VISUAL PERCEPTION AND MEMORY AFTER ANTERIOR TEMPORAL-LOBE LESIONS IN HUMANS

by

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Abstract

The impairments in human behavior that follow right temporal lobectomy occur in the domains of perception and memory. This consensus has emerged from numerous past studies of patients with unilateral anterior temporal-lobe lesions, but four outstanding issues remain. First, previous studies have concluded that right temporal lobectomy results in abnormal visual discrimination, recognition, and recall of pictorial material that cannot be easily specified verbally, such as geometric designs and faces. However, the exact nature of these deficits is still unclear, and no complete description of the properties of the stimuli that elicit difficulties exists; such stimuli are still often defined by exclusion as "nonverbal." Most stimuli that have been employed are conceptually rich as well as perceptually complex. It is unclear whether semantic content is necessary to elicit deficits. Second, the patterned nature of images is believed to be important, but this variable has not been explored systematically. Third, it has been claimed that the memory deficits result from a deficit in retrieval rather than encoding. It was hypothesized that new tests with sufficiently rigorous encoding demands may demonstrate encoding deficits. Finally, the observed deficits in perception have sometimes been characterized as separate from memory impairments. This characterization needs to be tested with experiments that vary memorial and perceptual demands independently.

The subjects of this study included patients with cerebral lesions due to surgical excision or head injury, and normal subjects. Nine subjects underwent an anterior temporal lobectomy in the left hemisphere, and nine subjects had this resection performed in the right hemisphere. Case 1 sustained bilateral anterior temporal-lobe lesions due to a head injury. H.M. underwent a bilateral medial temporal lobe resection that resulted in a profound global anterograde amnesia. Chapter 1 describes basic visual discrimination abilities after anterior temporal lobectomy. Chapter 2 describes basic visual discrimination abilities in Case 1. Chapter 3 describes recognition memory abilities after anterior temporal lobectomy, in Case 1, and in H.M. Chapter 4 pursues some issues raised by Chapter 3 more fully using young, healthy subjects.

Experiments with subjects who had a unilateral anterior temporal lobectomy demonstrated that basic visual discrimination capacities were essentially intact. No evidence was obtained that perceptual impairments were limited to the domain of pattern perception, or generalizable to non-meaningful stimuli. Consistently, subjects with left or right anterior temporal lobectomy showed normal performance on recognition memory tasks when retrieval demands were low despite high encoding demands.

Only when retrieval demands were high did subjects with left and right anterior temporal lobectomy show impaired performance. Case 1 provided the first demonstration of impaired visual discrimination of less prominent targets restricted to pattern vision after bilateral temporal-lobe lesions. The role of global features and stimulus complexity in normal recognition memory was explored further through an experiment with healthy subjects.

The results of these experiments combined with past studies provide a strong dissociation between basic perceptual encoding abilities (largely intact in subjects with left or right anterior temporal lobectomy), and the storage and retrieval mechanisms that support memory function (compromised after anterior temporal lobectomy).

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Preface

This thesis is comprised of four articles. Each article is intended to stand alone, so references and figures are found at the end of each article As a group these articles address related and complementary issues.

Visual Discrimination after Anterior Temporal Lobectomy

The behavioral consequences of unilateral anterior temporal lobectomy (ATL) in humans varies with the side of the lesion. Left ATL selectively disrupts verbal memory and perception (Meyer & Yates, 1955; Milner, 1958) reviewed in (Smith, 1989a). Right anterior lobectomy causes parallel difficulties in tasks of nonverbal perception and memory (Kimura, 1963; Milner, 1968). The deficit in verbal memory after left ATL, but not after a similar right-sided lesion, and the impairments in nonverbal memory when the lesion is on the right, but not on the left, constitutes an important double dissociation of brain functional anatomy.

Neuropsychological studies have demonstrated that lesions of the right temporal lobe in humans results in impaired visual perception (Doyon & Milner, 1991b; Kimura, 1963; Lansdell, 1968; Meier & French 1965; Milner, 1971; Milner, 1974; Milner, 1980; Mooney, 1956; Warrington & James, 1967; Warrington & Taylor, 1973). The perceptual deficits reported are subtle. No blindness or visual agnosia is present. It is often stated that in order to elicit an impairment, the stimuli must minimize the perceptual cues that contribute to stimulus redundancy (Milner, 1990). The stimuli used to elicit impairments are usually made challenging by ambiguity, reduced information, or brief exposure times. Although the evidence is limited, it is generally believed that mild perceptual deficits result from removal of the anterior temporal-lobe neocortex rather than the medial limbic structures. The large body of evidence that anterior inferotemporal neocortical lesions result in impaired visual discrimination learning in monkeys supports this assumption. Further, Milner has reported normal performance on the Mooney Closure Faces Test (a test that elicits deficits in patients with right ATL) for three patients with selective right amygdalo-hippocampal resections (Milner, 1990).

One disadvantage of the stimuli that have been used with humans is that they are conceptually rich as well as perceptually complex (classification of half-tone faces, identification of incomplete objects, discrimination of anomalous scenes). Few studies report deficits in perception of figures that have no semantic content. Three exceptions to this trend are studies that presented simple patterned stimuli under time pressure (Dorff, Mirsky, & Mishkin, 1965; Kimura, 1963; Meier & French, 1965). Kimura presented overlapping nonsense shapes for 200 msec, and then immediately tested for recognition. Patients with right anterior temporal lobectomy (RTL) were impaired relative to patients with left anterior temporal lobectomy (LTL). In a study by Meier and French, subjects performed a simultaneous odd-ball-out visual discrimination on four sets of fragmented concentric circles. Exposure duration ranged from 4-16 sec. RTL patients were impaired relative to LTL patients. Dorff et al. employed letter stimuli (groups of four consonants) that were presented for 150 msec. RTL and LTL patients were impaired at recognizing the letters, particularly when flashed in the visual field contralateral to the lesion. However, when two groups of letters were flashed simultaneously in both visual fields, the LTL patients showed impairment only in the right visual field, whereas the RTL patients displayed depressed recognition in both visual fields. The results were interpreted to support a partially dominant role for the right temporal lobe in visual perception.

No studies have assessed basic visual discrimination abilities after ATL with a group of tests that sample a spectrum of perceptual abilities. Thus, Experiment 1 compared visual discrimination across a range of basic visual cues. In Experiment 2, we used a more complex task in which subjects extracted shape information from limited contours, from motion information only, or from texture information only. These experiments allowed us to address three questions. Is pattern or shape vision is particularly vulnerable after right ATL? Was the semantic content in many previously employed stimuli critical for eliciting impairments after right temporal lobectomy? Does the dissociation between left and right ATL still obtain when simple meaningless stimuli are used?

