INTERHEMISPHERIC COMMUNICATION AFTER SECTION OF THE FOREBRAIN COMMISSURES

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Introduction

Recent studies of patients with complete forebrain commissurotomy suggest that the cerebral hemispheres may have more channels for cross-communication than formerly supposed. Even subtle shades of emotional and semantic information seem to transfer from one hemisphere to the other through midbrain or brainstem channels as shown in tests for self-recognition and social awareness in the right hemisphere (Sperry, Zaidel and Zaidel, 1979). Other recent studies (Johnson, 1984a; Trevarthen and Sperry, 1973) appear to revise the early disconnection findings with reports that human split-brain subjects can occasionally cross-integrate information projected to the separate hemispheres. There are additional reports that these subjects can sometimes name or vocally describe stimuli presented exclusively to the right hemisphere (Butler and Norsell, 1968; Levy, Trevarthen and Sperry, 1972; Trevarthen and Sperry, 1973; Teng and Sperry, 1973; Johnson, 1984b), further suggesting the possibility of channels by which information may be transmitted across the midline to the speaking hemisphere.

Before it can be concluded that such findings unequivocally establish the cross-communication of cognitive information via subcortical channels, it is necessary to rule out alternative possibilities such as the use of peripheral cross-cuing, emergence of right hemisphere speech, or the use of ipsilateral sensory systems to circumvent the intended lateralization of input. Similar questions are raised by the general absence of disconnection symptoms with congenital agenesis of the callosum (Sperry, 1970; Milner and Jeeves, 1979; Chiarello, 1980) and by the apparent presence of bilateral speech in some callosum-sectioned patients (Gazzaniga, Volpe, Smylie, Wilson and LeDoux, 1979; McKeever, Sullivan, Ferguson and Rayport, 1982), although for both of these latter conditions transfer

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through the intact anterior commissure must be added as a possibility (Myers, 1984).

The presence of some vocal naming ability in the right hemisphere after complete commissurotomy has been strongly supported by recent evidence in which split-brain patient LB was able to name pairs of stimuli flashed one to each visual hemifield but was unable under similar conditions to make a simple cross-comparison of whether the stimuli were the same or different (Johnson, 1980, 1984a). Patients NG and RY, however, could correctly make the cross-comparisons on these same tests but could name only the stimulus in the right visual hemifield. This latter favors subcortical interhemispheric transfer in which, as noted previously (Sperry et al., 1979), the general context or "sense" of the stimulus is communicated but apparently not the name or identity.

The present study was undertaken to first reconfirm that patients with complete forebrain commissurotomy can, under adequately controlled conditions, name stimuli presented only to the right hemisphere or cross-compare stimuli projected to the separate hemispheres, and if so, to then try to ascertain the means by which such exceptional behaviors are now accomplished. It is critically important that the mechanism of these forms of cross-integration be better understood to enable us to design and properly interpret further commissurotomy studies. A new lateral limits technique for prolonged exposure of lateralized visual input (Myers and Sperry, 1982) was employed, permitting the application of special tests and control procedures designed to better distinguish among possible mechanisms such as right hemisphere speech, bilateral projection of input, peripheral cross-cuing or subcortical interhemispheric transfer.

Material and Method

Subjects

Split-brain patients NG and LB were selected for this study because they have been prominent in previous reports of the exceptional left visual field naming and cross-integration phenomena in question. They also are relatively free of extra-commissural brain damage and are considered most representative of the symptomology of hemisphere disconnection (Sperry, Gazzaniga and Bogen, 1969). Each had undergone complete surgical division of the forebrain commissures for relief of intractable epilepsy, involving midline section of the entire corpus callosum along with the anterior and hippocampal commissures (and the massa intermedia of the thalamus if encountered). The surgeries were performed by Drs. P. J. Vogel and J. E. Bogen upon NG, a female, in September 1963, at age 30 and upon LB, a male, in April 1965, at age 13. Both subjects are right-handed and right eye dominant and detailed case histories have been published (Bogen and Vogel, 1975; Sperry et al., 1969).

Stimuli and apparatus

Stimuli were selected to include items similar to those found previously to permit crossed responses contrary to the usual disconnection symptoms. Visual stimuli included single digits, uppercase letters and line drawings of common household objects, all 1-4 cm in size and drawn in black ink with lines 1 mm thick on standard white index cards. These stimuli were presented at a viewing distance of 57 cm, approximately 2 degrees eccentric from the midline subtending a visual angle of 1-4 degrees. Tactual stimuli consisted of plastic 5 cm digits and uppercase letters. Tactual tests were conducted with the hands of the subject positioned under and behind a screen to exclude the use of vision.

