Left and Right Hemisphere Contributions to Physiognomic and Verbal Discrimination

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The relative contributions of the right- and left-temporal lobes in rapid recognition of faces and letters were studied in patients with anterior right- or left-temporal lobe excisions and a matched control group. On the basis of findings in patients with unilateral and bilateral brain damage, it was hypothesized that left hemisphere damage would not change the reaction time of letters analyzed by the right hemisphere and that right hemisphere damage would not change the reaction time of faces analyzed by the left hemisphere. The hypothesis was supported for letters but not for faces. Patients in the right-temporal group, particularly those with large hippocampal removals, were slow to recognize faces in both visual fields. Two possible explanations for the findings with faces are explored: One holds that right hemisphere mechanisms are involved even when a face is presented to the left hemisphere for rapid recognition; the other holds that specialized encoding is carried out by the right hemisphere during learning, with the encoded template then being used by each hemisphere independently.

Descriptions of face recognition disorders can be found as early as in nineteenth century neurological writings (e.g., Charcot, 1883), but it was only in the mid-1900s that patients were described in whom a disproportionate loss of face recognition existed in the absence of other visual problems (Bodamer, 1947). Bodamer (1947) named the condition prosopagnosia (literally, loss of person knowledge; from Greek prosopon meaning person and agnosia meaning ignorance). Subsequent work has shown that the right cerebral hemisphere plays a predominant role in analyzing and learning complex visual material such as familiar (but not famous-see below) faces. The most complete theory to date of face recognition (Bruce & Young, 1986) posits an initial structural encoding followed by several analytical processes (carried out by face recognition units), which probably act in parallel, followed by recognition and

Correspondence concerning this article should be addressed to Henry A. Buchtel, Neuropsychology Program, 480 Med Inn, University of Michigan, Ann Arbor, Michigan 48109-0840. Electronic mail may be sent to gusb@umich.edu. naming. The Bruce and Young (1986) model focuses on functional requirements in facial recognition and does not attempt to designate which cerebral hemisphere is responsible for a particular analytical component, though many of the units (e.g., analysis of emotional expression) are likely to be organized by the right hemisphere (e.g., Anderson, Spencer, Fulbright & Phelps, 2000; Buchtel, Campari, De Risio, & Rota, 1978), even in chimpanzees (Morris & Hopkins, 1993).

Evidence that the right cerebral hemisphere has a major responsibility for learning and remembering familiar faces comes from studying patients with lateralized brain damage (e.g., Benton & Van Allen, 1968; De Renzi & Spinnler, 1966; Milner, 1968; Warrington & James, 1967) and from tachistoscopic studies in which normal participants view lateralized visual stimuli that are sent initially to one or the other cerebral hemisphere (e.g., Geffen, Bradshaw, & Wallace, 1971; Rizzolatti, Umiltà, & Berlucchi, 1971). Recent work showing activation of the right fusiform gyrus in face tasks supports these conclusions (e.g., Kanwisher, McDermott, & Chun, 1997; Kim et al., 1999; O'Craven & Kanwisher, 2000). It is noteworthy that individuals with defects in face recognition do not show this fusiform activation (Schultz et al., 2000). Right-hemisphere activation with face stimuli has been seen in nonhuman species as well (Broad, Mimmack, & Kendrick, 2000).

Hypotheses about the origin of this right-hemisphere superiority in face perception have ranged from classifying faces as a special category of visual-spatial stimuli, which would fit with the lateralization of mechanisms to the right hemisphere along with other spatial skills involved in analyzing stimuli that are difficult to translate into a verbal code (e.g., De Renzi, 1982). For some time it was thought that the analysis and recognition of faces and other complex nonface stimuli (e.g., buildings) were subserved by the same mechanisms because deficits in one were almost invariably asso-

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ciated with deficits in the others (for a recent treatment of this topic, see Gauthier, Behrmann, & Tarr, 1999); new functional magnetic resonance imaging evidence has shown that the areas activated in remembering faces and buildings are within millimeters of each other, but clearly dissociable (O'Craven & Kanwisher, 2000). The question of why the right hemisphere might be dedicated to analyzing this kind of stimulus is beyond the scope of this article, but it is possible that spatial skills were pushed into the right hemisphere because this part of the brain had not already become dedicated to speech processes. Finally, Sergent (1982) has demonstrated that the right hemisphere is superior to the left hemisphere in the analysis of stimuli with low spatial frequencies. Because face stimuli are richer in low spatial frequencies than in high spatial frequencies (which are more characteristic of letters and words), Sergent proposed that the right hemisphere superiority for faces could simply be secondary to the lateralization of spatial frequency sensitivity. Although the explanation for face lateralization based on spatial frequencies has now been called into question, even by Sergent herself (1987), it has served the purpose of highlighting the fact that the two hemispheres are differentially sensitive to spatial frequencies and that studies of visual-field differences need to take this potential confound into account.

