EVIDENCE FOR PARACALLOSAL VERBAL TRANSFER AFTER CALLOSAL SECTION

A POSSIBLE CONSEQUENCE OF BILATERAL LANGUAGE ORGANIZATION

by MICHAEL S. GAZZANIGA, JOHN J. SIDTIS, BRUCE T. VOLPE, CHARLOTTE SMYLIE, JEFFREY HOLTZMAN *and* DONALD WILSON

(From the Division of Cognitive Neuroscience, Department of Neurology, Cornell University Medical College, New York, New York 10021, and the Department of Neurosurgery, Dartmouth-Hitchcock Medical Center, Hanover, New Hampshire 03755, USA)

INTRODUCTION

BEHAVIOURAL studies of patients who have undergone surgical section of the corpus callosum for seizure control have generally supported the view that the cortical representation of expressive language is limited to the left hemisphere. However, one of the commissurotomy patients in our series has been the focus of intense interest largely because the representation of his language ability departs from this organizational principle. Unlike other commissurotomy patients in either the Bogen and Vogel series (Bogen and Vogel, 1962) or the present Wilson series (Wilson, Reeves, Gazzaniga and Culver, 1977; Wilson, Reeves and Gazzaniga, 1980), P.S. demonstrated a strong right hemisphere language capacity shortly after operation (Gazzaniga, LeDoux and Wilson, 1977). Moreover, this language capacity has not remained static following callosal section, but has undergone a change that has apparently allowed the right hemisphere to access speech (Gazzaniga, Volpe, Smylie, Wilson and LeDoux, 1979). Thus, in addition to having the capacity for sophisticated linguistic comprehension in each hemisphere, P.S. appears to have the ability to generate speech from each of these systems.

The question of access to the speech production system is critical to the issue of how the right hemisphere can generate speech in this case. Several possibilities exist in this regard. One possibility is that language systems, including the neural mechanism for the control of the vocal apparatus, may exist independently in each hemisphere. In this case, one system would remain naïve with respect to information lateralized to the other until the informed system vocalized the critical information. Under such circumstances, interhemispheric communication would require auditory feedback from the spoken expression. A second possibility is that language

systems in each hemisphere rely on a common system for speech production. If this were the case, the point of convergence between these systems might provide an avenue for the paracallosal integration of information between the hemispheres. The distinction between language and speech is used in the present context to differentiate between language comprehension and language production. While comprehension has been shown to occur independently in each of P.S.'s separated hemispheres, the degree of independence of each hemisphere's production is less clear.

The present research was conducted to examine several issues with respect to the right hemisphere's capacity to generate speech. An associative learning paradigm was used to determine the following: whether vocalization is required for the interhemispheric exchange of information; whether interhemispheric communication is specific to linguistic information; and whether shared linguistic information is specifically speech-like in nature (that is, phonological or articulatory).

GENERAL METHODS

Subject

P.S. is a right-handed male, 19 years of age at the present testing. His history includes a series of seizures at the age of 2 years, with a left temporal focus identified by electroencephalography. Subsequent development was normal until aged 10 years when seizures recurred and over the next five years proved intractable. At the age of 15 years, P.S. underwent complete surgical section of the corpus callosum. Since his operation, which was performed in January 1976, the patient has remained largely free of seizures. Additional information on the patient has been published elsewhere (Wilson *et al.*, 1977).

Procedure

All lateralized stimuli were presented using a two-field projection tachistoscope. Stimuli were presented at least 5 deg to the left or right of a central fixation point for a duration of 150 ms. On a typical trial, the subject, seated approximately 1 m from a rear projection screen, was instructed to fixate a dot located in the centre of the screen. When fixation was achieved, the experimenter initiated the stimulus presentation. Eye movements and facial gestures were carefully monitored through the use of a video recorder and camera fitted with a remote control 10:1 zoom lens. There were no indications of overt muscular activity prior to an actual spoken response, nor did fixation deviate during presentation of the stimuli.

Each of the tests described in the present report employed the following associative learning procedure. At the beginning of each test sequence, the subject was presented with a critical target stimulus lateralized to one visual field. The subject was instructed not to name the target, but rather to respond by naming the associate specified by the experimenter. This was rehearsed during a learning phase at which time the critical stimulus was presented to a single visual field, embedded in a sequence of non-target stimuli which were to be named properly. Once the association was established, the critical stimulus was presented under various conditions during a test phase. In both learning and test phases, the subject was urged to respond as rapidly as possible, and successive stimuli were presented immediately after the subject's previous response. This rapid rate of presentation was used to minimize any possible opportunity for cross-cuing or sub-vocal rehearsal. Response latencies were not measured. However, there were no gross systematic differences in response latencies observed across the between and within conditions.