EXPERIMENT 1

Methods

Subjects

The subjects were 18 patients with unilateral anterior temporal-lobe resection to treat intractable epilepsy (Table 1). Nine patients underwent resection on the left side (LTL), and 9 patients on the right side (RTL). The operation included removal of anterior temporal neocortex, part of the rostral perirhinal, and most of entorhinal cortex, most of the amygdala, and part of the hippocampus. Operation reports documented the resection size for lateral neocortex and for mesial structures (Table 2). T-tests showed that the size of the medial excision did not differ between the LTL and RTL groups (p= 0.2), whereas the lateral excisions in the RTL were significantly larger than in the LTL group (p= 0.002). At the time of testing, the patients varied in time elapsed since operation with a range of 1 to 7 years. The LTL and RTL groups did not differ with respect to time elapsed since operation (p= 0.7). All patients were seizure free, or experiencing only rare seizures, and most were taking therapeutic doses of anticonvulsant medication.

Nineteen normal control subjects (NCS) who did not differ with respect to age (p= 0.994; $F[1,37] = 0.1$) or education (p= 0.858; $F[1,37] = 0.2$) from the resection patients were also tested (Table 1). In a few instances, not all subjects participated in every test due to constraints of time and equipment. In no case was there a significant difference among the subject groups (LTL, RTL, NCS) in age and education. The number of subjects who participated in each test is indicated in the Results section. All subjects gave informed consent to the testing.

As a prelude to the basic visual testing, all subjects performed the Mooney Closure Faces Test (Mooney, 1956), a test of the ability to perceive faces in ambiguous black and white images. The goal was to use this test as a reference point to determine whether our subjects would show a similar pattern of performance as has been seen previously. In past studies, subjects with RTL were impaired, while subjects with LTL were not (Milner, 1980; 1990). The results of our testing indicated that subjects with LTL (p= 0.012; F[1,35] = 7.0) and RTL (p= 0.006); F[1,35] = 8.8) were impaired relative to NCS (Figure 1). The reason why both lesion groups were impaired is unclear, but may relate to the modest sample size in this experiment. We were reassured by these results, however, that some perceptual deficits similar to those elucidated previously could be demonstrated for the subjects used in this study.

All testing was conducted at the MIT Clinical Research Center (CRC). Concurrent with the vision testing, all patients and NCS received a physical examination in order to ensure that they met the inclusion and exclusion criteria, and to document retino-calcarine abnormalities. The physical examination included funduscopy, evaluation of fixation, pupillary function, extraocular movement, and visual fields by response to confrontation.

In addition, 5 LTL subjects and 4 RTL subjects received a neuro-ophthalmological examination performed at the Massachusetts Eye and Ear Infirmary by Dr. Joseph F. Rizzo. It included applanation tonometry to detect glaucoma and nonglaucomatous ocular hypertension; examination of the anterior segment and lens to detect and describe cataract and other lens opacities; determination of refractive error to ensure appropriate correction; funduscopy to inspect the retina and optic nerve; evaluation of fixation, pupillary function, and extraocular motility; and Snellen acuity. Formal Goldman perimetry was performed to detect and delineate field defects on confrontation testing. All subjects demonstrated a corrected near Snellen acuity of 20/30 or 20/20.

Of the 4 subjects with RTL, 2 subjects demonstrated a history of "lazy left eye" or amblyopia. Accordingly, visual acuity was reduced unilaterally, and stereopsis was poor or absent. The amblyopia was not judged to be related directly to the surgical procedure. The other 2 subjects with RTL had a normal neuro-ophthalmological examination. Of the 5 subjects with LTL, 2 subjects had a normal examination. One subject was judged to have a "monofixation syndrome" in the left eye, which is a subtle form of strabismus with subsequent loss of stereopsis. Finally, the 2 other subjects with LTL displayed some optic neuopathy (moderate constriction and pallor of optic nerves) thought to be related to a period of high intracranial pressure early in life. One of these 2 subjects also had a history of "lazy right eye" that lead to strabismic surgery at the age of 8. Naturally, we considered the optic abnormalities found in the subjects with ATL a possible confound in the attribution of visual deficits to ATL. The results of this study are interpreted with this consideration in mind.

Apparatus and Stimuli

Subjects performed a group of 9 tests intended to evaluate a wide range of basic visual capacities. All tests were computerized, and 8 of the 9 have been used extensively in previous research on monkeys (Schiller, 1993). They were adapted for use with human subjects. For the assessment of basic visual capacities a discrimination paradigm was used, and the method of constant stimuli was employed. For each test several levels of difficulty were employed, and mixed randomly, so that a range of performance could be assessed.

Of the 9 tests, 8 used a discrimination paradigm in which 4 or 6 stimuli appeared following the presentation of a fixation spot. One of the stimuli, the target, was different from the other identical comparison stimuli on any one of several dimensions (e.g., size, color, motion). The stimuli appeared equidistant from the fixation spot at 6^0 or 8^0 eccentricity on a polar coordinate system. The subject's task was to press a key on a keypad that corresponded to the spatial location of the target stimulus.

Although this test used simple stimuli that assessed basic visual capacities, it also tapped a visual function of a higher level when the prominence of the target was varied. For example, when discrimination of an oddball target was based upon size differences, the target was either larger or smaller than the distracters. In a similar fashion, the remaining tests were designed with a target that was either "greater" or "lesser" along the relevant stimulus dimension compared to the distracters. Thus, we created two prominence conditions: "greater-than" (G) and "lesser-than" (L), (Figure 2). Previous work in monkeys has shown that the L condition can be especially impaired following a visual cortex lesion (Schiller, 1993). The absolute difference between targets and distracters was varied in order to create several levels of difficulty (independent of prominence). Difficulty level and target position were randomized. When discrimination tasks contained G and L conditions, the prominence conditions were separated in blocks of trials.

Size. Following presentation of the fixation cross, six squares in a hexagonal arrangement were flashed for 250 msec. The size difference between the target and comparison stimuli was varied. The difficulty levels corresponded to size differences of 30, 20, and 10%. The absolute size of the squares was 1.6, 1.76, 1.92, and 2.08^{o2}. The target was either larger (G) or smaller (L) than the distracters. The test comprised 288 trials.

Contrast. Following presentation of the fixation cross, six squares (1.8^{o2}) in a hexagonal arrangement were flashed for 250 msec. The luminance difference between the target and comparison stimuli was varied. The absolute luminance values used were 1.41, 2.20, 4.18, and 10.81 cd/m^2 with background luminance at 84.04 cd/m^2. The target was either darker (G) or lighter (L) than the distracters. The test comprised 192 trials.