Although there is a convergence of findings that the right hemisphere is superior to the left hemisphere in face analysis and face memory, both the left and right cerebral hemispheres appear to possess mechanisms that allow them, in isolation, to recognize certain classes of faces. In the case of unilateral right-hemispheric lesions in adulthood, patients may be extremely impaired in the learning of new, previously unknown faces (Benton & Van Allen, 1968; Milner, 1968; Warrington & James, 1967), but they are usually still able to recognize, for example, family members, perhaps by using mechanisms located in the intact left hemisphere. It should be noted that clinical observations and CT scan findings in living patients have suggested that right hemisphere damage alone may be capable of producing a complete loss of memory for faces, including family members (e.g., De Renzi, 1986; Landis, Cummings, Christen, Bogen, & Imhof, 1986; Sergent & Poncet, 1988; see also Sergent & Villemure, 1989, for a case of prosopagnosia after right hemispherectomy at the age of 13 years), but cases of prosopagnosia that have come to autopsy have shown damage in both cerebral hemispheres (Meadows, 1974) or have shown right-hemisphere damage plus an interruption of critical pathways to posterior left cortical areas (Damasio, Damasio, & Van Hoesen, 1982). Ettlin et al. (1992) have documented a case in which progressive infarcts of the right hemisphere did not cause prosopagnosia until the addition of a left-hemisphere infarct.

Further evidence of a left-hemisphere contribution to face recognition in normal individuals comes from findings with certain kinds of face stimuli presented tachistoscopically. For example, there is a right visual field (left hemisphere) superiority when the stimuli consist of famous faces (Marzi & Berlucchi, 1977), discrimination of expression in faces with a single salient feature (presence of visible teeth in judging emotional expressions; Buchtel et al., 1978), overlearned faces (Umiltà, Brizzolara, Tabossi, & Fairweather, 1978), and line drawings of faces with a few discriminative features (Patterson & Bradshaw, 1975; Sergent, 1982). Findings of this kind have led some authors to suggest that the lateralization of face analysis and discrimination depends on the degree of familiarity of the stimuli, with merely familiar faces being analyzed in a holistic manner, appropriate to the right hemisphere, and very familiar (famous) faces being analyzed in a more analytic and featureoriented manner, appropriate to the left hemisphere (e.g., Umiltà et al., 1978; Ross-Kossack & Turkewitz, 1984, 1986). Data in support of this characterization have come from studies on faces (e.g., Ross & Turkewitz, 1982; Ross-Kossack & Turkewitz, 1984; Turkewitz & Ross, 1983) and complex nonface stimuli (e.g., Japanese ideograms viewed by non-Japanese individuals; Kittler, Turkewitz, & Goldberg, 1989). Other authors have argued that figural and configurational information is usually interdependent in face recognition (Tanaka & Sengco, 1997).

Although mechanisms located in the left hemisphere may be capable of contributing to the analysis and recognition of faces, it has not been easy to determine what actually happens when a familiar face is presented in the right visual field (projecting to the left hemisphere). It is clear that left visual field (right hemisphere) presentation of familiar faces usually results in faster (Geffen, Bradshaw, & Wallace, 1971; Rizzolatti et al., 1971) or more accurate (Hilliard, 1973; Jones, 1979) recognition. However, it is not clear whether the slower, less accurate performance associated with right visual field (left hemisphere) presentation represents the outcome of relatively inefficient activities of the left hemisphere or rather the loss of time and precision caused by a transfer of information from the left to the right hemisphere for analysis. If Meadows (1974) was correct that severe face recognition deficits are seen only with bilateral brain dysfunction, one is led to conclude that the left hemisphere possesses face recognition mechanisms (the findings with famous faces are consistent with this conclusion). Therefore, one could hypothesize that right-hemisphere damage would not necessarily affect the time that the left hemisphere typically takes to recognize faces. The individuals in the present study have had temporal lobe resections for the control of intractable epilepsy. Because reading ability is affected in only a minor way, if at all, after left-temporal lobe resections (Milner, 1974), and because letter classification does not appear to be lateralized to one hemisphere or the other (Bruyer, 1986), one may analogously hypothesize that left-hemisphere damage would not substantially affect the time that the right hemisphere typically takes to recognize letters. The present study was designed to test these hypotheses by studying the time taken by the less competent hemisphere to recognize stimuli that are more appropriately handled by the other hemisphere, with the expectation that whereas reaction times associated with presentation to the damaged hemisphere may be elevated, reaction times associated with presentation to an intact incompetent hemisphere will change little or not at all. If, on the other hand, lateralized damage to the competent hemisphere were found to disturb the abilities of both the damaged and intact hemispheres, the most parsimonious interpretation would be that the competent hemisphere plays a role in the rapid analysis of appropriate stimuli regardless of which hemisphere receives the information directly.