Experiment 1. Single Field Associative Learning (Meaningful Stimuli)

The sequence of events for single-field associative learning is summarized pictorially in fig. 1. The patient was told that he had to name a series of words or pictures of objects presented to one or the other hemisphere by lateralized stimulation of the contralateral visual hemifield. Prior to the presentation of the first item in a test series, the subject was instructed to call the target stimulus some specified associate. Thus if the first word was *apple* the correct response for the subject might be *petunia*. On subsequent test trials, the target was embedded in a series of stimuli presented sequentially to either visual field in a random order. The target stimuli could first occur in either the trained or untrained visual field.

Verbal transfer

EXAMINER:	PATIENT:
CALL THE NEXT THING YOU SEE 'PETUNIA'	'O.K'
CAT·	'PETUNIA'
·APPLE	'APPLE'
CAT·	'PETUNIA'
HOUSE·	'HOUSE'
·CAT	'PETUNIA'

FIG. 1. Schematic example of the single-field associative learning in which the target is the word *cat* and the associate is the word *petunia*. The last box in this example represents paracallosal transfer of the learned association.

If vocalization provided the only means of interhemispheric transfer and each hemisphere controlled vocalization independently, no evidence for the interhemispheric transfer of the learned association would be expected, since the critical information was never vocalized. However, if interhemispheric transfer occurred, each system must share information by some means other than auditory feedback.

Results and Discussion

The results of this procedure are summarized in Table 1, which contains only those trials during which the actual name of the target stimulus was not accidentally used as a response by the subject during training. It can be seen that under single-field conditions, the subject virtually always referred to the target stimulus as the associate, whether it was first tested in the trained or the untrained field. In the untrained left visual field, accuracy of the responses to target stimuli was significantly better than chance for both pictures and words (binomial $P < 0.05$). In the untrained right visual field, this was also observed for words (binomial $P < 0.01$), but the performance on pictures was only marginally significant (binomial $P < 0.06$) because of the small number of trials. Thus, under unilateral stimulus conditions, P.S. demonstrated the capability of transferring a learned association to the hemisphere that did not receive direct stimulation. Since vocalization was not required for the interhemispheric exchange of this information, P.S.'s rich bilateral capacity must have allowed each hemisphere to transfer information *via* some paracallosal pathway.

TABLE 1. ACCURACY OF PERFORMANCE (% CORRECT) IN THE UNTRAINED VISUAL FIELD FOLLOWING SINGLE-FIELD ASSOCIATIVE LEARNING.

	Untrained visual field	
Stimuli	Left	Right
Pictures	89	86
	(8/9)	(6/7)
Words	83	91
	(10/12)	(10/11)

The number of trials for each condition are presented in parentheses.

There are two possible explanations for the present results, however. As noted earlier, the first is that the exchange occurs *via* some mechanism involved in language function, possibly at the point where language in each hemisphere accesses speech production. That point could be either where independent production systems in each hemisphere access common articulatory musculature or where independent comprehension systems access a common production system. Presumably, if the linguistic interaction occurred where independent comprehension systems accessed a common production system, it might be based on

information most like that transferred through the callosum. If, on the other hand, the point of interaction is at the common articulatory musculature, transfer might be based on each hemisphere's reading of sub-vocalizations produced by the opposite hemisphere. While sub-vocalization cannot be strictly ruled out, it seemed unlikely in the present paradigm, which utilized a rapid rate of stimulus presentation and the overt vocalization of the paired associate. Moreover, facial movements were carefully monitored with the video system, and no articulatory gestures other than those used in overt responding were observed.

A second possible explanation is that the interhemispheric transfer of visual information has been reinstated as a consequence of a post-operative functional reorganization. The second experiment was designed to evaluate the latter possibility using the same paradigm in which verbal transfer was observed.

Experiment 2. Single Field Associative Learning (Nonlinguistic Stimuli)

The results of the first experiment raise questions as to the nature of the interhemispheric communication that is evident in P.S. Does it represent transfer of actual features of the stimulus presented to one of the hemispheres or is some linguistic encoding of the stimulus required before any interhemispheric exchange of information can take place? One way to examine this question is to require a discrimination from within a set of stimuli which vary along a sensory dimension not ordinarily distinguished linguistically. For example, one can readily discriminate figurally identical objects at differing orientations despite their semantic identity. If successful interhemispheric transfer of a learned discrimination of this type obtained in P.S., it would suggest a capacity for the interhemispheric exchange of sensory information, while a failure to obtain such transfer would suggest that interhemispheric communication in P.S. is mediated by processes which do not have direct access to sensory input.

