, S.Y. responded faster with his right than with his left hand, a finding typical of strongly right-handed individuals (cf. Tassinari et al., 1983, Table 2). The interaction

of visual field $\times$ responding hand, measured as RT difference between ipsilateral and contralateral responses (5.66 msec—3.40 msec at high intensity and 7.92 msec at low intensity), failed to reach a reliable level of significance [$t(99) = 1.53$, $p > .05$], although it was of larger magnitude than the estimate of 3 msec for the general population (Bashore, 1981). This absence of significance may be due to the smaller number of trials employed and/or to the greater variability formed among trials of a single subject than would be obtained between the means of subjects in a group analysis. The same outcome occurred in the analysis of the effect of intensity on RT differences between ipsilateral and contralateral responses, which showed a greater increase for the latter than for the former with a reduction in light intensity. This finding departs from Milner and Lines's group results, which showed no influence of stimulus intensity on estimates of ITT with manual responses. Although little can be deduced from the results of a single subject, this finding at least suggests possible intersubject variations, or that an initial effect of intensity on ITT in the manual task disappears with practice.

The blowing task yielded an advantage for RVF over LVF presentations of 1.16 msec, which was nearly identical at the two intensity levels. This RT difference failed

to reach significance ($p > .30$), and may confirm that no hemisphere has exclusive control over the musculature involved in such a blowing action, even though blowing requires the activation of muscles used in phonation. The verbal task yielded no advantage for RVF presentations, and resulted instead in a LVF superiority of 4.86 msec, which was not significant ($p > .05$). However, a comparison of differences in RT to LVF and RVF in the right-finger response and the verbal response indicated that the difference of 7.78 msec was reliable [$t(49) = 2.04$, $p < .05$], suggesting that information did not follow the same pathways from the right to the left hemisphere in the two tasks.

Commissurotomed subjects. Response latencies and standard errors of patients L.B. and N.G. are presented in Table 2, for each task as a function of visual field and intensity level. Also presented in Table 2 are the relevant RT differences in the three tasks (ipsilateral minus contralateral RTs in the manual task, and LVF minus RVF RTs in the blowing and verbal tasks). One notable aspect of these results is that the latencies were considerably larger and response variability was higher for the two patients than for the control subject, as well as for acallosal subjects (Jeeves, 1969; Milner, 1982). Since Smith (1947) found that reaction performance was slower postopera-

Table 2
Mean Reaction Time (in milliseconds) and Standard Error (S.E.)
for L.B. and N.G. in the Three Tasks, as a Function of
Stimulus Intensity, Visual Field, and Responding
Hand, and Estimates of Transfer Time

High Luminance						Low Luminance			
		LVF		RVF		LVF		RVF	
Subject	Hand	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Manual									
L.B.	Left	324.0	8.64	336.7	8.61	352.4	8.94	368.2	9.08
	Right	352.9	6.44	325.2	12.27	362.5	8.01	303.8	8.81
N.G.	Left	300.8	10.94	339.8	8.91	341.2	11.79	344.4	5.95
	Right	451.5	16.07	352.3	6.26	419.2	17.18	358.8	6.67
Blowing									
L.B.		417.7	7.94	415.6	12.92	430.7	10.46	429.2	12.54
N.G.		436.5	25.27	444.7	21.79	504.4	26.71	505.3	25.07
Verbal									
L.B.		411.3	7.76	397.6	6.14	436.1	10.75	440.2	11.42
N.G.		472.4	25.57	464.0	17.03	478.4	21.57	481.0	18.31

Estimates of Transfer Time					
Subject	High Luminance		Low Luminance		Mean
Manual—Ipsilateral minus Contralateral					
L.B.	20.32		37.28		28.75
N.G.	69.08		31.74		50.41
Blowing—LVF minus RVF					
L.B.	2.04		1.48		1.76
N.G.	-8.20		- .96		-4.58
Verbal—LVF minus RVF					
L.B.	13.69		-4.12		4.79
N.G.	8.40		-2.64		2.88

Note—LVF=left visual field; RVF=right visual field.

tively than preoperatively in the same patient, it would seem that the longer simple reaction found in our split-brain patients was due to the section of the commissures per se rather than to brain damage associated with epilepsy.

Both L.B. and N.G. displayed an interaction of visual field $\times$ responding hand in the manual task, at both intensity levels, and this finding proved highly reliable [L.B., 355.09 and 326.34 msec for contralateral and ipsilateral responses, respectively, $t(99) = 2.89$, $p < .01$; N.G., 388.71 and 338.3 msec, respectively, $t = 5.13$, $p < .01$]. This finding is consistent with the evidence (Brinkman & Kuypers, 1973) that the contralateral hemisphere controls the movements of distal limbs. The fact that the two patients were at all capable of producing a finger response in the contralateral hand-field combination indicates that some information about the light stimulus was crossing the midline, necessarily at a subcortical level, for manual response initiation. The section of the forebrain commissures obviously had detrimental effects on this transfer, and the RT difference between ipsilateral and contralateral responses was considerably larger than that observed in intact subjects. This may indicate that this subcortical route is not normally operative in the simple manual RT task.