Color Hue. Following presentation of a fixation spot, four squares (1.4^{o2}) in a diamond arrangement were flashed for 200 msec. The color hue of the target stimuli relative to the comparison stimuli was varied systematically as described by Schiller (1993). The stimuli were generated using the coordinate system devised by MacLeod and Boynton (1978), and as elaborated by Derrington et al. (1984) and Schiller (1993). We created two tests that assessed discrimination for two cardinal axes in the color space. The four difficulty levels corresponded to an color angle difference of 11.25. 22.5, 33.75, and 45^0 from the cardinal axis. All colors were isoluminant (65.8±1 cd/m^2). Qualitatively, the target stimulus appeared as a blue color that looked slightly more green than the distracters, or in the other case, a shade of red that looked slightly more pink than the distracters. The test comprised 160 trials.

Color Saturation. Following presentation of a fixation spot, four squares (1.4^{o2}) in a diamond arrangement were flashed for 200 msec. We assessed color saturation discrimination along two axes in the MacLeod color space. In one case the color of the squares systematically varied from pure white to pale blue. In the other case the color varied from white to pale red. For both red and blue axes there were 4 difficulty levels corresponding to saturation differences of 4, 2, 1, and 0.5%. For both red and blue axes, a G version with the target more saturated and a L version with the target less saturated were used. The test comprised 160 trials.

Pattern. Following presentation of a fixation spot, six squares (2.1^{o2}) in a hexagonal arrangement were flashed for 250 msec. The squares contained high-contrast checkerboard patterns, with the target pattern having a different spatial frequency from the other identical comparison stimuli. The checkered patterns were 3 x 3, 4 x 4, 5 x 5, or 6 x 6, with check size 40, 30, 24, or 20 min. respectively. The check pattern size was either larger (G) or smaller (L) than the distracters. The test comprised 288 trials.

Flicker. Following presentation of a fixation spot, four squares (1.4^{o2}) in a diamond arrangement were flashed for 1000 msec. The rate of flicker as well as the degree of +/- luminance shift of the two flicker values were varied systematically relative to the background. The mean luminance of the flickering stimulus was equal to the background luminance. Four levels of difficulty corresponded to a +/- luminance shift of 2.6, 4.6, 6.4, and 8.7 cd/m^2. Absolute values of luminance levels were 26.6, 29.2, 31.2, 33.0, and 35.3 cd/m^2. The flicker values employed were 3, 7.5, and 15 Hz. The test comprised 240 trials.

Texture. In this case, following presentation of a fixation cross, an array of vertical lines filled the screen. In six small areas (3^{o2}), the lines were tilted along the diagonal. Difficulty was varied by systematically increasing the amount of tilt difference between the target and distracters. In the G condition, the target area lines were more tilted, and the distracters blended easily into the background of vertical lines. Conversely, in the L condition the target area contained lines less tilted than the distracters. The test comprised 192 trials.

Motion. Following presentation of a fixation cross, six windows, each containing 50 moving dots, were displayed on the screen for 1000 msec. One window contained dots moving at a different speed than the other 5 identical windows. The speed was varied systematically, and corresponded to 4 difficulty levels with speed ratios between target and distracters of 1.5, 2, 2.5 , and 3. The absolute speed of the dots was 1.5, 2.25, 3, 3.75, or 4.5 °/second. In this test, each individual moving dot had a limited lifetime, that is, it traveled a particular course for just 100 msec before it disappeared and was randomly repositioned to a new location to move for 100 msec, disappear, and so forth. The result was a pure motion signal not confounded by position cues. The correct response could not be determined by following a particular dot. Instead, a global motion field was perceived by integrating the motions of all the dots in the field. The target moved either faster (G) or slower (L) than the distracters. The test comprised 192 trials.

Contrast Sensitivity. For this test, we used a two-alternative forced-choice format (Vision Metrics, Berkeley, CA) (Higgins, et al., 1984). Spatial sine-wave luminance gratings were generated with an oscilloscope, each with a mean luminance of 5 cd/m^2. Subjects received trials randomly distributed across 6 spatial frequencies (0.5, 1.0, 2.0, 4.0, 8.0, and 14.0 cycles/degree [cpd]). Each trial consisted of two temporal intervals of 700 msec separated by a 300 msec gap. The first interval was associated with a high-pitched tone, and the second with a tone approximately one octave lower in pitch, but equal in amplitude. The tones were easily audible. For each trial, a vertical grating filled the screen for one interval, and a homogeneous field, matched in mean luminance (5 cd/m^2), appeared during the other interval. The grating appeared randomly in either the first or the second interval. The subject responded "one" if the grating appeared in the first interval, and "two" if it appeared in the second interval. Response accuracy was measured; the microcomputer automatically adjusted difficulty based upon performance feedback using a staircase procedure. The algorithm sought the 75% correct threshold by reducing contrast by 1 dB for each correct response, and increasing contrast by 3 dB for each error, until 20 reversals were completed for each spatial frequency. The performance measure was the log of sensitivity, which was the reciprocal of the threshold contrast.

Procedure

Subjects sat 14 in. in front of a computer monitor in a dimly lit room. They were shown a sample stimulus printed on paper, and told to find the oddball target in each briefly flashed picture. Subjects knew whether to look for a G or L target. Additionally, they were told that the difficulty level was mixed randomly, that they should try to fixate the cross at the center of the screen, and that they should guess when unsure of the correct choice. Before the onset of the stimuli, a warning tone was given and a central fixation cross was presented for 2 sec. The subjects indicated their response by pressing 1 of 6 keys that corresponded to the hexagonal arrangement of stimuli. The subjects rested at several points during the test, indicated by a "please rest" screen. A block of trials ranged from 96 - 144 trials, and always contained stimuli of the same basic domain (e.g., size or contrast), and of the same prominence condition (G or L). There was no practice set. Subjects required 10 - 15 minutes to complete a block of trials.

For the contrast sensitivity test, subjects sat in a darkened room and viewed the oscilloscope, which subtended 7.1° by 5.7° at a distance of 1 meter. Ten practice trials with high contrast preceded the test. For each trial, they verbally responded "one" if they thought lines appeared coincidentally with the first tone, or "two" if they thought lines appeared coincidentally with the second tone. Subjects were told to guess when unsure of the correct response.

Results

For each test we performed a mixed within and between subjects ANOVA with 2 or 3 factors: group (LTL, RTL, NCS); difficulty (3 or 4 levels); and when applicable, condition (G, L).

