The disconnection syndrome Basic findings reaffirmed

S. E. Seymour, P. A. Reuter-Lorenz and M. S. Gazzaniga³

¹Department of Psychology, Dartmouth College, the ²Department of Psychology, University of Michigan and the ³Center for Neuroscience, University of California at Davis, USA Correspondence to: M. S. Gazzaniga, Center for Neuroscience, University of California at Davis, Davis, CA 95616, USA

Summary

Recent challenges to the traditional view of the disconnection syndrome have been based primarily on evidence of information shared between the hemispheres in commissurotomy patients L.B. and N.G. of the West Coast series. In order to evaluate the generality of these claims, patients J.W., V.P. and D.R. were tested using a series of experiments which replicated and extended some of the experiments carried out in the West Coast series. Using comparisons of numerical identity and value as the model tasks, we found no indication that the separated hemispheres of J.W. or D.R. could share information on any

of the tasks they performed. V.P., who has spared callosal fibres and has shown highly specific transfer in previous investigations, performed above chance (60%) in one out of three between field conditions. Together the data fail to support the claims that splitbrain patients show evidence of unified cognitive functioning particularly for more abstract, nonperceptual tasks. The data are consistent with the traditional view of the corpus callosum as the primary interhemispheric pathway by which sensory and high-level cognitive integration is achieved.

Key words: disconnection syndrome; corpus callosum

Introduction

The pioneering commissurotomy research by Sperry and Gazzaniga demonstrates the disconnection of higher cognitive functioning between the two hemispheres following section of the forebrain commissures. The disconnection syndrome is characterized by the absence of interhemispheric transfer of information derived from a stimulus presented unilaterally. The separated hemispheres are unable to share information about stimulus identity, shape, and higher-order associations (Gazzaniga et al., 1962; Sperry et al., 1969). The classic example of the disconnection syndrome is the patient whose speaking left hemisphere cannot name or identify an object held in his left hand, but who can select the object under guidance from his right hemisphere. Evidence of this sort led to the view that the split brain patient possessed two separate minds operating in parallel (Sperry, 1966–7; Gazzaniga, 1970).

Exceptions to this general characterization were eventually reported. These include the transfer of emotional or aesthetic tone (Gazzaniga, 1970) and the transfer of motion and crude form information from stimuli presented in the extreme visual periphery (Trevarthen and Sperry, 1973). This shared information, however, is too vague to be used for stimulus identification. The subcortical mechanisms invoked to account for these effects are only capable of transferring information

which is 'largely connotative, contextual or orientational in nature' (Myers and Sperry, 1985, p. 258). Holtzman furthered this description by demonstrating interhemispheric cooperation in attentional and oculomotor control (Holtzman *et al.*, 1981; Holtzman, 1984, 1985; and cf. Reuter-Lorenz and Fendrich, 1990; Hughes *et al.*, 1992). Thus, the prevailing view of the disconnection syndrome, as it concerns stimulus identity, associative processing and higher-order cognition, was not seriously challenged by these reports.

A number of authors have expressed doubt that this description of subcortical transfer goes far enough to explain the essentially unified everyday behaviour of these patients who are said to have two minds. It has been argued (e.g. Sergent, 1987) that the early studies found what they set out to find; namely, examples of hemispheric isolation in perception and processing. Several more recent studies have therefore been carried out with the opposite goal—finding to what extent the hemispheres can be said *not* to be disconnected. These studies claim to have found evidence of 'interhemispheric influence' (Lambert, 1991), integration (Sergent, 1983, 1986, 1987), cross-comparison (Johnson, 1984; Sergent, 1987, 1990) and unity of intent (MacKay and MacKay, 1982). Almost all of these studies have been carried out on a group of patients from the

Bogen and Vogel series (L.B., N.G., A.A. and R.Y.), with a majority of the studies focussing on L.B. and N.G. Several are based on data from L.B. alone. Even when other patients were included (e.g. Johnson, 1984; Sergent, 1990) almost all the positive results were from L.B. and N.G. Two studies examined interhemispheric effects in subject J.W. (MacKay and MacKay, 1982; Sergent, 1983). MacKay and MacKay's study concerned the unity of evaluative criteria and priorities in the two hemispheres, an aspect of cognition which is considerably different from and likely unrelated to those which are under examination in the other studies mentioned here. The Sergent (1983) study, in which J.W. was the only subject, had design weaknesses which the author noted herself in a later paper (Sergent, 1986).

Thus the bulk of the data used to support the 'reunified' view of the split brain is derived from only two subjects, L.B. and N.G. Unfortunately, there has been some question as to the completeness of the section in L.B., the patient who has been most studied. Of three post-operative MR scans taken on different occasions, only the most recent has shown a complete section of the corpus callosum (Bogen et al., 1988), while the earlier two each showed a 'small patch of filmy substances' in the area of the splenium (Sergent, 1987). There are also several suggestive instances in which L.B.'s performance is closer to that of normals than to other commissurotomy patients. He is the only one of these subjects who has consistently been able to perform cross-field same/different comparisons (cf. Myers and Sperry, 1985; Sergent, 1990; however, see Johnson, 1984); he can frequently name (after some delay) stimuli presented to the right hemisphere, although there is no evidence that he is capable of right hemisphere speech (Johnson, 1984; Myers and Sperry, 1985; Sergent, 1987, 1990); in a word categorization task he shows interhemispheric semantic influence which closely resembles that seen in normals (Lambert, 1991), although interhemispheric semantic transfer has not been seen in other split-brain subjects (Gazzaniga et al., 1984b); and like normals but, unlike other commissurotomy subjects, he shows little neglect of the left visual field stimulus in bilateral displays (Teng and Sperry, 1973). At the least it may be said that L.B. is not very representative of the splitbrain population.