Prolonged lateralized exposure of visual material was obtained without attachments to the eye by use of the lateral limits technique (Myers and Sperry, 1982). With this method, stimuli can be presented to either visual hemifield at the corresponding lateral limits of horizontal eye rotation where further eye movements cannot be used to transfer the stimuli into the view of the unintended hemisphere. A biteboard, clamped to the edge of a table, is used to hold the head of the subject in a fixed position and the visual midlines at the limits of lateral eye rotation are determined with monocular vision using the blindspot of each eye as a reference. Once these limits have been determined no eyecover is needed and lateralization to the right hemisphere can be achieved by having the subject look to the extreme left while stimuli or response arrays are presented to the left hemifield just beyond the left lateral limit of the center of gaze (and vice versa for input to the left hemisphere). Movable panels, placed in front of the stimuli or response arrays, were used to control the timing of presentation.

Procedure

The subjects were tested individually. During testing, they were seated at a table with their hands placed in clear view. Stimuli were presented in random order in blocks of 24 trials either to one visual hemifield or to one hand. Generally only a few seconds were allowed for the inspection of a stimulus and formulation of a response. Guesses were encouraged and immediate vocal corrections were permitted but noted as such. A few trials on which there was reason to suspect interhemispheric cross-cuing because of unusual hand, eye or facial movements or extra delay in the response were excluded and repeated later in the same session. All data were analyzed using one-tailed binomial probability distributions.

Naming of left visual field and left hand stimuli

The patients were first tested for their ability to name stimuli projected to the right hemisphere. Single letters, digits or line drawings were used in the visual naming tests and letters or digits in the tactual tests. Prior to a block of trials the subjects were either shown the stimuli and given practice rehearsing the names (informed) or were told only the category of the stimuli to be presented (uninformed). The subjects were then instructed to name each stimulus in the subsequent test presentations. A block of trials consisted generally of eight different stimuli repeated three times each in dispersed random order. However, since NG performed poorly under these conditions (as expected from previous results), additional blocks of trials were administered in her case with the number of alternative stimuli reduced to two (repeated twelve times each) or three (repeated eight times each).

Tests for left hemisphere participation

To assess possible involvement of the left hemisphere when correct verbal responses had been made to stimuli projected to the right hemisphere, selected blocks of trials were repeated under similar conditions but a response other than naming was requested. In one such test the subjects were asked to silently point to the corresponding digits in choice arrays restricted by the lateral limits method to either the left or right visual hemifield. In another control test the subjects were instructed to respond on each trial by generating a novel rhyme to the digit name. In previous tests of these subjects with words and pictures, the right hemisphere has been shown to fail even to recognize rhymes (Levy and Trevarthen, 1977; Zaidel, 1978; Zaidel and Peters, 1981).

Cross-comparison tests

As noted above, a previous study using bilateral tachistoscopic presentations (Johnson, 1980, 1984a) found that NG could make simple same-or-different judgments across the visual midline although she was unable to name both of the stimuli whereas LB performed in the reverse fashion. Present tests assessed the ability of these same subjects to make such cross-comparison judgments under other conditions in which the stimuli were presented either tactually, to the two hands simultaneously; or visually, to right and left hemifields in alternate succession.

RESULTS

Naming of left visual field and left hand stimuli

Results of tests for the ability to name aloud stimuli projected to the right hemisphere are shown in Table I. The data are presented separately for the two subjects because different test conditions were employed in accordance with their individual abilities. In calculating binomial probability distributions, the chance probability of a correct response was derived from either the actual or expected number of stimulus alternatives (i.e., for the informed conditions, $p = 1/2$, $1/3$, or $1/8$; for the uninformed conditions $p = 1/10$ for digits and $1/26$ for letters).

Subject LB named letters or digits each from a set of eight presented to the left visual hemifield or left hand virtually without error even though he was not preinformed of their identities. When simple line drawings of familiar objects were similarly presented to the left visual hemifield, however, and LB was told beforehand only that the stimuli were pictures of common objects, he failed to name any of the eight drawings presented three times each. Yet, when the test was repeated after LB was told the names and shown the drawings in free vision (where the information reached both hemispheres), he correctly named them all. The near perfect performance for both letters and digits with tactual or visual presentations suggests that the naming ability was unlikely to have been mediated through ipsilateral channels in either modality.