Contrast Sensitivity. For this test, there was no main effect of group (p= 0.144; [F2,33] = 2.1). There was a main effect of spatial frequency (p= 0.0001; [F5,165] = 137.2), reflecting the well known decrease in sensitivity at high and low spatial frequencies (Figure 3).

Texture. In this case there was no main effect of group p= 0.653; [F2,32] = 0.4). There was a main effect of difficulty (p= 0.0001; F3,96] = 130.0), and of condition (p=

0.0001; [F1,32] = 66.10). The L condition was significantly more difficult than the G condition (Figure 4).

Pattern. We found no main effect of group (p= 0.560; [F2,33] = 0.6). There was a main effect of difficulty (p= 0.0001; [F2,66] = 42.1) (Figure 5).

Size. There was no main effect of group (p= 0.514; [F2,34] = 0.7). We found a main effect of difficulty (p= 0.0001; [F2,68] = 175.7), as well as condition (p= 0.033; [F1,34] = 4.9). The L condition was harder than the G condition (Figure 6).

Motion. In this case there was no main effect of group (p= 0.789; F2,27] = 0.2). We found a main effect of difficulty (p= 0.0001; [F3,81] = 62.2), as well as condition (p= 0.0001; [F1,27] = 32.3). The L condition was more difficult than the G condition (Figure 7).

Flicker. Once again, there was no main effect of group (p= 0.071; [F2,31] = 2.88). We found a main effect of difficulty (p= 0.0001; [F3,93] = 117.4). We did not employ a G vs. L condition in this test. In the present analysis, the factor of condition corresponded to fast (15 Hz), medium (7 Hz), and slow (3 Hz) flicker (p= 0.0001; [F2,62] = 101.9). The slow flicker condition was more difficult than the fast flicker condition. For this test, we found significant interactions between group and difficulty (p= 0.028; [F3,93] = 2.5), as well as between group and condition (p= 0.011; [F4,62] = 3.56). The RTL and LTL groups showed somewhat poorer performance with slow flicker relative to fast flicker, and relative to NCS.(Figure 8).

Color Hue. Again, we found no main effect of group (p= 0.302; [F2,34] = 1.2). We found a main effect of difficulty p= 0.0001; [F3,102] = 127.4) and condition (p= 0.011; [F1,34 = 7.2). A prominence condition was not possible for this test. In this analysis, the factor of condition corresponded to the blue axis vs. the red axis. The significant effect of condition indicated that the blue and red axis hue discriminations were not equally difficult, although no strong systematic trends were apparent (Figure 9).

Blue Saturation. This test is the only one in which we found a main effect of group (p= 0.012; [F2,33] = 4.46). We also found a main effect of difficulty (p= 0.0001; [F3,99] = 145.4), as well as condition (p= 0.0001; [F1,33] = 23.1). Inspection of the data showed that the RTL group was impaired when making L discriminations. Consistently, there was a significant interaction between group and difficulty (p= 0.004; [F6,99] = 3.4), as well as between group and condition (p= 0.012; [F2,33] = 4.5) (Figure 10).

Red Saturation. In this case, the main effect of group just missed significance (p= 0.066; [F2,31] = 2.96). Performance for the LTL and the RTL groups were depressed compared to NCS. We found a main effect of difficulty (p= 0.0001; [F3,93] = 196.7), as well as condition (p= 0.0001; [F1,31] = 196.7). The L condition was more difficult than the G condition (Figure 11).

Contrast. Once again the main effect of group just missed significance (p= 0.058; [F2,32] = 3.1). Performance for the LTL and RTL groups were depressed compared to NCS. We found a main effect of difficulty (p= 0.0001; [F3,96] = 107.0) (Figure 12).

Discussion

Overall, the results indicate little impairment of basic visual discrimination capacity after left or right ATL. Given the large number of significance tests that we performed, we must be sensitive to the possibility of significant effects occurring due to chance. Even conservative interpretation, however, suggests that a subtle weakness for color and contrast discrimination may result after RTL. We demonstrated that the L prominence condition evoked poorer performance for many tests. The increased difficulty of the L condition appeared to elicit the noticeable impairment of the RTL group for blue saturation discrimination. The results of Experiment 1 are discussed further in the final General Discussion section.

EXPERIMENT 2

Methods

Subjects

The subjects in this experiment were the same as those in Experiment 1.

Apparatus and Stimuli

The stimuli appeared on a Sony Trinitron color monitor controlled by a TIGA graphics board (Number Nine Corp.). Stimulus presentation and response collection was managed by a PDP-11 and a Gateway P4D-66 PC computer. The stimuli consisted of 4 simple geometric shapes: circle, triangle, cross, and star subtending 2° of visual angle (Figure 13). The stimuli were made visible by luminance contour information, motion information, or texture information.

In the **Limited Contour Test**, the screen was filled with a grid of diagonal white lines on a black background. The shapes were also drawn and filled with black, so that they appeared to occlude the white grid. The intersections of the grid with the shapes were the only sources of contour information, which was varied systematically by changing the density of the grid to create 3 difficulty levels.

In the **Shape From Motion Test**, the display consisted of randomly placed white dots on a black background. The dots within the boarders of the shapes were moving. Thus, the shape contours could only be extracted from the boundaries between moving and stationary dots. Three difficulty levels were created by systematically altering the density of dots on the screen.

In the **Shape from Texture Test**, the shapes contained a texture of randomly placed oriented line segments oriented 90^{0} from a similar background texture. Shape contours could only be extracted from texture boundaries. The density of oriented lines was varied to create three levels of difficulty.

Procedure

We employed a match-to-sample paradigm. To begin each trial, a sample stimulus appeared in the center of the screen. After a delay of 500 msec four additional choice shapes appeared at four locations in the visual field, one of which was identical to the sample. The other three stimuli were different shapes. The subject's task was to select the stimulus that matched the sample by pressing the appropriate key. On each trial, the sample was one of the four figures in the stimulus set. The particular shapes shown at the four positions were varied randomly from trial to trial. The sample stimulus was always presented with full contour information. The choice stimuli were visible by limited contour, motion, or texture information as described above.

Results

We performed 3 mixed within and between subjects ANOVAs and found no main effect of group for the limited contour, motion, or texture tests; the respective *p* values were: (*p*= 0.752; [*F*2,29] = 0.5) (*p*= 0.344; [*F*2,29] = 1.1) *p*= 0.699; [*F*2,28] = 0.3) (Figure 7). There was a significant effect of difficulty for all of the tests; the respective *p* values were: (*p*= 0.003; [*F*2,58] = 6.5) (*p*= 0.003; [*F*2,58] = 6.3) (*p*= 0.001; [*F*2,56] = 176.0) (Figure 14).