These considerations suggest the importance of replicating the results which support the 'reunified view' in other callosotomy patients before assuming that they can be generalized beyond subjects N.G. and L.B. In the present investigation subjects J.W., V.P. and D.R. of the East Coast series were studied using tasks modelled largely on those of Sergent (1990) with a variety of methodological changes and additions. Sergent's (1990) work represents some of the strongest claims that subcortical pathways can mediate the interhemispheric integration of higher level abstract information. Sergent argues, in fact, that it is the very abstract nature of the information which makes interhemispheric comparison possible. The subcortical pathways are less efficient at, or incapable of, transfer or cross-comparison of stimulus identity (presumably based on perceptual attributes). She reports that

performance may be compromised when physical identity is emphasized, whereas performance improves when the same stimuli are compared for meaning.

The present investigation attempts to replicate a critical subset of Sergent's findings using tasks that require comparisons of single digits presented bilaterally. Tasks involving numerical comparisons have figured prominently in a number of Sergent's reports (1987, 1990; Corballis and Sergent, 1992) and are, therefore, an appropriate starting point for evaluating the generalizability of her claims. We also tested Sergent's proposal that abstract representations but not sensory information can transfer in the split brain (see also Cronin-Golomb, 1986). This idea was tested in a task that required comparison of numerical values represented by a digit and a group of dots (Experiment 4) and could therefore only be performed if abstract representations were shared between the hemispheres. Sergent (1990) has also suggested that brief, tachistoscopic exposure interferes with subcallosal transfer. We, therefore, included a condition which allowed for extended lateralized viewing using the technique of image stabilization (Experiment 3, Part 3).

Methods

Experimental design

The methods described here were similar in all the experiments. Variations will be noted where they apply. Each experiment examined the ability of the callosotomy patients to compare different types of numerical information (i.e. digit identity and value) derived from stimuli (digits or dots) presented to the separated hemispheres (i.e. 'between field' condition). In order to ascertain whether each hemisphere could independently carry out the task, the subjects were also tested on 'within field' conditions in which the two stimuli to be compared were presented to the same hemisphere. The within and between field conditions were run in separate blocks. In the within field blocks, right visual field and left visual field trials were presented in a random order with the constraint that no more than three consecutive trials be presented to the same hemisphere. Intermixing the presentation field encouraged central fixation because the subject could not predict where the next stimulus would appear. Subjects' fixation was monitored by the experimenter to discourage eccentric fixation and ensure that the eyes remained stationary. For the between field conditions, the inner edge of the stimulus was >4° from the fovea so that any attempt to look at the stimulus would be readily detectable.

Subjects

The subjects were three patients with callosal section (J.W., V.P. and D.R.) who have been tested extensively in the past and are, thus, familiar and comfortable with the testing procedures. J.W., 38 years old at the time of testing, is a right-handed male who underwent a two-stage callosotomy at the age of 25 years. His MR scan demonstrates a complete section of the corpus callosum (Gazzaniga et al., 1985). V.P., a 40-year-

old right-handed woman, underwent callosotomy in two stages at the age of 27 years. Her MR scan and some behavioural findings indicate the presence of spared fibres in the rostrum and splenium (Gazzaniga et al., 1985), although in most respects, behaviourally, she presents the classic disconnection syndrome (Gazzaniga et al., 1984b; Holtzman, 1984; Fendrich and Gazzaniga, 1989, 1990). D.R., a 47-year-old right-handed woman, underwent callosotomy at the age of 40 years. Her MR scan and surgical report indicate a small area of spared fibers in the inferior rostrum (Baynes et al., 1992). All three subjects have intact anterior commissures. Thorough case histories of these patients have been published elsewhere (Gazzaniga et al., 1984a; Tramo and Bharucha, 1991; Baynes et al., 1992). This experiment had ethical committee approval and all patients gave informed consent.

Equipment and stimuli

The stimuli for Experiments 1-3 were the digits 1-9 presented in black on a white field by a Macintosh computer (Macintosh II for J.W. and Macintosh SE or Classic II for V.P. and D.R.). In the within field condition two digits were presented one above the other in the same visual field; and in the between field condition they were presented one in each visual field. The digit stimuli subtended ~5° of visual angle vertically and 2.75° horizontally and were centred $\sim 7^{\circ}$ horizontally from fixation in the between field condition. In the within field condition the stimuli were centred ~4° above or below the horizontal meridian at 7° from the vertical meridian. For subject J.W., peripheral response buttons were sampled with millisecond accuracy using the Macpacq data acquisition system. Because portable equipment was used to test V.P. and D.R., these subjects responded by pressing one of two keys on the computer keyboard and response timing was omitted.

Procedure

For J.W., data were collected in a series of sessions carried out over a 24-month period. He was tested in a private testing room, seated 57 cm from the screen with his chin supported in a chin-rest. The response box was positioned comfortably for whichever hand was being tested. His index finger rested just between the two buttons which were ~1 cm apart. The buttons were labelled (e.g. 'S' for same and 'D' for different) for the subject to refer to, although this was generally not necessary. V.P. and D.R. were tested at their homes, V.P. on five different days and D.R. on three. In order to maintain equivalent visual angles with the smaller computer screen, a viewing distance of 43 cm was used. These subjects rested their index finger on a computer key and pressed the key to the left or right of it in order to respond.

Each experiment began with several practice trials in which sample stimuli were drawn on paper in a free-field viewing condition. This was repeated between blocks as seemed necessary and particularly before switching hands. Each trial began with the presentation of a fixation point, followed 500 ms later by a warning beep. The stimuli were then presented for ~ 150 ms timed to the screen refresh rate. The next trial began 3 s after the subject responded.

Experiment 1

The task in Experiment 1 consisted of making a same/different judgment about two digits. It is generally held that split-brain subjects are unable to perform such tasks when the stimuli to be compared are presented separately to the two hemispheres. L.B., it seems, has been an exception to this rule, since, according to Sergent (1990), he is able to perform a task basically identical to this one. The present experiment examines whether this ability exists in J.W., V.P. or D.R.