Although L.B. was about as efficient at responding with his left hand to the right field as he was at responding with his right hand to the left field, N.G. showed much more difficulty responding with her right hand to the left field than vice versa. Although, because of the relatively small number of trials involved, care should be taken not to overstress the importance of this finding, it may nonetheless provide a hint to suggest an asymmetric efficiency of subcortical transfer in N.G., as well as variations among commissurotomy patients in this efficiency. It is also noteworthy that the level of stimulus intensity had no consistent effect on RT, which contrasts with the results of the control subject obtained in exactly the same experimental conditions.

The blowing task yielded no significant visual-field difference in either L.B. or N.G. (1.76 msec in favor of the RVF for L.B. and 4.58 msec in favor of the LVF for N.G. [$t(49) > .40$]). However, stimulus intensity influenced RT in both subjects, as indicated by an increase of 13.3 and 64.25 msec for L.B. and N.G., respectively, with a reduction in luminance. This effect was not reliable in L.B. ($p > .05$) but reached an acceptable level of significance in N.G. ($p < .01$); there was no indication of interaction between intensity and visual field in either subject.

The verbal task produced no significant visual-field difference in either patient. Although there was a tendency for RVF stimuli to be responded to faster at high luminance, the difference did not reach a reliable level of significance and was completely eliminated at low luminance. These results suggest a different type of information transfer from that implied by the results of the manual task. In fact, a comparison of visual-field differences in the verbal task and the right-finger manual task

revealed significant differences between the manual and the verbal responses (L.B., 38.52 msec, $p < .01$; N.G., 76.88 msec, $p < .01$), which does not concur with Milner and Lines's model.¹

DISCUSSION

Asymmetric response to lateralized flashes in simple RT tasks may result from differential hemispheric efficiency at processing the stimulus or from lateralized mechanisms' mediating the production of the response, but spatial compatibility between visual field and responding hand does not seem to be a determining factor, as suggested by the lack of influence of hand position on the pattern of simple RTs (Anzola et al., 1977). The present results confirm previous findings from research with normal subjects, that it is the lateralization of the response mechanisms that is responsible for the different RTs to laterally presented light stimuli, since both the two commissurotomy patients and the control subject responded equally fast to LVF and RVF stimulation in the blowing task, which requires activation of muscles that can be controlled by either hemisphere. The two hemispheres can thus be assumed to be equally efficient at processing the light stimuli, and any asymmetry observed in the manual and verbal tasks must be assumed to involve longer, and/or less effective, neural circuits linking light receiving with the responding hemisphere. In the absence of forebrain commissures, such circuits must follow a subcortical route which previous research has shown to be capable of conveying visual, emotional, semantic, and patterned information (Johnson, 1984a; Sperry, Zaidel, & Zaidel, 1979; Trevarthen & Sperry, 1973; Zaidel, 1982).

The simple manual RT task provided further evidence of subcortical transfer of information after section of forebrain commissures, and each "disconnected" hemisphere was able to react to stimulation of the other. A finger response was chosen to ensure that response production would be initiated and controlled by the contralateral hemisphere (see Brinkman & Kuypers, 1973), and the results showed that the subcortical pathway was highly inefficient in transmitting the information across the hemispheres. The RT difference between ipsilateral and contralateral response averaged 28.75 msec for L.B. and 50.41 msec for N.G.; it was 5.66 msec for the control subject and is an estimated 3 msec for the population of normal subjects (Bashore, 1981).

These estimated times of interhemispheric transfer for L.B. and N.G. in the manual task stand in sharp contrast to those derived from the verbal task, which averaged 4.79 and 2.88 msec, respectively. If information received by the right hemisphere was crossing the midline through the same pathway as that used in the manual task, the RT difference between LVF and RVF presentations in the verbal task should have been larger than that obtained. Yet, despite the inherent advantage of the left hemisphere, which subserves language-production mechanisms, information projected directly to this hemisphere did not lead

to significantly faster responses than did a stimulation of the right hemisphere. This suggests that different mechanisms are involved in the interhemispheric transfer of information, depending on whether the response is manual or verbal, which does not concur with the prediction of Milner and Lines's (1982) model that the two tasks should yield about equal estimates of transfer time. Instead, the results are consistent with Tassinari et al.'s (1983) suggestion that the initiation of a verbal response is not lateralized but depends on nonlateralized subcortical mechanisms.² Before examining this suggestion further, an alternative account of the results should be considered.