The stimuli used to distinguish between these possibilities were single lines which differed only in their angular orientations (step size = 10 deg). These stimuli were incorporated into a paradigm analogous to the single-field testing procedure described above. During the initial training period, a series of lines were presented tachistoscopically in a random order exclusively to either the right or the left visual field. Prior to the presentation of each stimulus, P.S. was informed whether the following stimulus did or did not depict the target stimulus. The target line for right visual field training was orientated at 110 deg (measured counter-clockwise from the horizontal), while that for left visual field training was orientated at 70 deg.

A period of single-field testing followed each unilateral training period. In a randomized sequence, 9 examples of the target stimulus and 9 examples of 4 alternative stimuli (figurally identical lines at a variety of different orientations relative to the horizontal) were presented tachistoscopically to the trained and untrained visual fields, for a total of 90 stimulus presentations. P.S. was instructed to say 'yes' for each presentation which matched the target stimulus, and 'no' when any of the alternative stimuli had appeared.

Results and Discussion

The combined results of the testing periods for left visual field training and right visual field training are presented graphically in fig. 2A and B, respectively. Within each figure, separate curves are presented depicting left visual field (filled squares) performance and right visual field (open squares) performance. The abscissa for each figure indicates the angular orientation of the target stimulus (70 deg for left visual field training; 110 deg for right visual field training) and that of the four alternative stimuli. The ordinate in each figure represents the proportion of the total testing trials that P.S. responded to a particular stimulus as the target.
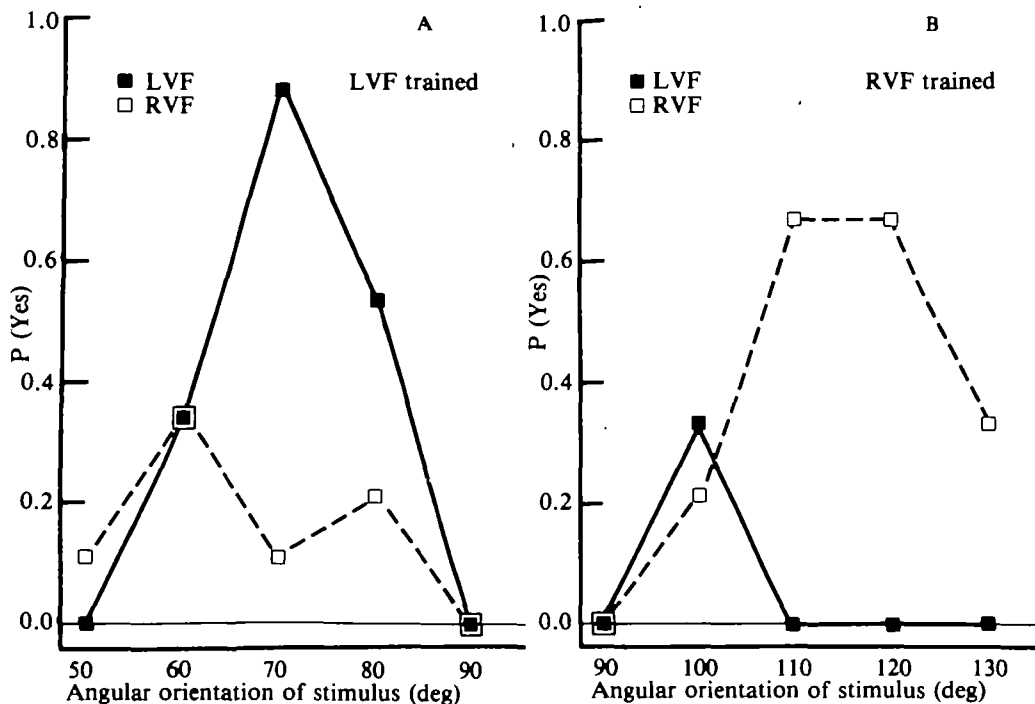

FIG. 2. Results obtained for single-field associative learning with nonlinguistic stimuli. The target stimuli for left and right visual field training were orientated at 70 and 110 deg., respectively. Results are depicted in terms of proportion (P) of trials in which a stimulus was identified as the target. Unlike the results observed for linguistic stimuli, training in one hemisphere failed to transfer to the naïve hemisphere.