Methods

Generating all possible combinations of the nine digits in both visual fields (or quadrants in the within field condition) gave 72 'different' trials and nine 'same' trials. The same trials were presented eight times each, such that the total of 144 trials was comprised of 50% 'same' and 50% different trials. J.W. was tested on two within and four between field blocks with each hand. Hand order was counterbalanced. V.P. was tested on one within and two between field blocks with the right hand and with the left hand, she was tested on one between field block and half a within field block which consisted of 144 randomly selected trials. D.R. was tested on two within field blocks and two between field blocks with each hand.

Results and discussion

Occasional trials were omitted when V.P. or D.R. pressed an extraneous key on the keyboard. Across the entire series of experiments, between 0 and 0.7% of V.P.'s data per block was excluded. For D.R., exclusions ranged from 0 to 4.9% of the data. Exclusions for J.W., due to a failure to respond, amounted to only two trials in a single test block (Experiment 3, Part 2) or 0.007% of the data in that block.

As can be seen in Table 1, both J.W. and V.P. were able to perform the same/different comparison with a high degree of accuracy in the within field condition regardless of the combination of responding hand and visual field of presentation (in all cases $159 > \chi^2_1 > 280$, P < 0.001). D.R.'s right hemisphere performed poorly at the within field task regardless of which hand was used for responding (left hand: $\chi^2_1 = 0.46$, P > 0.5, right hand: $\chi^2_1 = 0.064$, P > 0.8). She also performed poorly at the between field task: 50.5% correct with the right hand ($\chi^2_1 = 0.032$, P > 0.8) and 48.6% correct with the left hand ($\chi^2_1 = 0.23$, P > 0.5). Since her right hemisphere could not perform the within field task, it is impossible to know whether her poor performance at the between field task was due to a failure of interhemispheric integration or to a failure of the right hemisphere to comprehend

Table 1 Percent correct, number of trials (in parentheses), and mean reaction times in the same/different comparison of digits (Experiment 1)

	J.W.		V.P.		D.R.	
	Right hand	Left hand	Right hand	Left hand	Right hand	Left hand
Within left visual field Mean reaction time	87.2 (288) 1040 ms	99.0 (288) 994 ms	97.9 (144)	100.0 (72)	51.6* (283)	53.7* (283)
Within right visual field Mean reaction time	99.3 (288) 988 ms	92.7 (288) 1098 ms	99.3 (144)	97.2 (72)	92.3 (284)	88.5 (280)
Between visual fields Mean reaction time	47.6* (576) 794 ms	53.6* (576) 1032 ms	55.4* (287)	44.1* (143)	50.5* (287)	48.6* (282)

^{*}Not significantly different from chance performance.

a task which required its participation. The case is clearer for J.W. and V.P. Although they both were obviously able to perform the same/different task easily in either hemisphere, when interhemispheric comparisons were required in the between field condition their performance fell to chance levels. J.W. was 47.6% correct with his right hand ($\chi^2_1 = 1.36$, P > 0.2) and 53.6% correct with his left hand ($\chi^2_1 = 3.06$, P > 0.05). V.P. was 55.4% correct with her right hand ($\chi^2_1 = 3.35$, P > 0.05) and 44.1% correct with her left ($\chi^2_1 = 2.02$, P > 0.1).

Mean reaction times for correct responses are given in Table 1 for subject J.W. Mean reaction times in both of the left hand within field conditions and the right hand right visual field condition are based on only a single block of trials each, due to a data collection error. Although, J.W.'s poor right hand performance in the between field condition is consistent with the possibility of a speed-accuracy trade-off, his left hand performance could not be explained in this manner. Furthermore, it is apparent in the subsequent experiments that J.W.'s between field accuracy is always at chance, regardless of whether his between field reaction times are faster or slower than the corresponding within field conditions.

The results demonstrate, as expected, that callosotomy patients are unable to compare the identity of stimuli presented to the two visual fields. It has been reported (Sergent, 1990), however, that some patients may be able to compare information related to such stimuli even when they are unable to compare the identities of the stimuli. This possibility was evaluated in the next experiment.

Experiment 2

Sergent (1990) has reported that two commissurotomy patients, N.G. and L.B., were able to compare digits presented bilaterally, as in the previous experiment, when the instructions given to the subjects caused them to focus on the value of the digits instead of their identities, i.e. they are able to perform above chance when deciding whether the digits are equal or unequal, but not when deciding whether the digits are the same or different. This experiment attempted to find evidence of this ability in J.W.

Methods

The stimuli and procedures were identical to those in the between field condition of the previous experiment. Only the instructions differed. The terms 'same' and 'different' were not mentioned; instead, he was encouraged to consider the values of the numbers and to decide whether or not they were equal. This experiment and Experiment 1 were run in separate sessions at least 1 week apart. Two blocks of 144 trials were run with each hand for a total of 576 trials.

Results and discussion

As in the previous experiment, the subject was unable to perform beyond the level of chance. He was 52.4% correct with his right hand ($\chi^2_1 = 0.68$, P > 0.3), and 44.8% correct with his left hand ($\chi^2_1 = 3.12$, P > 0.05).

Despite the efforts to emphasize numerical quantity rather than identity in this task, it became clear by the second block that J.W. was still treating this as a same/different task. When asked to repeat the instructions, he persisted in using the same/different terminology. He was corrected and again instructed to judge whether or not the digits were equal rather than same or different. Although he was informed that he could do better by thinking of the values rather than the names or appearance of the digits, he nevertheless insisted that it was the same thing as same/different. His performance in the two trial blocks after this coaching was no different than that in the two earlier blocks.

The present results clearly fail to replicate the reported ability of L.B. and N.G. However, the possibility exists that J.W. may have demonstrated similar abilities had he not noticed a fundamental similarity in the equal/not equal and same/different instructions. In order to examine this issue further, we went on to test the callosotomy subjects on several tasks which would force them to evaluate the digits.