Discussion

Despite the more complex task employed in this experiment, we obtained no evidence for a deficit after RTL or LTL. Numerous past studies of the effects of bilateral temporal-lobe lesions in monkeys have indicated loss of shape discrimination ability. The perceptual deficits that follow RTL in humans also have been reported to diminish shape perception on some tasks. However, the current task, which employed simple geometric shapes with little semantic meaning, did not appear to tap the perceptual problems that subjects with RTL have demonstrated in other studies. These issues are discussed more fully in the following general discussion.

GENERAL DISCUSSION

In this study, we assessed a wide range of visual discrimination performance for subjects with left or right ATL. The aim of the study was to determine whether the previously reported mild perceptual deficits after right ATL extended to non-meaningful stimuli, and also if impairments of pattern or shape perception would dominate. We answered both of these questions in the negative. The following discussion reviews our results and previous studies of the effects of temporal-lobe lesions monkeys and humans.

Visual Discrimination Performance after ATL

Overall, the performance of subjects with ATL was remarkably good. The lack of main effects of group for so many tests largely allayed our concerns regarding the amblyopia of some subjects, as well as any effects of anticonvulsant medication. We also believe that our efforts to keep the groups well matched with respect to age and education contributed to the clear lack of differences between groups. One question that arises is how to interpret the single significant effect of group for discrimination of blue axis color saturation, which was restricted to the RTL group when making L discriminations. The considerable size of this deficit combined with the borderline significance of impairments for red saturation and contrast discrimination argues for serious attention.

Impaired discrimination of hues at the blue end of the spectrum with relative sparing of the ability to discriminate other hues (incomplete achromatopsia) has been described previously in cortical lesion studies (Meadows, 1974; Pearlman, Birch & Meadows, 1979; Rizzo et al., 1992). Zeki (1990) suggested that this pattern of performance may result from the fact that short-wavelength-sensitive neurons are less common in visual cortex, making blue discrimination capacity more sensitive to partial loss of brain tissue. Lesion studies and recent PET studies conclude that the fusiform and lingual gyri subserve color vision in normal subjects (e.g., Damasio et al., 1980; Green, & Lessel, 1977; Pearlman, Birch & Meadows, 1979. Zeki et al., 1991). A deficit for blue color discrimination has been reported in patients with Alzheimer's disease (AD) (Cronin-Golomb, 1993). Given that the cerebral lesions in AD are not focal, it is difficult to correlate the impairment with any particular visual cortical locus; however, the neuropathological changes in AD are prominent in the temporal neocortical regions (areas 20, 21)(Arnold, 1991). According to Arnold and colleagues areas 20 and 21 are among the areas with the highest density of neuropathological changes; only the medial temporal-lobe structures are more severely affected. Additionally, behavioral experiments have suggested that the temporal neocortex and the associated ventral visual information processing pathway are particularly compromised in AD (Mendola, 1995; Kurylo, 1996). Thus, there is evidence that temporal-lobe damage may cause some loss of blue color discrimination in AD and after ATL.

Another issue is the selective impairment for lesser than discrimination of blue axis saturation. The ability to make such lesser-than discriminations appears to be particularly sensitive to the effects of brain lesions. Experiments in monkeys have demonstrated that lesions to area V4 cause difficulties making lesser-than discriminations across many visual domains (e.g., size, contrast, motion) (Schiller, 1993). We have found in our laboratory that Case 1, a subject with bilateral lesions of the anterior temporal lobes, manifests an impairment making lesser-than discriminations in the pattern domain. The results of this study (described in detail in Chapter 2) clearly showed that the lesser-than condition is harder for normal subjects than the greater-than condition. So, it is possible that the increased difficulty causes the increased sensitivity to brain lesions. However, the specificity of the effect for patterns in Case 1 and for color in patients with right ATL argues against a generalized effect of difficulty. It is possible that discrimination of less prominent elements in a given visual domain requires special mechanisms that are disrupted when the visual cortical areas relatively dedicated to that domain are damaged.

The lack of a deficit in the domain of pattern or shape perception is somewhat surprising. As discussed in the introduction, there has been some suggestion that pattern perception is disrupted after right ATL. Further, there is stronger evidence that pattern perception is affected by bilateral inferotemporal lesions in monkey. Detailed comparison between the human and monkey literature is limited by several factors: First, modern surgical lesions of the anterior temporal lobe in humans are always unilateral in order to avoid the dense global amnesia associated with bilateral anterior, medial temporal-lobe removal, as witnessed in the patient H.M. (Milner, 1968; Scoville & Milner, 1957). In contrast, only bilateral temporal-lobe lesions in monkeys typically produce impairments (Chow, 1951; Mishkin & Pribram, 1954). Second, the lesions in monkeys are larger than those in humans, include more posterior temporal neocortical tissue, and exclude more medial limbic structures. Third, the nature of the stimuli and tasks that have been employed in human studies has differed from those used in monkey experiments. Despite the above mentioned limitations, the human and monkey research should be used to inform each other. This effort clarifies the extent of inter-species similarities among primates, and is essential to a unified theory of temporal-lobe function.

Studies of Monkeys with Temporal-Lobe Lesions

There is general agreement that many simple capacities (minimum separable visual acuity, visual fields, critical flicker frequency, flash detection threshold, backwards masking) are spared after bilateral anterior inferotemporal neocortical (IT) removal (reviewed in (Gross, 1973)). Initially, the deficit resulting from bilateral IT lesions was characterized such that the degree of impairment depended on the difficulty level (as assessed by the length of acquisition by normal monkeys) across tests of luminance, color, and 2- and 3-dimensional forms (Gross, et al., 1971). However, according to many later studies the patterned nature of the stimuli seems to be critical, echoing the literature on human temporal-lobe lesions. Gross found that monkeys with posterior IT lesions manifest greater difficulties on an object discrimination versus a color discrimination task that was disproportionate to the relative difficulty level (Gross, et al., 1971). Another study found that monkeys with posterior IT lesions (TEO) showed only transient difficulties relearning an oddball-out task, but persistent difficulties making form discriminations, but not discriminations of luminance, color, or size (Iversen & Humphrey, 1971). According to Iversen (1973), color, size, and brightness are more easily discriminated than patterns under similar conditions. However, deficits are demonstrable using non-pattern tasks if testing proceeds in an interleaved manner that requires flexible discrimination behavior.