Inspection of fig. 2A and B reveals that during the testing period, P.S. was able to reliably discriminate the target stimulus from its alternatives when they were presented to the trained visual field. However, while learning had occurred in the trained field, it is clearly evident that the learned discrimination did not transfer to the untrained field. This is most striking when the left visual field-right hemisphere received the training. It can be seen that, while the solid curve in fig. 2A (left visual

field testing) reveals accurate right hemisphere training on the discrimination task, the comparable dashed curve (right visual field testing) shows no evidence of transfer of this training to the left hemisphere. In general, performance in the untrained field was significantly worse than chance (binomial $P < 0.05$) on 7 of the 10 orientations indicating a reluctance to use the target name in the untrained field. For the remaining 3 orientations, performance was not significantly different from chance.

Thus, when learning within a hemisphere involves the discrimination of stimulus features that are not conducive to linguistic coding, we find a failure of this training to transfer to the untrained hemisphere. Overall, then, these data support the notion that interhemispheric communication of the learned association for words and pictures reported above is not mediated by direct transfer of the sensory features of the critical stimulus.

Experiment 3. Semantic vs Phonetic Transfer

The failure to obtain sensory transfer in P.S. makes it unlikely that, when the learned discrimination involves words, the untrained hemisphere has access to the orthographic features of the target stimulus. However, interhemispheric transfer after further encoding could involve any of several possible linguistic representations. Experiment 3 attempted to ascertain whether paracallosal transfer in P.S. involved only the phonetic or articulatory correlates of the name of the stimulus or a more general linguistic representation including a semantic referent. For this purpose, a number of homophonic pairs were employed as stimuli. If P.S. could make semantic discriminations between homophonic pairs within the untrained hemisphere, this would suggest that paracallosal transfer included more than just phonetic or articulatory information. On the other hand, confusions between the target stimulus and its homophonic pair would suggest that the transferred information is largely speech-like.

The stimuli used in this experiment were 12 pairs of 3 or 4 letter homophones. Again, P.S. was trained under single-field presentation to call one homophone (for example, *meat*) a specified associate, and to call all other words, including the nontarget homophone (for example, *meet*), ·by their correct names. After the discrimination was learned during unilateral training, the opposite hemisphere was tested. The set of 12 homophones was presented under both within-field and between-field testing conditions.

Results and Discussion

During testing, the discrimination was made successfully within the trained hemisphere where accuracy was at 92 per cent (11/12 correct), which was significantly better than chance (binomial $P < 0.005$). However, when the association was tested in the opposite hemisphere, confusions between homophones occurred and accuracy fell to 58 per cent (7/12), which was not significantly better

than chance. While P.S. only responded to members of the homophone pair as targets in the between-field conditions, he was correct in his discrimination only about half of the time. This suggests that the information available for paracallosal transfer was not semantic. Rather, the untrained hemisphere responded to both members of a homophonic pair as if they were targets, but was unable to discriminate between the phonetically similar stimuli.

Experiment 4. Simultaneous Bilateral Associative Learning

The results of the preceding experiments reveal that interhemispheric communication in P.S. does not consist of either direct sensory input from the stimulated hemisphere or the semantic referent of the target item. Rather, it seems to involve a phonological or articulatory representation of the stimulus. Since the language systems in each hemisphere must converge at some level in order to share the common articulatory structures, it was postulated that if each system was simultaneously presented with a task that engaged some phonological processing, paracallosal transfer would not occur.

As in the previous experiments, a series of stimuli were presented to be named. In this experiment, however, two pictures were simultaneously flashed during training, one in each visual field. The subject was told to label both items in the first stimulus pair as the target associate. For example, a picture of a gun and a picture of a car might be simultaneously presented to the left and right visual fields, respectively. After the subject vocalized the specified associate, other stimulus pairs were presented for naming following the training procedure outlined in the previous studies. Thus, in this experiment each associate was simultaneously paired with a different target in each hemisphere. On the test trials, the double simultaneous nature of the stimulation was maintained by pairing a pictorial stimulus in one visual field with a pronounceable four-letter nonsense syllable in the other. Thus, only a single hemisphere would have to respond on any given trial, but both would be receiving information that could be coded phonetically. The positioning of the critical target stimulus was varied, with either of the trained stimuli occurring in either the visual field in which it was trained, or the field which was trained on a different target. Thus, during the test phase, the left hemisphere's target appeared in both the trained right visual field and the untrained left visual field. The same was true for the right hemisphere's target.

Results and Discussion

Typically, under these conditions of bilateral stimulation, P.S. was only capable of learning the association for a single member of the target pair. Both associates were learned on only one of the six learning sets. Collapsed across visual fields, accuracy on the first occurrence of a target stimulus was 75 per cent correct in the appropriate field. Transfer of the learned association was never observed, however. It should also be noted that once established, the association failed to transfer even

during the test phase, when in trials in which a critical stimulus was presented to the untrained hemisphere, it was correctly named.