Experiment 3: Part 1

Determining which of two numbers is greater requires that one consider the value rather than the identity of the numbers. Sergent (1990) has reported that three commissurotomy patients

Table 2 Percent correct, number of trials (in parentheses), and mean reaction times in the which-is-larger comparison of digits (Experiment 3)

	J.W.		V.P.		D.R.
	Right hand	Left hand	Right hand	Left hand	Left hand
With strategy					
Between visual fields	72.7 (216)	77.8 (144)	-	-	_
Without strategy					
Within left visual field Mean reaction time	75.2 (432) 1102 ms	95.9 (647) 1276 ms	83.7 (215)	91.8 (158)	60.4 (321)
Within right visual field Mean reaction time**	99.3 (432) 952 ms	96.8 (647) 1125 ms	90.2 (215)	93.9 (164)	62.3 (321)
Between visual fields Mean reaction time	49.1* (216) 1197 ms	55.5* (216) 1121 ms	59.9 (429)	57.0 (214)	51.2* (640)
Image stabilized					
Between visual fields Mean reaction time	54.6* (108) 788 ms	_	-	_	-

^{*}Not significantly different from chance performance; **mean reaction times for J.W. in the left-hand right visual field condition are based on three of the six blocks due to a programming error.

can perform this task with a high degree of accuracy. Unfortunately, her design is not well suited to examine interhemispheric transfer since it is possible to obtain 78% accuracy by simply applying a strategy based on the digit in a single visual field (i.e. if the digit is ≤ 4 , guess that the other side is higher; if it is ≥ 6 , guess that this side is higher; and if it is 5 simply guess). We ran the experiment nonetheless to determine whether J.W. would show the pattern of results reported in N.G. and L.B. We also attempted to verify that J.W. used the single-field strategy by including trials in which the digits were the same. He was told that on such trials he should simply guess since these trials would not be scored. If one hemisphere takes control of performance and adopts the unilateral strategy described above, we would expect that hemisphere to choose the contralateral visual field when the digit is >5 and the ipsilateral field when the digit is <5, despite the fact that both fields contain the same digit. An analysis of 'same' trials cannot, however, distinguish between the case in which this strategy is not used and that in which the control of responses shifts from one hemisphere to the other. In the former case, responses would be random guesses, and in the latter, the hemispheres would choose opposite responses given the same stimulus so that, again overall, responses would appear random.

Methods

The stimuli were all the pairs of digits used in the previous two experiments. The digits were presented bilaterally and the subject was instructed to press the button on the side of the digit with the higher value. Blocks again consisted of 144 trials, but only half of these, the 'different' trials, were scored for

accuracy. J.W. was tested on three right hand and two left hand blocks.

Results and discussion

J.W.'s performance was better than that expected by chance when chance is defined as 50% correct (Table 2). He had 72.7% correct with the right hand ($\chi^2_1 = 44.46$, P < 0.001) and 77.8% correct with the left ($\chi^2_1 = 44.44$, P < 0.001). Perfect use of the unilateral strategy described above would have predicted 78% correct, and in fact during testing J.W. described using this strategy. An examination of the 'same' trials showed his use of the strategy in the right hand blocks based on the digit in the right visual field (85% 'left side greater' responses for the digits 1-4, 42% for the digit 5, and 13% for the digits 6-9). No pattern appeared in the left hand data (47% 'left side greater' responses for the digits 1-4, 31% for the digit 5, and 42% for the digits 6-9), but as noted above, this is still consistent with use of the strategy, although it is not conclusive.

Experiment 3: Part 2

Although performance in the previous experiment was better than chance (i.e. >50%), this result is likely due to the use of a unilateral strategy rather than to interhemispheric transfer. This interpretation would be supported if chance performance is obtained when the strategy is made ineffective. To test this possibility, we redesigned the stimulus set in the following way. The set was restricted to those pairs of 'different' digits which were one unit apart (e.g. 1 and 2, 2 and 1, 2 and 3, 3 and 2, etc.). Each digit was paired, an equal number of times, with one higher or one lower than itself. Trials with a 1 or a 9 in

either the left or the right visual field were included in the stimulus set, but were not scored since the strategy could be applied to them. No 'same' trials were included in this experiment.

Methods

Each pair of digits was repeated nine times for a total of 144 trials per block, of which 108 per block were scorable after removing trials with ones and nines. All three subjects, J.W., V.P. and D.R., were tested on both within field and between field comparisons. As in the previous experiment, on between field blocks the subjects were instructed to press the left button when the digit on the left was higher, and the right button when the digit on the right was higher. For within field blocks the left button was assigned to the digit in the upper quadrant and the right button to the digit in the lower quadrant. J.W. was tested on four within field blocks with the right hand and six with the left; and two between field blocks with each hand. The two extra left hand within field blocks were meant to ensure that he could still perform the task when the left hand, between field data were collected at a later date than the original within field and right hand data. V.P. was tested on two within field blocks and four between field blocks with her right hand. With her left hand she was tested on two between field blocks and, due to time constraints, only one and a half within field blocks (the half block consisting of the first 144 randomly selected trials of a block, 106 of them scorable once trials with ones and nines were eliminated). In this and the following experiment, D.R. was tested with her left hand because in Experiment 1 her left visual field scores were better with left hand responses whereas right visual field performance was less affected by response hand. She was tested on three within field blocks and six between field blocks. Because D.R. showed a great deal of variability in her performance on the first three between field blocks, additional blocks were run to ensure a stable estimate of her abilities. More specifically her scores on the six blocks were 50.5%, 65.4%, 58.5%, 45.8%, 45.8% and 41.7%, with only the second block being significantly above chance $(\chi^2_1 = 10.18, P < 0.005).$

Results and discussion

All subjects demonstrated that they were capable of performing the task in the within field version (Table 2). When using the hand ipsilateral to the visual field of presentation, J.W. was at least 95.9% correct ($\chi^2_1 \ge 545.23$, P < 0.001) and V.P. was at least 90.2% correct ($\chi^2_1 = 139.20$, P < 0.001). D.R. did not perform as well but her scores for both visual fields were significantly above chance (left visual field, 60.4% correct, $\chi^2_1 = 13.98$, P < 0.001; right visual field, 62.3% correct, $\chi^2_1 = 19.44$, P < 0.001).