Method

Participants

Participants were 76 right-handed individuals consisting of 62 patients who had undergone temporal lobectomy at the Montreal Neurological Hospital for surgical relief of intractable temporal lobe epilepsy and 14 matched controls. All patients signed an informed consent form and control participants gave their oral informed consent. All patients were left-hemisphere dominant for speech according to the intracarotid amobarbital procedure and/or surgical stimulation. Thirty-three had right-temporal lobe excisions (16 women, 17 men), and 29 had left-temporal lobe excisions (13 women, 16 men). The general characteristics of patients have been described in previous publications (see Milner, 1975). During the operation, varying amounts of the hippocampus and parahippocampal gyrus were removed; the entire amygdaloid complex was removed in all cases. The extent of hippocampal removal was recorded by the surgeon at the time of surgery and was later coded for data analysis according to a method developed by Corsi (1972; Milner, 1974). If less than 2 cm of hippocampus or hippocampal gyrus were removed (Corsi's Groups I and II), the patient was placed in the Small Removal subgroup; if 2 cm or more were removed (Corsi's Groups III and IV), the patient was placed in the Large Removal subgroup. Some of the patients had upper-quadrant visual defects contralateral to the temporal lobe removal, but these defects never impinged on vision within 10° of the fovea and therefore did not interfere with the visual discrimination tasks used in this study. A control group of 14 individuals (6 women, 8 men) was equivalent in age to the patients (for the 12 individuals who completed the testing, mean age was 28.4 years ± 7.6 compared with 28.2 \pm 7.6 for the patients who completed the testing) and consisted of relatives of the patients and ancillary staff of the hospital. Patient characteristics for the 54 patients who were able to learn the task and perform at adequate levels of accuracy are as follows: 25 patients were seen 2 weeks postsurgery (11 left temporal, 14 right temporal), and 29 patients were seen from 6 months to 16 years postsurgery (17 left temporal, 12 right temporal). Time since surgery was also equally distributed among the patients with small mesial excisions (18 seen at 2 weeks postsurgery, 21 seen at least 6 months postsurgery) or large mesial excisions (7 seen at 2 weeks postsurgery, 8 seen at least 6 months postsurgery). The right-temporal group contained 18 patients with small excisions and 8 patients with large excisions. The left-temporal group contained 21 patients with small excisions and 7 patients with large excisions. Patient groups were equivalent in terms of age (lefttemporal group mean age = 28.5 years \pm 8.2, right-temporal group mean age = 27.9 ± 7.1) and Full Scale IQ (left-temporal group mean = 110.7 ± 11.7 , right-temporal group mean = 110.3 ± 14.8). There were nonsignificant trends (p > .2) for Verbal IQ to be slightly lower in the left-temporal group than in the right-temporal group (107.3 \pm 13.4 vs. 110.5 \pm 15.4) and for the Performance IQ to be slightly lower in the right-temporal group than in the left temporal group (108.5 \pm 15.5 vs. 112.3 \pm 10.5). The educational levels of the patient groups were similar (left-temporal group mean = 12.1 years \pm 3.3, righttemporal group mean = 11.8 ± 2.4) and occupations varied from unemployed (n = 11), through student status (n = 10), and

skilled/professional (one lawyer, one policeman, etc). The IQ and educational level of the control group were not obtained, but the characteristics of the patient groups (IQ values within one standard deviation of the mean of the general population; educational levels in the high school range) are such that a demographic differences between the control group and the patient groups are very unlikely.

Stimuli and Apparatus

Stimuli consisted of four faces from the set described by Rizzolatti et al. (1971) and four vertically oriented letter pairs (AN, BS, AS, BN). Letters were 24 point in size, similar in style to Helvetica Light, and written in India black ink on white stimulus cards, one letter above the other.

The face stimuli subtended $1.3^{\circ} \times 2.0^{\circ}$ of visual angle. During the test session, the center of the face appeared 2.3° of visual angle to the left or right of a central fixation spot, which consisted of a red spot of light subtending 0.2° of visual angle. The near edge of the face was approximately 1.6° of visual angle from the fixation spot. Both light and dark versions of the faces were used to ensure that the discrimination could not be made on the basis of simple brightness differences between the stimuli (see Reynolds & Jeeves, 1978). The faces were centered on a rectangular black background subtending $1.79^{\circ} \times 2.55^{\circ}$ of visual angle. The letter pairs subtended $0.26^{\circ} \times 0.9^{\circ}$ of visual angle, with the center of the stimulus 2.3° of visual angle from the fixation spot. Stimuli were presented in a three-field tachistoscope (Scientific Prototype Manufacturing Co., Waltham, MA), and between stimuli the participants looked at a blank white field. Pilot work with the patient groups had shown that the addition of a secondary task to check for central fixation (e.g., McKeever & Huling, 1971; Sperry, 1974) interfered with the patients' ability to identify the faces, so it was decided not to use such a task. However, the participants could not predict the visual field of the next stimulus and the distribution of reaction times is consistent with central fixation (i.e., reaction times to lateralized stimuli were slower than when stimuli were shown in central fixation during training trials as described below).