Subject NG failed to name either one of just two different letters or digits randomly presented to her right hemisphere if she was not given advance knowledge of the identities. She could, however, occasionally name one of two line drawings under these conditions apparently on the basis of information which had transferred subcortically. After being shown any two stimuli and rehearsing their names in advance, NG correctly named the two stimuli at a level substantially above chance when they were randomly presented to the right hemisphere. When the size of the stimulus set was increased to three or to eight, the number of correct identifications dropped although remaining above chance. These results suggest that the mental set of the left hemisphere was important and when informed of the stimuli to be presented, correct identifications were perhaps prompted by a single transmitted cue. This is further supported by a few occasions on which NG gave long sequences of reversed responses for a given pair of visual or tactual stimuli (e.g., saying "S" when

TABLE I

Naming of Stimuli Projected to the Right Hemisphere

Subject	Condition	Modality of presentation	Stimulus set size	Percentage of stimuli named correctly		
				Digits	Letters	Line drawings
LB	Uninformed	Visual	8	100**	100**	0
		Tactual	8	100**	96**	
	Informed	Visual	8			100**
NG	Uninformed	Visual	2	17	12	8
		Tactual	2	8	0	
	Informed	Visual	2	100**	96**⁻	100**
			3	62*	46	42
			8	29*	29*	33*
		Tactual	2	67	100**⁻	
			3	54*	58*	
			8	33*	8	

*$p < 0.05$; **$p < 0.001$; ⁻Actual responses were reversed (see text).

the letter was "N" and vice versa) similar to reversals noted earlier for LB during a tactual cross-matching test (Levy, 1970). The close conformance of the results when either visual or tactual stimuli were used, along with the occurrence of reversals in both modalities again argues against explanations in terms of ipsilateral projection systems.

Tests for left hemisphere participation

The ability of the left hemisphere to respond to stimuli projected to the right hemisphere paralleled the respective oral naming abilities of the subjects for these same stimuli. On the rhyming tests, when preinformed of the identities, NG gave appropriate rhymes for one of two different digits on 18 of 24 trials (75%, $p<.05$) and on 9 of 24 trials (38%) for three different digits. LB, even though not preinformed, responded with appropriate rhymes to 22 of 24 presentations (91%) of one of eight different digits ($p<.001$).

Nonverbal tests involving the manual selection of digits projected to the right hemisphere from choice arrays confined to either the left or right visual hemifield concur with the rhyming results in support of left hemisphere involvement in the oral naming results (Table II). Both subjects could easily point out the matching digit with the left hand (right hemisphere) from an array of eight choices presented in the left visual hemifield. They could also, with somewhat less success, select the correct match in a right hemifield display using the right hand (presumably guided by the left hemisphere). This right hemifield performance suggests that the left hemisphere sometimes has access to stimuli projected to the right hemisphere and so may be responsible for the similar oral naming performance for these stimuli. The less than perfect performance of LB in the right hemifield may be attributable to visual field anomalies (Myers, 1982).

Cross-comparison tests

Both subjects could sometimes judge whether two stimuli presented visually to opposite hemispheres were the same or different (Figure 1). NG failed to make correct judgments when the stimuli were presented tactually and LB appeared least able to cross-integrate the line drawings. Nearly 75% of all errors by LB were misjudgments in which two similar stimuli were reported as different.

Since LB showed some ability to make accurate cross-comparison judgments in contradiction to previous tachistoscopic findings (Johnson,

TABLE II

Oral and Manual Identification of Digits Projected to the Right Hemisphere

Subject	Stimulus set size	Percentage of correct identifications		
		Manual selection left hemifield choice array	Oral naming	Manual selection right hemifield choice array
LB (uninformed)	8	100**	100**	67**
NG (informed)	2	96**	83**	88**
	8	96**	42**	42**

**p< .01

1980, 1984a), he was retested with bilateral tachistoscopic presentations of letters (1.5 degrees in size, backprojected for 100 ms, 2 degrees to the right and left of a central fixation mark). His responses on this test were similarly accurate (18 of 24 or 75% correct, $p<.05$), in contrast to the earlier reports under these conditions, although all of the errors were incorrect "same" decisions for two stimuli which were actually different. LB commented that the letters in the left visual hemifield were difficult to recognize and that in order to make the same or different judgments he had to first identify both letters.