Another theory of IT function postulates that IT plays an important role in perception of object invariances: the ability to recognize an object's identity despite an infinite variety of viewing angles, sizes, and lighting conditions, as well as many possible means of creating visibility, including luminance, chrominance, motion, texture, and depth. Several kinds of evidence support this theory: First, anatomical and physiological studies clearly imply a convergence of input on to IT neurons. Most neurons have large, bilateral receptive fields, and the exact position of a stimulus inside the receptive field is not critical (Gross, et al., 1972). Second, IT lesions impair the perceptual constancy of rotated 2-dimensional patterns, as well as 3-dimensional objects transformed in size, viewing angle, or lighting (Gross, 1978;

Gross & Mishkin, 1977; Weiskrantz, 1990). Third, electrophysiological studies of IT cortex report single cell responses that are invariant with respect to object size (Lueschow, Miller, & Desimone, 1994) and object viewing angle (Logothetis & Pauls, 1995).

Studies of Humans with Anterior Temporal Lobectomy

Given the evidence for perceptual deficits after temporal-lobe lesions in humans and monkeys, it striking that we found such normal performance for our subjects. One possibility is that the mild 'perceptual' difficulties of subjects with right ATL are only tapped by tasks more complex than those employed here. In particular, it may necessary to use stimuli with semantic content. The difficulty may lie not in the analysis of basic visual cues, but in extracting meaning from nonverbal stimuli such as faces, designs, and scenes. Another unresolved issue is whether human brains can be expected to have visual areas homologous (or at least analogous) to visual areas in monkeys, and whether such areas are located in grossly analogous regions of the human brain, which is much larger than that of monkeys. There is some evidence (from recent imaging studies, e.g., [Sereno, 1995]) that the visual areas in humans do not extend as far anteriorly into the temporal lobe in humans as they do in monkeys. The advent of imaging methods for measuring cortical activity in the normal active human brain should allow a large step forward in further answering questions about the cortical substrates of visual discrimination capacities in human subjects in the future.

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Table 1: Subject Characteristics

Group	Number of Subjects [M, F]	Mean Age [SD]	Mean Education [SD]
L-ATL	[3, 6]	32.9 [11.9]	14.4 [2.8]
R-ATL	[2, 7]	32.7 [11.4]	14.0 [1.8]
Normal Control	[9, 10]	32.8 [8.9]	14.2 [1.3]

Table 2: Excision Characteristics

Group	Number of Subjects	Lateral Cortex* [SD]	Mesial Structures* [SD]	Months Since Surgery
L-ATL	9	3.7 [1.2]	5.2 [1.1]	40.4 [27.7]
R-ATL	9	5.6 [0.6]	4.6 [1.3]	34.4 [30.7]

*Measured in cm

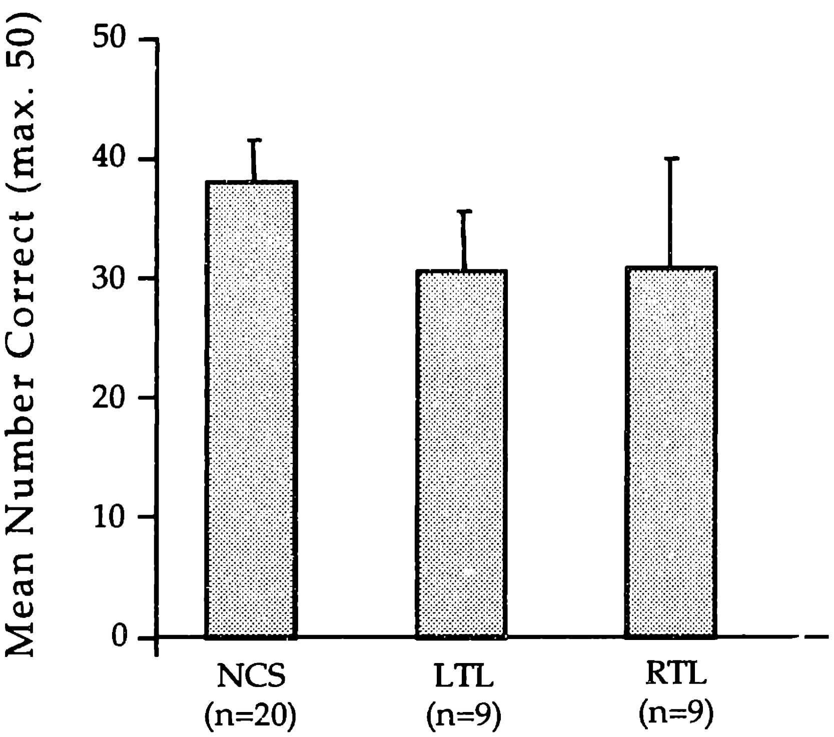


Figure 1. Experiment 1. Results of Mooney's Closure Faces Test. Left and right anterior temporal lobectomy impairs performance relative to control subjects.