Procedure

Participants within each group were assigned alternatively to one of two subgroups. One subgroup first learned and responded to the faces and then learned and responded to the pairs of letters; the other group learned the letter pairs and then the faces. In both cases the stimuli were first shown to the participants under normal lighting conditions with approximately 5-10 s of exposure to each stimulus. In the case of faces, the participants were told that they should press a button when they saw either Face 1 or 2 (Figure 1A, first two faces in upper row) but not when they saw Face 3 or 4 (Figure 1A, last two faces in upper row). In the case of letters, they were told to respond to AN and BS but not to AS and BN. For the purpose of this article, we refer to these stimuli as "positive stimuli" and "negative stimuli," but when they were introduced to the patients, they were simply referred to as "stimuli to be responded to" or "stimuli not to be responded to." In each case, during this introductory phase, the two positive stimuli were shown both singly and together, as were the negative stimuli. Positive and negative stimuli were never shown simultaneously in order to discourage the participants from trying to base the recognition on single feature differences between the faces or head coverings.

The participant was then given a microswitch to hold in his or her right hand and instructed how to respond by pressing with his or her thumb. The room lights were dimmed and the participant



Figure 1. A: The four faces used in face discrimination task. Faces 1 and 2 were responded to by the participants; Faces 3 and 4 were not to be responded to. B: Same faces as in A but with the eyes and mouth exchanged. Participants relying on a single detail for their discrimination would be expected to have less trouble identifying these "scrambled" faces than a participant who has learned to recognize the face as a complex visual stimulus. The faces in A are from "Opposite Superiorities of the Right and Left Cerebral Hemispheres in Discriminative Reaction Time to Psysiognomical and Alphabetic Material," by G. Rizzolatti, C. Umiltà, and G. Berlucchi, 1971, *Brain, 94*, p. 432. Copyright 1971 by Oxford University Press. Reprinted with permission.

was instructed to look into the tachistoscope where the stimuli were shown in central vision for 150 ms. A 400-ms tone preceded the stimulus by 50 ms, and the central fixation spot disappeared during the visual presentations. Stimuli requiring or not requiring a response were still identified by the experimenter for 4-10further exposures per stimulus, until the participant reported that the recognition had been mastered. An incorrectly identified stimulus was repeated, for a longer duration if necessary, until the participant recognized it. With completion of this phase of training, the durations were set permanently to those of the test conditions (150 ms), lateralized stimuli replaced the centrally presented stimuli, and final criterion training was begun. Stimuli were presented either in the left or right visual field according to pseudorandom sequences (Gellerman, 1933).

Participants made button press responses to the positive stimuli, and feedback as to the accuracy of the response was given until the participant completed 12 consecutive responses with no errors (button presses to the negative faces were counted as errors). Participants were given a maximum of 100 trials to learn to recognize the stimuli. Then a sequence of test trials was begun with 101 trials total (5 practice and 96 test trials; 12 test trials per visual field per stimulus). Halfway through the sequence the participant was given an opportunity to rest for 3–5 min. If a rest was taken, the second half was preceded by another set of five practice trials, which were not analyzed. Time between trials was approximately 5 s. Reaction times from the onset of the stimulus to the initiation of the button press were recorded in milliseconds. Errors of omission (false negatives) were noted but the trial was not replaced, and trials on which the patient erroneously responded to a negative stimulus (errors of commission, false positives) were counted but the reaction times were not analyzed. Pilot work with a pilot group of neurologically intact participants indicated that a cutoff of 40% errors (false positives + false negatives) would be appropriate for distinguishing between individuals who could learn the task and those who could not.

Testing with the second type of material (faces or letters) followed immediately upon completion of the first type, using the same procedure. When both tasks were finished, the participants were asked if they found one kind of material easier or harder than the other, and whether they had used any particular strategies to remember which were the positive and negative stimuli. Responses to these questions were recorded for later qualitative analysis. Finally, participants were shown, one at a time, the rearranged versions of the faces (Figure 1B, lower four faces) and were asked to identify which were the negative and positive faces. Latency to make this decision was recorded to the nearest 0.5 s. This task was administered because it was hoped that it might reveal whether a participant had learned to use a single feature or a small number of features for identifying the faces. Such participants might be expected to have less trouble identifying the scrambled faces than

those using the total configuration of the face, because the scrambling disturbed the spatial relations between face parts (distance between eyes and nose, for example). It was predicted that a strategy based on single details might be seen more frequently in the right-temporal group than in the left-temporal group and the control group.