When the task required comparing information held in the two hemispheres (the between field task) the performance of all the subjects dropped drastically. J.W.'s performance with the right hand at 49.1% correct and with the left at 55.5% was not significantly different from chance in either case

 $(\chi^2_1=0.07,\,P>0.75;\,\chi^2_1=2.67,\,P>0.1$, respectively). D.R.'s score of 51.2% correct was also not statistically different from chance $(\chi^2_1=0.40,\,P>0.5)$. V.P.'s between field performance, although only 57.0% correct with her left hand and 59.9% with her right, was significant given the large number of trials (left hand: $\chi^2_1=4.21,\,P<0.05$; right hand: $\chi^2_1=16.84,\,P<0.005$). It should be noted, however, that V.P. is known to have some spared callosal fibres. Their role in her above chance performance cannot be ruled out. We return to this issue in the general discussion.

These results demonstrate that two of the three subjects are completely unable to make cross-hemisphere comparisons when the stimulus set is properly controlled to eliminate response strategies. Contrary to Sergent's hypothesis, no transfer was evident despite the fact that digital value, rather than identity, was emphasized.

Experiment 3: Part 3

It has been suggested by Sergent (1990) that interhemispheric comparison in callosotomy patients may require additional processing time for one hemisphere to become aware of information held by the other. Thus, the rapid tachistoscopic presentation typically used may be detrimental to the observation of subcallosal transfer, whereas longer stimulus presentation time would improve performance. We tested this suggestion using image stabilization, thereby nullifying the effects of eye movements which occur with extended presentations and ensuring that the stimuli remained lateralized.

Methods

The task and the stimuli were identical to those used in Part 2 of this experiment. The subject's eye movements were monitored by a Purkinje image eyetracker which was connected to a stimulus deflector system. The subject viewed the stimuli through mirrors controlled by the eyetracker outputs, such that if the eye moved, the stimulus deflector compensated by moving the visual field with the eye. Stimulus presentation was terminated when the subject made a response. Subject J.W. was tested on one block of the between field comparison (144 trials total; 108 of them scorable once trials with ones and nines were eliminated).

Results and discussion

In spite of the fact that viewing times were on the average three times longer, J.W. showed no ability to perform this task (54.6% correct; $\chi^2_1 = 0.93$, P > 0.3; Table 2). This result suggests that the absence of interhemispheric transfer cannot be attributed to brief tachistoscopic exposures.

Experiment 4

While the 'which side is higher?' judgment should, in principle, require comparison of numerical quantity, perhaps the most direct way of ensuring this form of encoding is to ask the subject

	J.W.		V.P.	D.R.
	Right hand	Left hand	Right hand	Left hand
Within left visual field	50.0* (120)	68.3 (240)	92.5 (120)	85.0 (120)
Mean reaction time	1272 ms	1415 ms		
Within right visual field Mean reaction time	86.7 (120) 1235 ms	76.3 (240) 1384 ms	95.8 (120)	79.0 (119)
Between visual fields Mean reaction time	50.0* (120) 1349 ms	55.4* (240) 1593 ms	52.5* (240)	50.5* (360)

Table 3 Percent correct, number of trials (in parentheses), and mean reaction times in the equal/not equal comparison of digits and dots (Experiment 4)

to compare the value of a digit with some quantity of dots. In order to compare these physically dissimilar stimuli, each must be recoded into a common abstract representation of quantity or value. Thus the presentation of an array of dots to one hemisphere and a digit to the other requires that each hemisphere determine the numerical quantity present in order to make the necessary comparison. Identity comparison is useless in this situation.

Methods

The set of digits and dots was restricted to the numbers 1-6, because pretesting with J.W. showed that the sets of dots above six tended to be easily confused. The digits 1-6 were paired with groups of dots which were organized in a regular and fixed pattern (as on a dice with the exception that '2' and '3' ran horizontally rather than diagonally). The dot stimuli took up approximately the same amount of screen space as the digits, ranging from 1.1 to 4.5° high and from 1.1 to 3.75° wide, and were centred at ~ 6.5 ° from fixation.

All possible combinations of dot array-digit pairs were used. Each combination was presented twice in each condition, once with the dots in one visual field (or quadrant) and once with the dots in the other. Each 'equal' pair was repeated five times, resulting in 60 'equal' trials to balance the 60 'not equal' trials for a total of 120 trials in the between field condition. In the within field condition these numbers were doubled (120 'equal' trials, 120 'not equal' trials) so that each combination appeared twice in each visual field.

The subject was instructed to press one button if the two stimuli represented an equal value and the other if they were not equal. For J.W. one left and two right hand blocks were run for both the within and between field conditions. V.P. was tested on one within and two between field blocks with the right hand. D.R. was tested on one within field block and three between field blocks, all with the left hand.

Results and discussion

All subjects performed well in the within field condition (Table 3), particularly when responding with the hand contralateral to the hemisphere which received the information. J.W.'s

unusually poor performance with the right hand when responding to left visual field stimuli was likely due to fatigue he experienced during this session. Regardless, each of J.W.'s hemispheres was able to perform at a level of 68.3% or above in at least one condition ($\chi^2_1 \geq 32.27$, P < 0.001) demonstrating that each hemisphere was able to perform the task. V.P. was able to perform above 92.5% with either hemisphere ($\chi^2_1 \geq 86.70$, P < 0.001), and D.R. performed at 79.5% or better with either hemisphere ($\chi^2_1 \geq 40.01$, P < 0.001). These results demonstrate that either hemisphere was able to judge the value of both types of stimuli (dots and digits) in order to make equal/not equal comparisons.

In contrast to their within field performance, all subjects again demonstrated an inability to transfer the relevant information between the hemispheres in the between field condition. J.W. performed at 50% correct with his right hand ($\chi^2_1 = 0.00$, P > 0.995) and 55.4% with his left ($\chi^2_1 = 2.82$, P > 0.05). V.P. was 52.5% correct ($\chi^2_1 = 0.60$, P > 0.3), and D.R. 50.5% correct ($\chi^2_1 = 0.04$, P > 0.8). No transfer was observed even though the task could only be solved by comparing information about value.