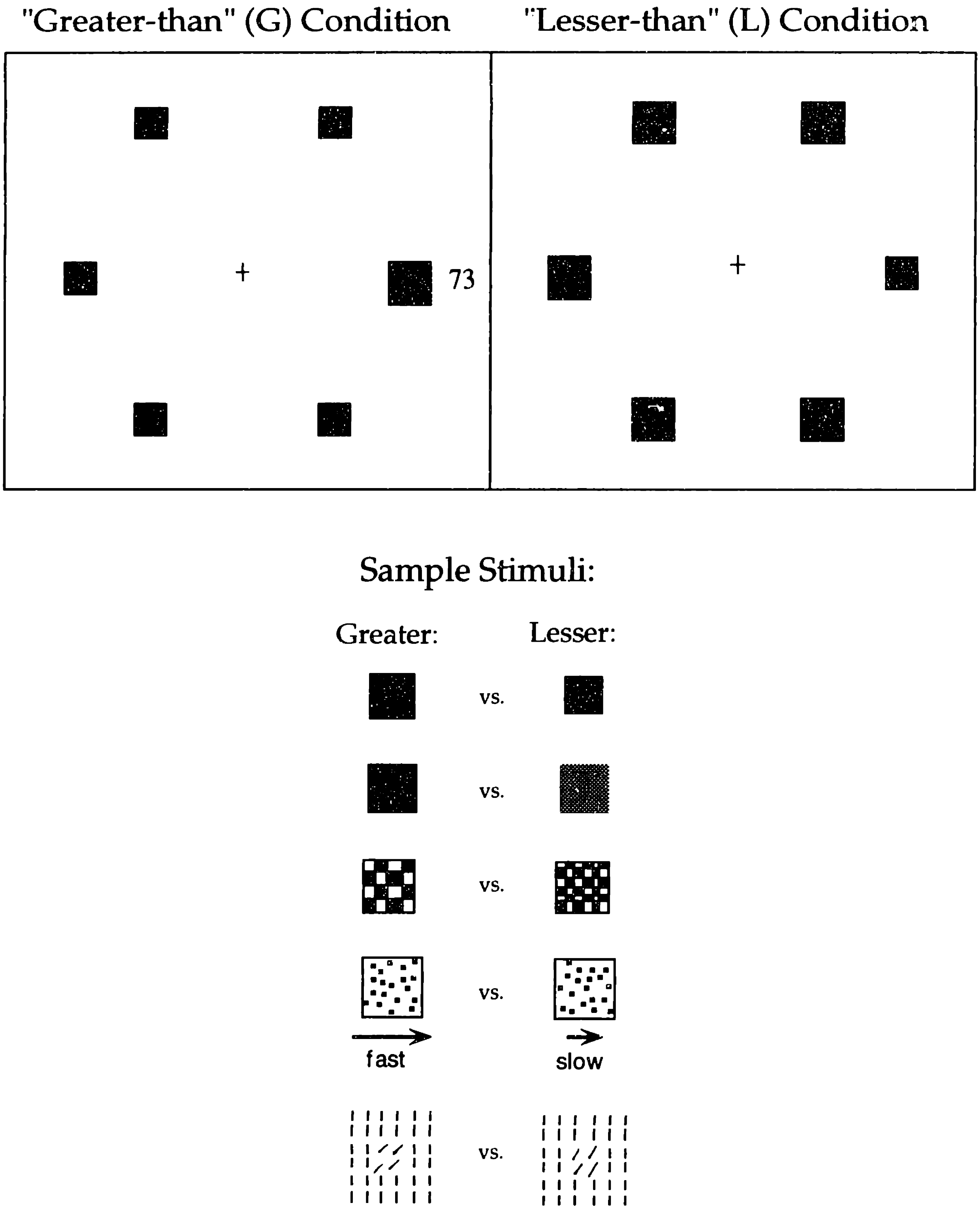


Figure 2. Experiment 1. Depiction of stimulus array for the greater-than and lesser-than condition. Size discrimination is shown as an example. Examples are also shown of the greater-than and lesser-than stimuli for the visual domains of size, contrast, pattern, speed of motion, and oriented texture.

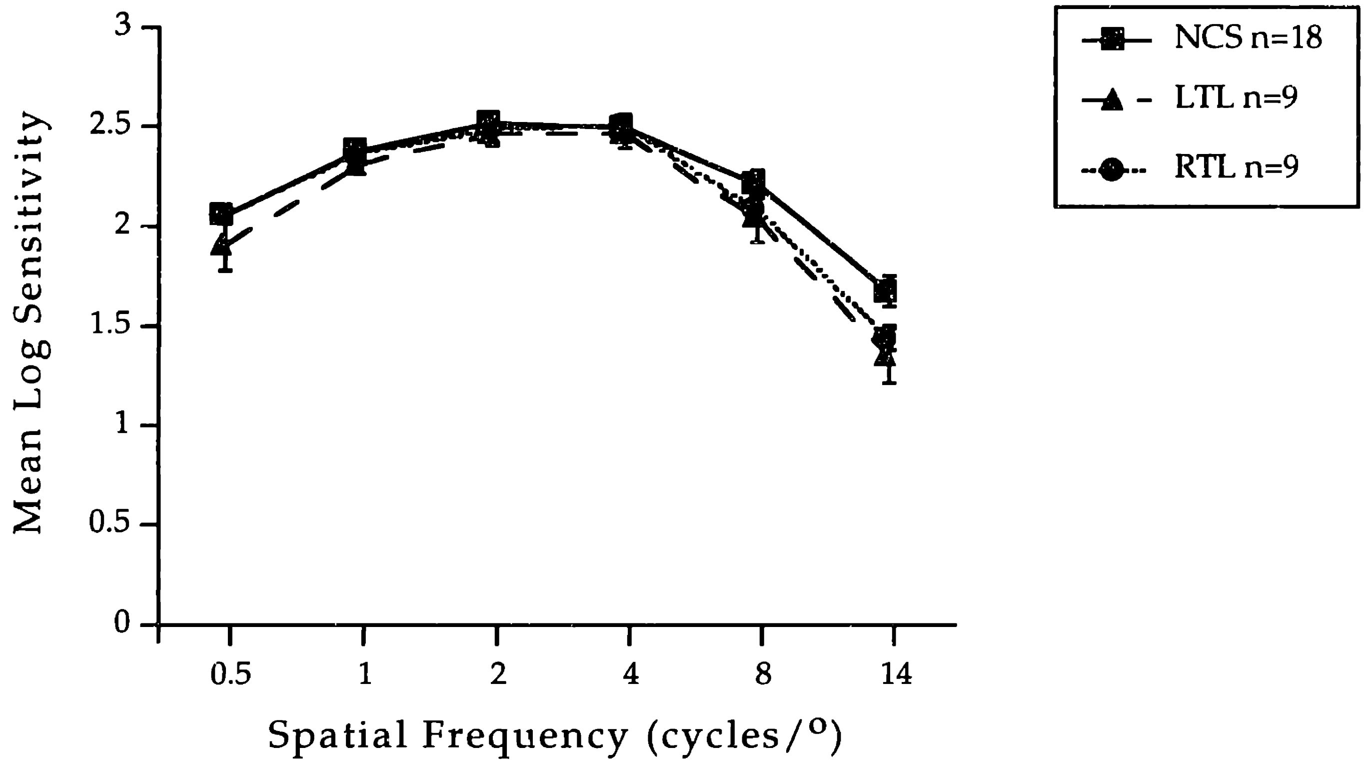


Figure 3. Experiment 1. Contrast sensitivity is normal after left or right anterior temporal lobectomy.