Results

Statistical analyses were carried out with analysis of variance (ANOVA), with repeated measures (BMD-P2V and StatView), and t tests, with Tukey-Kramer post hoc analyses and p < .05 to indicate statistical significance. The Mann-Whitney U Test was used when assumptions underlying the parametric tests were violated. All participants learned the letter task within 100 trials. Six participants were dropped from the study because they were unable to learn the faces within 100 trials (four from the right-temporal group: one with a small removal, three with large removals; one from the left-temporal group: large removal; and one from the control group). Mean trials to learn the letter task were 12.6 \pm 1.5 for the control group, 14.1 \pm 2.9 for the left-temporal group, and 14.5 \pm 3.9 for the righttemporal group (group differences were not significant by Mann–Whitney U Test). Mean trials to learn the faces to criterion were 25.0 \pm 10.5 for the control group, 20.5 \pm 11.3 for the left-temporal group, and 26.1 \pm 14.6 for the right-temporal group. Although there was a trend for the right-temporal group to take longer to learn the faces, the difference did not reach statistical significance, F(2,63) = 1.23, ns. Even for the slowest patient, who made 14 errors in 84 trials before achieving 12 correct trials in a row, performance during the criterion trials was far better than chance (p < .00001). For those who learned the tasks, median reaction times to the two positive faces and the two positive letter pairs during the test session were calculated. Error rates during the test phase were also calculated for false positives (responses to negative stimuli), false negatives (lack of response to positive stimuli), and total errors (sum of false positives and false negatives). Because the interaction of error type and group was not significant for either letters or faces, only the total error score was used in subsequent analyses. Four further participants, three from the right-temporal group (one with a small removal, two with large removals) and one from the control group, were excluded because of high error rates with the face stimuli. This left 26 patients with right-temporal lobe excisions (11 women, 15 men; mean age = 27.7 years), 28 patients with left-temporal lobe excisions (12 women, 16 men; mean age = 28.5 years), and 12 participants in the control group (5 women, 7 men; mean age = 28.4 years).

Error rates during the test phase were considerably higher for faces than for letters, t(65) = 15.1, p < .0001. For letters, total errors ranged from 0% to 14.8% among the right-temporal group (mean error rate = $4.1\% \pm 3.5$), 0% to 18.8% among the left-temporal group (mean error rate = $4.9\% \pm 5.2$), and 0% to 10.2% among the control group (mean error rate = $2.9\% \pm 3.7$). Error rates were not statistically different for the three groups, F(2, 63) = 0.89, *ns*, but the two patient groups differ in the variance of their scores; a nonparametric analysis showed no difference between the patients groups (U = 363.5, Z = .009, ns). For faces, total errors ranged from 5% to 38.8% among the right-temporal group (mean error rate = $23.1\% \pm 8.1$), 4.8% to 34.5% among the left-temporal group (mean error rate = $18.0\% \pm 7.2$), and 6.7% to 29.2% among the control group (mean error rate = $16.4\% \pm 7.1$). Although there was considerable overlap between the groups, there was an overall effect of group, F(2, 63) = 4.41, p < .017, with the right-temporal group making significantly more errors than the left-temporal group (mean difference = 5.1, critical difference = 4.96) and the control group (mean difference = 6.7, critical difference = 6.4), but no difference between the left-temporal and control groups (mean difference = 1.6, critical difference = 6.3). The relatively higher error rate in the face task among the right-temporal group shows that their slower reaction times were not caused by a speed-accuracy trade-off.

Because the gender of the participant has occasionally been found to be relevant in research involving reaction times to faces (see McGlone, 1980; Rizzolatti & Buchtel, 1977), this factor was initially included as a grouping variable. However, because the only effect of gender was a trend for the women to respond faster than the men, F(1,60) = 3.51, p < .069, this factor was dropped from subsequent analyses.