This result is particularly noteworthy in the case of V.P. As the only case showing a modest amount of transfer in the 'which is higher?' task (Experiment 3, Part 2) she provides an opportunity to test the claim (Sergent, 1990; Cronin-Golomb, 1986) that successful transfer requires a high-level code. Her inability to compare dots and digits challenges this interpretation.

General discussion

The results of this series of experiments generally fail to replicate findings which have been reported for other split-brain subjects in tasks identical, or nearly identical, to those reported here. Sergent (1990) reported that L.B., N.G. and, to some extent, A.A. were able to perform tasks such as these, which emphasize stimulus meaning or abstract associations rather than the identity or low-level visual features of the stimulus. Sergent suggests that higher-order visual or amodal information may be more available to interhemispheric comparison than lower-order perceptual information, albeit at a level outside conscious

^{*}Not significantly different from chance performance.

awareness (Sergent, 1990). A similar claim has also been made concerning the same subjects in very different tasks by Cronin-Golomb (1986).

In contrast, the three callosotomy subjects tested here were unable to perform any of the between field tasks, with the exception of one of the tasks for case V.P., a subject with known sparing of callosal fibres. Apart from this exception, the subjects were no more accurate at tasks requiring abstract comparisons than they were in a same/different task requiring comparison on the basis of visual similarity. Even the digit/dot comparison, which was designed to enable solution only through abstract encoding of the physically dissimilar stimuli, could not be solved by these subjects in the between field condition.

We are left, therefore, with the question of how to account for the inconsistency between the East and the West Coast subjects. We address this problem by first considering how the present results fit with other attempts to find transfer of visual, as well as more abstract information, in the East Coast group. We then consider the potential role of unilateral strategies and response readiness as possible bases for the differences between the groups.

The present results reaffirm the numerous reports demonstrating the inability of split-brain subjects to compare the visual similarity of information presented to their separated hemispheres. For example, V.P. is unable to determine whether two patches of sinusoidal gratings presented simultaneously to her two visual fields have the same or different orientations (Fendrich and Gazzaniga, 1990). The same is true when she is required to cross-compare two non-nameable symbols drawn from a set of four possibilities (Fendrich and Gazzaniga, 1989) or two letters drawn from a set of only two (Gazzaniga et al., 1989). J.W. has been unable to cross-compare the orientation of sine wave grating patches, the shape of 4°×4° figures, the achromatic colour of 2° black or white squares on a gray background, and the vertical position of 2° squares offset vertically ±3° (Tramo et al., 1994). He is also unable to say whether two line drawings presented in opposite visual fields are the same or different (Sidtis et al., 1981). Another callosotomy subject, P.S., has repeatedly been found to be incapable of comparing words or pictures presented to his two visual fields despite his ability to name these stimuli when they were presented to either hemisphere (Gazzaniga et al., 1979). R.Y. and A.A., and in some cases N.G. and L.B., of the West Coast series, have also been unable to perform similar tasks when they were required to make same/different decisions (Cronin-Golomb, 1986; Johnson, 1984; Sergent, 1986, 1990).

Among the East Coast subjects, the only evidence for transfer that can be linked to subcortical pathways rather than spared callosal fibres involves low-resolution visual information. Holtzman (1984) reported that J.W. could reliably indicate whether a matrix of four 'X's (subtending altogether $2^{\circ} \times 2^{\circ}$ of visual angle) in the left visual field was above, below, or level with an identical reference matrix positioned at the horizontal meridian in the right field. He was most accurate at the largest discrepancies and reported difficulty with the smaller discrepancies because the left visual field stimulus,

which was presented for an extended duration, looked like a 'shadowy blob'. The residual visual information available to his uninformed hemisphere (i.e. the one ipsilateral to the stimulated hemifield), in fact, was not sufficient for discrimination of 0.25° shapes in that hemisphere's visual field. Thus, the cross-field comparisons were based on very gross visual form, possibly mediated by the superior colliculi.

Other reports bear directly on the hypothesis that abstract information can be transferred in the absence of a corpus callosum and the results are frankly inconsistent with this proposal. Gazzaniga *et al.* (1984b) have demonstrated that J.W. and V.P. are unable to compare semantic information about words presented in opposite visual fields, although they are able to perform within field comparisons. Specifically, they were unable to choose which of two words was semantically related to a word presented to the other hemisphere. This was found for each of four types of semantic relations: superordinate class, same class, attribute or function. Because this task required only associated semantic information, it would seem to be one for which Sergent's hypothesis would predict a high success rate.

In addition, Reuter-Lorenz and Baynes (1992) found no evidence that the hemispheres can share information about abstract letter codes. In a letter priming task, J.W. was required to decide whether an upper-case target letter was an 'H' or 'T'. The target was preceded by a lower case prime which was either an 'h' or 't'. In the between field condition the prime and target occurred in opposite visual fields. If information about abstract letter identity can be transferred, letter identification should be faster when the target is preceded by a prime of the same name than when prime and target mismatch. No evidence of this pattern was obtained for any of the between field conditions.

It has also been demonstrated that D.R. is unable to compare a picture and a word presented bilaterally (Baynes et al., 1992). The tasks included a same/different, picture/word comparison as well as a choice of which of two words matched a picture presented to the opposite visual field, or which of two pictures matched a word. She was unable to perform any of the tasks including those in which the relevant information for comparison was semantic information rather than perceptual identity.

V.P. is the only case for whom limited transfer has been previously reported. She was able to cross-compare words which both sounded alike (i.e. rhymed) and looked alike (R+L+), but not those which sounded alike but looked different (R+L-), looked alike but sounded different (R-L+), or both sounded and looked different (R-L-) (Gazzaniga et al., 1989). In other words, she was able to perform the cross-comparison only when aided by the visual perceptual information. She was not able to perform solely on the basis of phonetically coded information derived from the graphemic stimuli. The hypothesis that higher-order information can be cross-compared more readily than perceptual identity would seem to have predicted the converse result.