Discussion

The present results strongly indicate that subcortical channels are able to mediate communication of cognitive information between the cerebral hemispheres. The foregoing tests of patients who had undergone complete section of the forebrain commissures demonstrate that the left hemisphere can still obtain sufficient information about stimuli projected to the right hemisphere to allow correct naming or to allow comparison with stimuli projected directly to the left hemisphere under the experimental conditions described. The results argue against the use of ipsilateral sensory input, peripheral cross-cuing or right hemisphere speech in these tests. Hence, we conclude that the exceptional naming and cross-integrational performance observed in this and other recent studies (Johnson, 1984a, 1984b) is most likely mediated by subcortical communication channels. The extent to which these channels function also under normal conditions in the intact brain remains conjectural but no reason is seen to rule out normal function.

The exact nature of the information which crosses through subcortical pathways is difficult to determine from the present results. At most, it

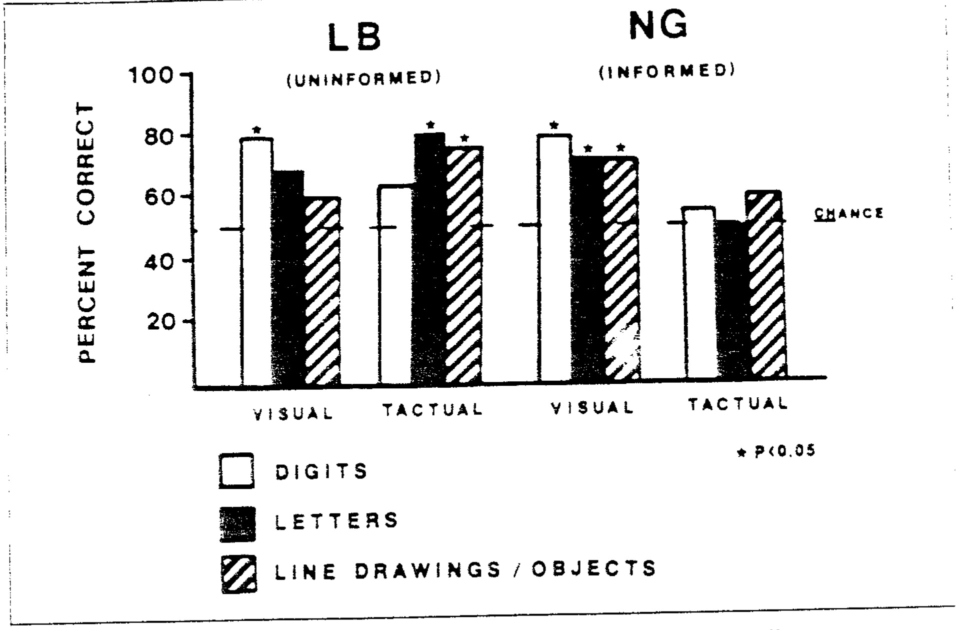

Fig. 1 — *Oral cross-comparison judgments of stimuli presented bilaterally.*

seems to be sufficient to allow the left hemisphere to recognize but not to generate recall of stimuli presented to the right hemisphere. The subjects' descriptions and behaviors suggest that what transfers is neither precise nor complete nor unprocessed. It appears to consist rather of limited arousal or orientational cues and partial, contextual or ambient impressions analogous to "mental block" or "tip of the tongue" sensations in which there is available some relevant information which is yet insufficient to trigger precise identification.

The apparently limited amount of information which crossed between the hemispheres in the present tests may, however, reflect in part the use of relatively simple, neutral stimuli. With stimuli which are richer is sensory or semantic associations or which are more emotionally arousing, there seems to be a corresponding increase in the transfer of information (Sperry et al., 1979) allowing the left hemisphere in some cases to identify the stimulus without using a rehearsal strategy.

The presence of these additional communication channels contradicts a contention (Gazzaniga and LeDoux, 1978) that the left hemisphere language system only becomes aware of right hemisphere processing through the observation of overt actions. It also supplies an explanation for certain unified responses to differential bilateral input recently described for split-brain patients (MacKay, 1981; Sergent, 1983). The disconnected left hemisphere, in the present tests, appeared to actively search for an appropriate response on the basis mainly of partial, sometimes ambiguous, information transmitted implicitly and subcortically, using cognitive strategies such as the rehearsal of likely alternatives. Peripheral cues or crude ipsilateral sensations would presumably also be used if available.