The main ANOVA factors were group (two groups of temporal lobe patients and one control group), task (faces, letters), and visual field (left vs. right). A separate four-way ANOVA was also carried out for the patients alone with extent of hippocampal removal (size) as a second grouping variable. Higher variance within the reaction times of the right-temporal group in the face task requires caution in interpreting the results of the following parametric analyses but, as shown later, the differences are confirmed and clarified by focused nonparametric analyses. Mean reaction times are shown in Table 1. It should be noted that because of the small amount of pretest training, the relatively few trials administered in a single session, and the smallness of the groups, it was not expected that the usual visual field

Table 1

Means and Standard Errors of Reaction Times to Letters and Faces in Control Participants and Patients With Small and Large Mesial Temporal Resections

Group	Letters				Faces			
	LVF		RVF		LVF		RVF	
	М	SE	М	SE	М	SE	М	SE
Control Left temporal	620	41	615	40	705	37	682	38
Small	703	38	736	45	749	28	790	25
Large Right	719	35	745	57	766	50	761	36
temporal Small Large	648 711	24 47	628 742	21 34	751 970	54 45	819 1,027	66 93

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

differences with verbal and physiognomic stimuli would necessarily emerge in the control group or in the patient groups. As can be seen in Table 1, the reaction times depend on the kind of material being presented, with responses to letter pairs being significantly faster than responses to face stimuli, F(1, 63) = 15.51, p < .0003. The group effect approached significance, F(2, 63) = 2.80, p < .069 (655 ms for the control group vs. 745 ms for the left-temporal group and 758 ms for the right-temporal group). The controls tended to be faster than both the left-temporal group (mean difference = 89.8, critical difference = 72.9) and the righttemporal group (mean difference = 102.7, critical difference = 73.7), whereas the two patient groups were equivalent (mean difference = 12.9, critical difference = 57.5). Finally, responses to left visual field (LVF) stimuli tended to be faster than responses to right visual field (RVF) stimuli (722 ms vs. 745 ms), F(1, 63) = 3.05, p < .086. The only significant interaction was of group and task, F(2,(63) = 3.65, p < .032, which derived from a reversal of the right- and left-temporal groups depending on the task: The rank order of reaction times from fastest to slowest for the face task was controls, left temporals, right temporals; the order for the letter task was controls, right temporals, left temporals.

The next finding of significance is found when only the reaction times of the two patient groups are considered. It is clear from Table 1 that the patients with right-temporal lobe excisions tended to respond more slowly to the face stimuli than the patients with the left-temporal lobe excisions. As can be seen in Table 1, the slowness in face recognition seen in the right-temporal lobe group derives specifically from slow reaction times in the patients with large removals. The effect of size of removal is weakly significant when the data are collapsed across groups and tasks, F(1, 50) = 4.23, p <.046 (729 ms for patients with small removals, 809 ms for patients with large removals), and the interaction between the size of the lesion and the side of removal approaches significance, F(1, 50) = 3.87, p < .055 (reaction times of the small and large left temporal removals are similar: 744 ms and 748 ms, respectively; small and large right temporal removals are associated with significantly different reaction times: 712 ms and 862 ms, respectively). Other statistically significant differences come from the factors of task (reaction times to faces were generally slower than to letter stimuli: 808 ms vs. 696 ms), F(1, 50) = 15.67, p < .0003, visual field (LVF times faster than RVF times: 736 ms vs. 767 ms), F(1, 50) = 6.44, p < .015, and the interaction of task and group, F(1, 50) = 7.15, p < .011. The latter interaction derives from the left-temporal group having roughly equivalent reaction times in the two tasks (723 ms for letters and 768 ms for faces), t(27) = 1.34, p < .10, whereas the right-temporal group was considerably faster with the letters than with the faces (665 ms for letters vs. 851 ms for faces), t(25) = 4.02, p < .0003, critical p =.025. The interaction of Visual Field \times Task was not significant. However, although the trends were generally in the expected direction, the number of trials was too few to obtain the usual significant visual field differences appropriate for the different tasks. Nor did visual field and task

interact significantly with group, as might have occurred if the left hemisphere in the right-temporal lobe group had been faster than the right hemisphere in the face task. As seen in Table 1, the slowest reaction times were associated with RVF presentation of faces in the right-temporal group. However, the three-way interaction suggested by this observation (Task × Group × Size) was not significant, F(1, 50) = 1.27, *ns*, nor was the four-way interaction including visual field, F(1, 50) = 0.06, *ns*. It is noteworthy, however, that the variance associated with these slow reaction times is also considerably higher than in the other subgroups. Using a nonparametric test, the reaction times for faces shown in the RVF do indeed tend to be slower for the right-temporal group with large removals than for the equivalent lefttemporal group (U = 8.0, Z = 2.32, p < .021).

There was no significant effect of time since surgery in either reaction times or errors, nor did this variable interact significantly with side or size of the removal. The reaction times associated with left and right visual fields of the right-temporal lobe patients are shown in Figure 2. No consistent differences between groups emerged in an analysis of the conscious strategy (or lack of strategy) in carrying out the tasks, nor were there any consistent trends in the participants' reaction times or accuracies in recognizing the scrambled faces (Figure 1B).