It is significant, then, that V.P. was also the only subject to show any ability to cross-compare in the present tasks. She performed slightly above chance when judging which of two digits was larger, but, by contrast, she was unable to say whether a digit was or was not equal in value to a group of dots even though both tasks require comparisons of values. This is reminiscent of the Gazzaniga (1989) study in which she was able to perform the R+L+ comparison but not the R+L-, R-L+, or R-L- ones. Gazzaniga and colleagues note the remarkable specificity of what could be successfully transferred via this subject's spared callosal fibres. The present findings can be taken as corroboration of such specificity.

It seems, then, that the only instances in which the East Coast subjects have shown evidence of transfer involve crude visual information or limited information crossing in residual callosal fibres. While the present results are consistent with these previous studies, they differ markedly from the results reported by Sergent (1987, 1990) for the West Coast patients on very similar tasks.

This divergence of results could be due, in part, to the possibility that the patients in Sergent's study employed a unilateral strategy such as the one clearly illustrated in the right hand data for J.W. in Experiment 3 (see also Sergent, 1986). The use of such strategies, however, cannot account for the fact that accuracy levels were sometimes >78%. Another possible explanation for positive results involving value comparison is that each hemisphere independently, and without any knowledge of the stimulus presented to the other, has a disposition to respond, which is determined by the magnitude of the digit presented to it. The hemisphere more disposed to respond then initiates the motor output. This would be a kind of integration that depends on hemispheric differences in response readiness whereby one hemisphere's motor command comes to dominate that of the other. However, with this type of mechanism, information about the stimuli themselves is never actually transferred between the hemispheres or compared at either a perceptual or higher level. We might speculate then that patients could vary in the extent to which differences in response readiness could provide a basis for seemingly integrated responding. Perhaps case L.B., for whom numerous reports of transfer have been obtained, is particularly adept at allowing differences in response readiness to determine which hemisphere controls performance.

While response readiness may not contribute to our subjects' performance in the present experiments, other investigations suggest that it may provide a basis for integrated responding for J.W. Gazzaniga et al. (1987) demonstrated that J.W. can name, or manually identify under left hemisphere control, digits which were presented tachistoscopically to the right hemisphere. This result occurs only when the entire stimulus set contains no more than two items. Although the left hemisphere is able to respond appropriately, it remains unaware of the item presented to the right hemisphere as evidenced, among other things, by its inability to perform a between field same/different comparison of the same stimuli. Thus, the right hemisphere seems able to set up a response readiness for one of the two responses to be produced by the left hemisphere. Nevertheless other information associated with the stimulus cannot be transferred. In addition, recent work by Reuter-Lorenz et al. (1994) demonstrates pronounced reaction time benefits in a

simple reaction time task when redundant targets are presented to the separated hemispheres simultaneously. Reaction time performance benefits from redundant targets even though detection accuracy under the identical stimulus conditions shows evidence of visual extinction. An extensive analysis of these effects suggests that motor readiness may also provide the basis for such redundancy gains in the bisected brain.

Together these findings suggest the need to distinguish between the transfer of information between the hemispheres via some extra-callosal route versus the integration of outputs from the two hemispheres by non-cortical structures. Evidence for the former class of effects has been the basis for the challenge to the traditional view of the split-brain syndrome (e.g. Sergent, 1990), whereas with the latter form of integration neither hemisphere has access to the processing operations of the other, but rather some other process coordinates the outputs of both (see also Sergent, 1986; Tramo et al., 1994). Sergent (1990) has distinguished between interhemispheric comparison and interhemispheric integration. However, she leaves open the possibility that transfer or 'information exchange' contributes to both processes. We emphasize that integration could very well take place in the absence of interhemispheric transfer. Thus, at least some of the results from the West Coast subjects that have been taken as evidence for transfer could be due instead to integration without transfer.

Finally, it is also worth noting that all of the subjects in the present investigation have intact anterior commissures which apparently played no useful role in the interhemispheric comparisons under study. This supports the conclusion, drawn from the numerous other studies discussed above which document the lack of interhemispheric transfer in these subjects, that the anterior commissure in humans, in contrast to that in other primates (Gazzaniga, 1966, 1988; Sullivan and Hamilton, 1973), does not transfer visual information. The presence of the anterior commissure in these subjects, and its absence in those West Coast subjects for whom subcallosal transfer has been reported, is the most notable difference between the groups. It is difficult to see how this difference could explain the discrepancies between the two groups, however, since it is precisely those subjects, who still have a major interhemispheric commissure, who cannot perform interhemispheric comparisons. Nevertheless, we cannot rule out the possibility that this neuroanatomical difference contributes to the performance differences between the East and West Coast groups since neither unilateral strategies nor response integration can entirely explain this variability.

The results of the present investigation are consistent with the traditional view of the corpus callosum as the major neural pathway by which interhemispheric transfer and integration are achieved. The present experiments provide little or no support for the claims that higher cognitive representations can be transferred or compared subcallosally. These results and those reviewed above suggest that such claims cannot be generalized to the population of callosotomy subjects as a whole and thus also question their implications for normal callosal and subcallosal function.

Acknowledgements

M. S. Gazzaniga and P. A. Reuter-Lorenz were supported by NINDS grant no. RO1 NS22626-07 and S. E. Seymour by the McDonnell-Pew Program.

References

Baynes K, Tramo MJ, Gazzaniga MS. Reading with a limited lexicon in the right hemisphere of a callosotomy patient. Neuropsychologia 1992; 30: 187-200.

Bogen JE, Schultz DH, Vogel PJ. Completeness of callosotomy shown by magnetic resonance imaging in the long term. Arch Neurol 1988; 45: 1203-5.

Corballis MC, Sergent J. Judgements about numerosity by a commissurotomized subject. Neuopsychologia 1992; 30: 8T 65-76.

Cronin-Golomb A. Subcortical transfer of cognitive information in subjects with complete forebrain commissurotomy. Cortex 1986; 22: 499-519.