It is conceivable that equal RTs to RVF and LVF presentations resulted from verbal response production by the left and the right hemispheres, respectively. Some findings obtained on the two commissurotomy subjects participating in the present experiments have been interpreted as indicating that the right hemisphere, especially L.B.'s, can produce speech (Johnson, 1984b). In addition, in the present task, the stimulus itself bore no direct relationship to the verbal output; it simply served as a signal to trigger the verbal-production mechanisms that were already "planned" and repeatedly used in trial after trial. Furthermore, the pattern of reaction times in the verbal task was similar to that of the blowing task, which was assumed to be controlled by either hemisphere. It is therefore possible that the absence of a significant RT difference between visual fields in the verbal task resulted from each hemisphere's producing the response after being stimulated, and that no transfer from the right to the left hemisphere was necessary for the production of the verbal response. There are, however, reasons to believe that the right hemisphere did not subserve the response in the verbal task. L.B. appears to be capable of identifying, by name, some stimuli projected to his right hemisphere, but N.G. is limited in this respect, although she displayed the same pattern of results as L.B. did in the present experiment and she was equally fast at responding to RVF and LVF stimulation. More importantly, when in Johnson's (1984b) study, L.B. could produce a verbal response to a stimulus presented in the LVF, his RTs were consistently at least twice as long as his RTs to a stimulus presented in the RVF, but both fields were responded to equally fast in the present experiment. The superiority of the left hemisphere in organizing the verbal output is certainly an undisputed fact, and it would seem most unlikely that the right hemisphere could match the left in generating the complex neural afferents necessary to activate the vocal motor system. This is not to argue against Johnson's (1984b) suggestion that the right hemisphere of some split-brain patients can produce speech in certain circumstances, but to suggest that there may be an alternative, and more efficient, route for access to the left-hemisphere "speech centers" when the task requires producing a pre-set verbal response to a signal sent to the right hemisphere.

Equal efficiency at responding verbally to LVF and RVF stimulation, in the context of equally efficient processing of the light stimulus by the two hemispheres,

implies that the verbal response, which is organized in the left hemisphere, must be initiated in structures to which both hemispheres can readily have access. Tassinari et al. (1983), following Penfield and Rasmussen (1968), have suggested a distinction between the initiation of a response and the organization of the patterning of activity of the muscles involved in a verbal response. Although there is considerable converging evidence for the lateralization of the latter to the left hemisphere, the verbal response seems to be initiated in mesencephalic centers that operate as functional units that show no asymmetry of function. These structures are left undivided in the surgical section of forebrain commissures and may thus be as operational in split-brain subjects as they are in normal ones. Information projected initially to the right or to the left hemisphere may thus reach these subcortical structures equally rapidly, with the organization of the response then proceeding within the left hemisphere.

It must be noted, however, that this pathway does not substitute for transfer through the corpus callosum when the verbal response is dependent on an analysis of the visual input, and it may act essentially as an alerting system that proves sufficient only when no such analysis is required. Thus, while this subcortical route may subserve information transfer efficiently in the simple verbal RT task for which the input acts as a signal to initiate the organization of the preset response, it is probably too rudimentary to convey complex information that would be necessary to organize a verbal response when the left hemisphere has no prior knowledge of the alternatives. In fact, the disconnection syndrome caused by section of the corpus callosum (Sperry, 1968) and the alexia caused by the destruction of the splenium and left occipital area (Geschwind, 1965) illustrate the limited efficiency of the subcortical route for transfer of information that would lead to a verbal response.

On the basis of our current understanding of the functional organization of the brain, one would not expect split-brain patients to display equally fast verbal responses to stimulation of the left and right hemispheres. Section of the forebrain commissures destroys the main means of communication between the two sides of the brain, and only subcortical pathways can subserve rapid interhemispheric transfer of information. The present results provide some indication that initiation of a verbal response is mediated by subcortical structures equally accessible by the two hemispheres, whereas both the initiation and the organization of a manual response appear to be lateralized to the hemisphere contralateral to the responding hand. These findings concur with the different patterns of visual-field differences found in manual and verbal simple RT tasks performed by normal subjects, and suggest that the verbal task cannot produce valid indexes of interhemispheric transfer. It was not possible, however, to specify the nature of the information transmitted from the right to the left hemisphere, mainly because of the absence of a reliable effect of stimulus intensity on visual field performance. The results nonetheless suggest that

there exist different ways through which subcortical structures can subserve interhemispheric transfer, and that the selection of these pathways depends on the structures responsible for the initiation of the motor response.

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NOTES

1. The manipulation of intensity did not result in consistent effects on visual-field performance across response modalities, and larger differences in energy level might be required to gather some indications concerning the nature of the information being transferred, depending on the mode of response.
2. The main question addressed in these experiments required the comparison of reaction times to visual field stimulation within each response modality, and the three subjects displayed essentially similar patterns of results. However, relative to the control subject, the commissurotomy patients showed a greater increase in RT for the blowing and the verbal responses than for the manual responses. One reviewer pointed out that this finding is not accounted for by the suggestion that both the blowing and the verbal responses can be initiated by response mechanisms that are equally accessible to each hemisphere, whereas manual responses cannot. The source of the greater increase in RT for the blowing and verbal responses by commissurotomy patients, relative to the control subject, is unknown, but there are reasons to believe that the control subject's results are, in fact, atypical in this respect. Tassinari et al. (1983) found verbal and blowing responses to be slower than manual responses, which is consistent with the results of L.B. and N.G. but not with those of S.Y. It may be that S.Y.'s equally fast responses in the three tasks reflected practice effects to which commissurotomy patients may be less susceptible.

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