Discussion

Several explanations have been proposed to account for the presence of hemispheric asymmetries in cognitive and perceptual tasks (see Allen, 1983, for a review of most of these approaches). In attempting to explain the faster and more accurate recognition of faces in the left visual field,



Figure 2. Relationship between reaction times (RTs) to face stimuli presented in the right visual field and left visual field for the patients with right-temporal lobe excisions. Each point represents a single patient. Points below the line are from patients with faster RTs with left visual field presentation than with right visual field presentation. Solid circles = patients with large excisions of mesial temporal lobe tissue; open circles = patients with small excisions of mesial temporal lobe tissue.

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two dimensions have been explored. One dimension concerns whether visual field differences are a direct or only an indirect consequence of the physiological substrate activated in the task. The possibility that large visual field differences arise because of an attentional bias has been proposed by Kinsbourne (1970), who argued that without such an attentional bias the difference between visual fields would only be in the order of a few milliseconds, reflecting commissural transmission time. Other authors (e.g., Berlucchi, 1972; Rizzolatti, 1979) have proposed that the visual field differences directly reflect the relative competencies of the two hemispheres, and they have obtained clear experimental support for their conclusion by randomly mixing trials of face and letter discrimination (Berlucchi, Brizzolara, Marzi, Rizzolatti, & Umiltà, 1974; see also the discussion of face familiarity in the introduction to the present article). The second dimension focuses on the nature of the differences in competency between the two hemispheres. One approach is to conclude that a difference of a certain number of milliseconds between discrimination times of right and left visual field presentation results from one hemisphere taking that number of milliseconds more than the other in carrying out the analysis. That is, both hemispheres are "competent," but one is more competent than the other (Umiltà, Rizzolatti, Anzola, Luppino, & Porro, 1985; see also Zaidel, 1983, for a discussion of the possible continuum between competency and noncompetency). The results of work with commissurotimized patients have contributed to the popularity of the notion of bilateral competency (see Sperry, 1974; Zaidel, 1994); work with chimeric faces (faces made up of two different faces split along the vertical meridian) has shown that split-brain patients can name faces shown in the right visual field and point with the left hand to a face that had been shown in the left visual field among a set of distractors (Levy, Trevarthen, & Sperry, 1972; see also Levy 1974). Although these split-brain studies show a potential role of the left hemisphere in face perception and discrimination, the most accurate performance was seen with left visual field (right hemisphere) presentation.

Alternatively, one of the hemispheres may be so incompetent in the particular analysis required that it never contributes to the final decision but rather transfers the information that it has to the other, competent hemisphere for analysis. In this case, visual field differences would reflect the time lost in transferring information plus any added analysis time caused by the degraded nature of the information that is received after transfer (poor quality would be attributed to distortions caused by the transfer process itself and perhaps to an inappropriate initial elaboration carried out by the incompetent hemisphere), plus any additional time taken for transfer of the motor output to the hemisphere controlling the response if this is different from the one making the decision to respond. This pattern appears to be appropriate for certain verbal tasks (Bruyer, 1986; Umiltà et al., 1985). Finally, there may be tasks in which the two hemispheres are able to carry out the necessary analyses in parallel; which hemisphere is ultimately responsible for organizing the response would depend on whether the time

lost in transfer of the motor command from the slower hemisphere to the hemisphere that controls the response is more or less than the difference in analysis times of the two hemispheres (Bruyer, 1986; Umiltà et al., 1985).

The present results with faces support the idea that righthemisphere mechanisms are used in tachistoscopic face recognition tasks regardless of the visual field of presentation, and the findings therefore do not support the hypothesis that the left hemisphere can act alone in recognizing faces in the tachistoscopic situation tested in this study. Before rejecting the hypothesis of independent left-hemisphere analysis, however, an alternative explanation needs to be evaluated. It is conceivable that the very slow reaction times to stimuli in the right visual field stimuli in the right-temporal group represent the usual time taken by left-hemisphere mechanisms to carry out the task (e.g., using "concrete structural codes"; Polster & Rapcsak, 1996), with these long reaction times not normally being seen, because in the intact brain the more efficient right hemisphere mechanisms "win" in the race between interhemispheric communication and intrahemispheric analysis as described above. However, if this were the case one might have expected to see a visual field difference in favor of the right visual field, whereas the opposite was found. Furthermore, the reaction times in the right visual field are very highly correlated with the reaction times in the left visual field (Figure 2; r = .832, p < .001), increasing the likelihood that the parallel increases in reaction times in both visual fields reflect the consequence of a disruption of mechanism(s) ordinarily subserved by the damaged right hemisphere. (Although it is true that high correlations between reaction times within an individual could reflect a subject variable rather than the activation of a single mechanism, it can be argued that independent activities of the left and right hemispheres in the task in these individuals would have led to less concordance between the LVF and RVF reaction times.)