The differences in the naming performance of the two subjects examined in this study duplicate previous findings (Johnson, 1980, 1984a, 1984b) and seem largely to reflect differences in the cognitive strategies they employed. Subject NG was generally able to make only dichotomous distinctions in her responses to stimuli lateralized to the right hemisphere as demonstrated by the failure to name stimuli when the number of alternatives in the stimulus set was increased beyond two or when she was not preinformed of the identities (but see the exception for line drawings above). The occasional sequences of reversed responses when only two stimulus alternatives were presented further demonstrate her reliance upon distinction rather than identification.

In contrast to NG, the strategy of LB permitted him to name alphannumeric stimuli presented to his right hemisphere when told merely that they would be either letters or digits. As noted on previous occasions (Gazzaniga and Hillyard, 1971), LB appeared to mentally rehearse the likely stimulus alternatives until a matching one "sticks out." Such a strategy was evident here when he was unable to name line drawings presented to his right hemisphere unless informed of their identities prior to testing and was further verified in his subjective reports. The same explanation would account also for results in an additional test (not reported) in which LB could name only the common primary colors from a Dvorine color wheel presented in the left visual hemifield while making poor guesses for somewhat less salient colors such as brown or orange.

The possibility that a capacity for oral naming exists within the disconnected right hemisphere, based initially on verbal identifications of left hemifield stimuli (Butler and Norsell, 1968; Levy, Trevarthen and Sperry, 1972; Trevarthen and Sperry, 1973; Teng and Sperry, 1973; Johnson, 1984b), has received recent support from evidence that some split-brain patients are able to name bilaterally presented stimuli but cannot cross-compare them under similar conditions (Johnson, 1978, 1980, 1984a; Gazzaniga et al., 1979; McKeever et al., 1982). However, the inability to cross-compare stimuli is not a sufficient control for interhemispheric transfer in tachistoscopic studies given the tendency to neglect one hemifield with bilateral presentations (Teng and Sperry, 1973; Levy, 1983). None of these prior studies entirely ruled out other possibilities such as the kind of interhemispheric transfer demonstrated here.

Correlated support for a second, right hemisphere, speech mechanism based on longer oral response times (Johnson, 1984b) could just as well be attributed to delays involved in subcortical transfer, rehearsal strategies and so forth. Additional controls, such as those included here, would seem to be required to ensure that it is not the left rather than the right hemisphere doing the speaking in these situations.

The present rhyming tests and lateralized manual responses, which both strongly implicate the *left* hemisphere in responses to left hemifield stimuli, counter recent indications of oral naming by the typical disconnected right hemisphere (Johnson, 1980, 1984b). Prolonged viewing of left hemifield stimuli, rather than allowing vocalization by the right hemisphere (Butler and Norsell, 1968), may serve mainly to facilitate the subcortical transfer of information. A few exceptional cases in whom there appears to be definite speech in the right hemisphere after section of the corpus callosum (Gazzaniga et al., 1979; Sidtis, Volpe, Wilson, Rayport and Gazzaniga, 1981; McKeever et al., 1982) seem best ascribed to the atypical bilateralization of language caused by early left hemisphere pathology (Rasmussen and Milner, 1977; Myers, 1984).

The possible role of subcortical structures in the interhemispheric transfer of cognitive information has only recently been revealed in tests of patients with complete section of the forebrain commissures. The present findings further reinforce the notion (Sperry et al., 1979) that these subcortical transmissions are largely connotative, contextual or orientational in nature and may not resemble typical commissural communications. It seems reasonable to infer that the kind of less structured information involved in these transmissions may normally play a role in cognitive processing, as in memory retrieval and in helping to regulate and direct attention.

ABSTRACT

Cognitive information is shown to be transmitted interhemispherically through channels other than the neocortical commissures, presumably through subcortical pathways. What crosses through these subcortical channels does not appear to include the name or identity of stimuli but rather is more contextual or associative in nature. Results obtained with a technique for prolonged visual lateralization indicate that this information, when used in conjunction with cognitive strategies, allows the cortically disconnected left hemisphere under certain conditions to verbally identify stimuli projected to the right hemisphere or to cross-compare bilateral input. The presence of this subcortical communication would thus appear to help explain some of the increasing exceptions to characteristic disconnection symptoms reported among split-brain subjects. In particular, the present results challenge reports which have attributed oral naming of stimuli in the left visual hemifield to the typical disconnected right hemisphere.