In short, there was no evidence of transfer when both hemispheres were simultaneously engaged in phonetic processing. This was true not only on the first critical test trial, but also throughout the course of each 72 trial test sequence. Moreover, it also appeared that the capacity for establishing a verbal association was limited: there was little evidence that both hemispheres could simultaneously learn the specified association. While this may reflect limits in some general capacity for dividing attention, it may also indicate a bottleneck at the point of interaction between the left and right hemisphere language systems. Both possibilities are currently under investigation.

GENERAL DISCUSSION

. Following the apparent emergence of right hemisphere speech after callosal section, the patient now realizes an ability to communicate between the two disconnected hemispheres by some covert neural mechanism. When a meaningful stimulus was lateralized to either hemisphere, it was identified by the opposite half-brain through a process that did not make use of either simple sensory transfer or overt cross-cuing mechanisms. Rather, this ability appeared to be tied to this patient's bilateral language organization. Although critical target stimuli were never overtly named, their identities were available to the naïve hemisphere *via* inter-hemispheric transfer of information that was either phonetically or articulatorily based. Articulatory information, of course, would have to have been available before overt vocalization, since the present results indicate that such expression was not necessary for transfer to occur.

The reorganization of language function in P.S. has been exhibited in a number of ways during his post-operative course. Beginning with excellent right hemisphere linguistic comprehension post-operatively, P.S. was able to generate brief spoken responses after the eighteenth post-operative month (Gazzaniga *et al.*, 1979). The apparent use of this bilateral speech capacity to provide paracallosal transfer is seen as a further developmental stage in this patient's post-operative course, emerging only after the thirty-sixth post-operative month. Prior to the emergence of the capacity for paracallosal transfer, the two hemispheres could only communicate to one another by overtly speaking, as previously reported.

The developmental aspect of this behaviour is also supported by our initial observation with a more recent patient, V.P., who has right hemisphere language comparable to that found in P.S. (Sidtis, Volpe, Wilson, Rayport and Gazzaniga, 1981). This young woman, in whom right hemisphere speech is just emerging, shows no evidence of paracallosal transfer at this point.

Based on these observations, it is clear that the question of interhemispheric transfer in this situation is intimately tied to another question: how is the patient's

right hemisphere generating speech? At this point, there is no single answer, but a range of alternatives bound at one end by the possibility that each hemisphere maintains its own speech-production system and at the other end by the possibility that the independent cognitive systems in each hemisphere access a common speech-production system. These possibilities represent a range rather than dichotomous alternatives because of the hierarchical organization of the speech-production system. Thus, while it is clear that the left and right hemisphere systems share the same articulators, convergence might occur at a higher level; for example, the level at which a phonetic sequence is translated into articulatory commands.

The range of functional alternatives for the explanation of paracallosal transfer is accompanied by a number of possible neural loci for this interaction. At the cortical level, the intact anterior commissure may provide the right hemisphere language system with access to speech production at a fairly early point in the production process. Functionally, this would fall at the extreme that postulates that each language system shares access to a common speech production system. At the opposite extreme, the interaction between two independent speech production systems, the explanation requires that the afferent connections with the peripheral articulators provide feedback that can be read by the naïve language system. In some sense, this extreme might be described as the capacity of one hemisphere to read any sub-vocalization that might be produced by the other. This latter extreme is considered unlikely, however, since there appears to be little physiological basis for supposing that there is sufficient afferent information to provide word recognition (Lenneberg, 1967).

Between the levels of cortical-cortical connection and peripheral afference, a number of other brain structures have been implicated in speech and language (Ojemann and Ward, 1971; Brown, 1979). It should be noted, however, that paracallosal transfer need not be confined to either extreme, nor to only a single level common to both systems. Regardless of the level at which paracallosal transfer occurs, it is clear that there has been a significant functional reorganization within this patient following callosal section, and that it is intimately tied to his bilateral capacity to generate language.

It remains for future studies to determine the actual mechanism of paracallosal transfer responsible for the present phenomenon. However, the nature of the transferred information strongly suggests that it is closely related to the ability of each hemisphere to generate speech.

SUMMARY

The covert interhemispheric transfer of linguistic information was demonstrated in a commissurotomy patient with bilateral language organization. It was found that under conditions of unilateral stimulation, a verbal association established in one hemisphere was available to the untrained hemisphere as well. Such inter-

hemispheric transfer was observed only for phonetically codable information. Moreover, transfer was not observed under conditions of simultaneous bilateral stimulation. These results suggest that the point of convergence between the left and right hemisphere language systems allows for the paracallosal transfer of linguistic information.

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