Thus, we are left with interpretations that implicate the right hemisphere in the performance of this face discrimination task regardless of the field of presentation of the stimulus. Interestingly, this means that although the study was designed to test the abilities of the noncompetent hemisphere, the findings presumably reflect the functions of the competent hemisphere. There are at least two ways the right hemisphere damage may be involved in producing the pattern of findings. First, under normal circumstances the right hemisphere may form a recognition template, presumably the outcome of the initial structural encoding of Bruce and Young (1986), which is stored bilaterally and can be used by each hemisphere independently when a stimulus arrives from the associated visual field (though if this occurs one would still need to explain why the left hemisphere remains slower than the right hemisphere using the template). In the absence of such a template, as in the right-temporal lobe group in this study, responses to both LVF and RVF stimuli would be slowed. The second possibility is that the right hemisphere may be called on in all phases of the task for help with the discrimination. This seems more likely because it would help explain the relative slowness with face recognition in the RVF.

In either case, the fact that the right-temporal lobe group's reaction times to RVF (left hemisphere) faces were much longer than normal suggests that the slightly elevated reaction times associated with RVF (left hemisphere) presentation in normal participants (e.g., Rizzolatti et al., 1971) do not simply represent slower facial analysis by the left hemisphere. Rather, these slower reaction times would reflect the consequence of transferring information to the right hemisphere for analysis or calling on right hemisphere mechanisms during the decision-making process in the task. This conclusion is consistent with other data (e.g., Berlucchi et al., 1974) that argue against interpreting visual field differences as simply secondary to differential hemispheric efficiency caused simply by attentional biases. Even if an attentional bias had been acting in a manner that was supposed to aid the damaged right hemisphere in its analysis of the faces, one would hardly have expected the intact left hemisphere to respond so much more slowly than in the normal intact person (e.g., see Posner, 1980, on the cost of attending to the wrong hemispace).

Although patients in the left-temporal group showed the expected tendency to have longer reaction times to RVF letter stimuli than the patients in the right-temporal group, t(52) = 1.76, p < .043, one-tailed, it is noteworthy that the findings with letter pairs differ from the findings with faces insofar as the patients with left-temporal lobectomies were not impaired to the extent that might be expected given the complementary material-specific nature of the right and left hemispheres (for reviews, see Benson & Zaidel, 1985; Bouma, 1990; Efron, 1990; Springer & Deutsch, 1998). This lack of symmetry in the findings may reflect the relative ease with which all subjects learned to recognize and remember the letter stimuli compared with the face stimuli (all individuals took fewer trials to learn the letters than the faces and the error rates with letters were on average about 20% of those with faces). Although the face and letter stimuli had been used in previous studies designed to show the relative superiorities of the right and left hemispheres in physiognomic and verbal tasks, respectively, it is nevertheless apparent from the number of trials to criterion during the training trials that learning to encode the letter pairs was faster than learning to encode the faces, especially when the faces (as in the present case) cannot be distinguished by single features.

The present data may indicate what happens when the left hemisphere is confronted by a familiar (though not famous) face but they do not answer the question of why the right hemisphere possesses its superior ability to handle such stimuli. A number of theories have been proposed to answer this question, and the present findings, even though they implicate the right hemisphere in face tasks regardless of the visual field of presentation, do not clarify the issue. The findings are, however, useful insofar as they demonstrate that under ordinary circumstances the processing time evident with right visual field presentation of familiar faces probably has little or nothing to do with the processing abilities of the left hemisphere, an assumption that is present in several theoretical treatments of tachistoscopic findings (e.g., Moscovitch, 1979). An ancillary implication of these findings is that the debate on the hemispheric organization of language abilities, that is, whether the left and right hemispheres both possess language (see Patterson & Besner, 1984), may benefit from an analysis of speech receptive abilities in the same way the face stimuli were studied in the present experiment, using more complex verbal stimuli and patients with damage to relevant lateralized structures, such as those studied here.

The findings with faces also raise the question of which right-hemisphere mechanisms are called on by the left hemisphere when confronted with a face stimulus. On the basis of the localization of the excisions in this study, it seems likely that right-hemisphere mesial or inferior temporal mechanisms play an important role in tachistoscopic recognition of faces, but this remains speculative. It is possible that the responsible mechanisms remained intact in the patients in this study but were deafferented owing to an interruption of pathways that bring this information. Specification of the neuroanatomical component(s) responsible for the findings will require further study now that it is clear that the right hemisphere is involved in face analysis regardless of the visual field of presentation; imaging studies in intact and brain-damaged patients may provide the answer by showing which areas are activated when a face is presented in the right visual field.

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