Fendrich R, Gazzaniga MS. Evidence of foveal splitting in a commissurotomy patient. Neuropsychologia 1989; 27: 273-81.

Fendrich R, Gazzaniga MS. Hemispheric processing of spatial frequencies in two commissurotomy patients. Neuropsychologia 1990; 28: 657-63.

Gazzaniga MS. Interhemispheric communication of visual learning. Neuropsychologia 1966; 4: 183-9.

Gazzaniga MS. The bisected brain. New York: Appleton-Century-Crofts, 1970.

Gazzaniga MS. Interhemispheric integration. In: Rakic P, Singer W, editors. Neurobiology of neocortex. Chichester: John Wiley, 1988: 385-405.

Gazzaniga MS, Bogen JE, Sperry RW. Some functional effects of sectioning the cerebral commissures in man. Proc Natl Acad Sci USA 1962; 48: 1765-9.

Gazzaniga MS, Volpe BT, Smylie CS, Wilson DH, LeDoux JE. Plasticity in speech organization following commissurotomy. Brain 1979; 102: 805-15.

Gazzaniga MS, Nass R, Reeves A, Roberts D. Neurologic perspectives on right hemisphere language following surgical section of the corpus callosum. Semin Neurol 1984a; 4: 126-35.

Gazzaniga MS, Smylie CS, Baynes K, Hirst W, McCleary C. Profiles of right hemisphere language and speech following brain bisection. Brain Lang 1984b; 22: 206-20.

Gazzaniga MS, Holtzman JD, Deck MDF, Lee BCP. MRI assessment of human callosal surgery with neuropsychological correlates. Neurology 1985; 35: 1763-6.

Gazzaniga MS, Holtzman JD, Smylie CS. Speech without conscious awareness. Neurology 1987; 37: 682-5.

Gazzaniga MS, Kutas M, Van Petten C, Fendrich R. Human callosal function: MRI-verified neuropsychological functions. Neurology 1989; 39: 942-6.

Holtzman JD. Interactions between cortical and subcortical visual areas: evidence from human commissurotomy patients. Vision Res 1984; 24: 801-13.

Holtzman JD. Eye movement control following corpus commissurotomy in humans. In: Posner MI, Marin OSM, editors. Attention and performance XI. Hillsdale, NJ: Lawrence Erlbaum, 1985: 425-40.

Holtzman JD, Sidtis JJ, Volpe BT, Wilson DH, Gazzaniga MS. Dissociation of spatial information for stimulus localization and the control of attention. Brain 1981; 104: 861-72.

Hughes HC, Reuter-Lorenz PA, Fendrich R, Gazzaniga MS. Bidirectional control of saccadic eye movements by the disconnected cerebral hemispheres. Exp Brain Res 1992; 91: 335-9.

Johnson LE. Bilateral visual cross-integration by human forebrain commissurotomy subjects. Neuropsychologia 1984; 22: 167-75.

Lambert AJ. Interhemispheric interaction in the split-brain. Neuro-psychologia 1991; 29: 941-8.

MacKay DM, MacKay V. Explicit dialogue between left and right half-systems of split brains. Nature 1982; 295: 690-1.

Myers JJ, Sperry RW. Interhemispheric communication after section of the forebrain commissures. Cortex 1985; 21: 249-60.

Reuter-Lorenz PA, Baynes K. Modes of lexical access in the callosotomized brain. Journal of Cognitive Neuroscience 1992; 4: 155-64.

Reuter-Lorenz PA, Fendrich R. Orienting attention across the vertical meridian: evidence from callosotomy patients. Journal of Cognitive Neuroscience 1990; 2: 232–8.

Reuter-Lorenz PA, Nazawa G, Gazzaniga MS, Hughes HC. The fate of neglected targets in the callostomized brain: a chronometric analysis. J Exp Psychol Hum Percept Perform 1994. In Press.

Sergent J. Unified response to bilateral hemispheric stimulation by a split-brain patient. Nature 1983; 305: 800-2.

Sergent J. Subcortical coordination of hemisphere activity in commissurotomized patients. Brain 1986; 109: 357-69.

Sergent J. A new look at the human split brain. Brain 1987; 110: 1375-92.

Sergent J. Furtive incursions into bicameral minds. Brain 1990; 113: 537-8.

Sidtis JJ, Volpe BT, Wilson DH, Rayport M, Gazzaniga MS. Variability in right hemisphere language function after callosal section: evidence for a continuum of generative capacity. J Neurosci 1981; 1: 323-31.

Sperry RW. Mental unity following surgical disconnection of the cerebral hemispheres. Harvey Lectures 1966-7; 62: 293-323.

Sperry RW, Gazzaniga MS, Bogen JE. Interhemispheric relationships: the neocortical commissures; syndromes of hemisphere disconnection. In: Vinken P J, Bruyn GW, editors. Handbook of clinical neurology, Volume 4. Amsterdam: North Holland, 1969: 273–90.

Sullivan MV, Hamilton CR. Interocular transfer of reversed and nonreversed discrimination via the anterior commissure in monkeys. Physiol Behav 1973; 10: 355-9.

Teng EL, Sperry RW. Interhemispheric interaction during simultaneous bilateral presentation of letters or digits in commissurotomized patients. Neuropsychologia 1973; 11: 131–40.

Tramo MJ, Bharucha JJ. Musical priming by the right hemisphere post-callosotomy. Neuropsychologia 1991; 29: 313-25.

Tramo MJ, Baynes K, Fendrich R, Mangun R, Phelps EA, Reuter-Lorenz P, Gazzaniga MS. Hemispheric specialization and interhemispheric integration: recent insights from experiments with commissurotomy patients. In: Reeves A, Roberts D, editors. Epilepsy

and the corpus callosum, second edition. New York: Plenum Press, 1994. In press.

Trevarthen C, Sperry R. Perceptual unity of the ambient visual field in human commissurotomy patients. Brain 1973; 96: 547-70.

Received June 1, 1993. Accepted September 25, 1993