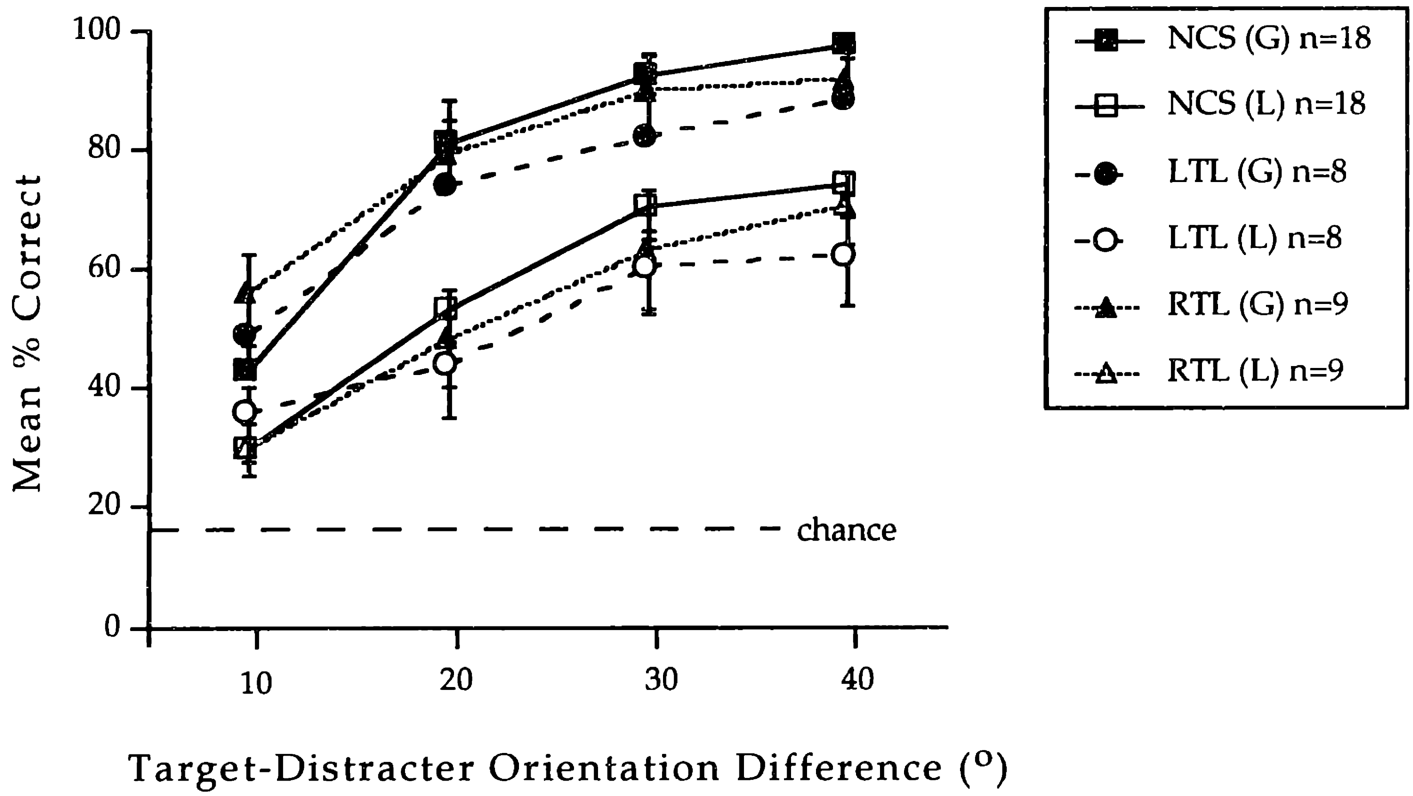


Figure 4. Experiment 1. Texture discrimination is normal after left or right anterior temporal lobectomy. Results are shown for the greater-than (G) and lesser-than (L) condition.

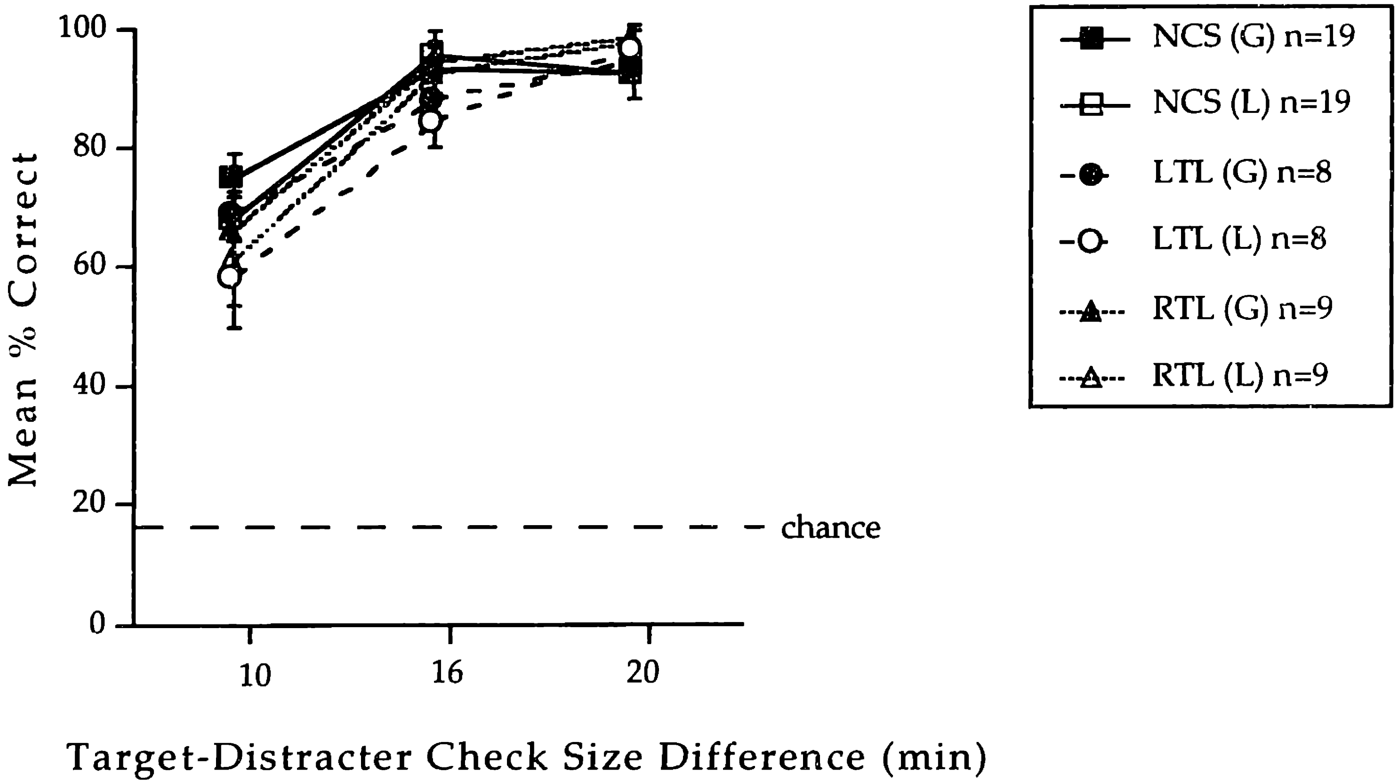


Figure 5. Experiment 1. Pattern discrimination is normal after left or right anterior temporal lobectomy. Results are shown for the greater-than (G) and lesser-than (L) condition.

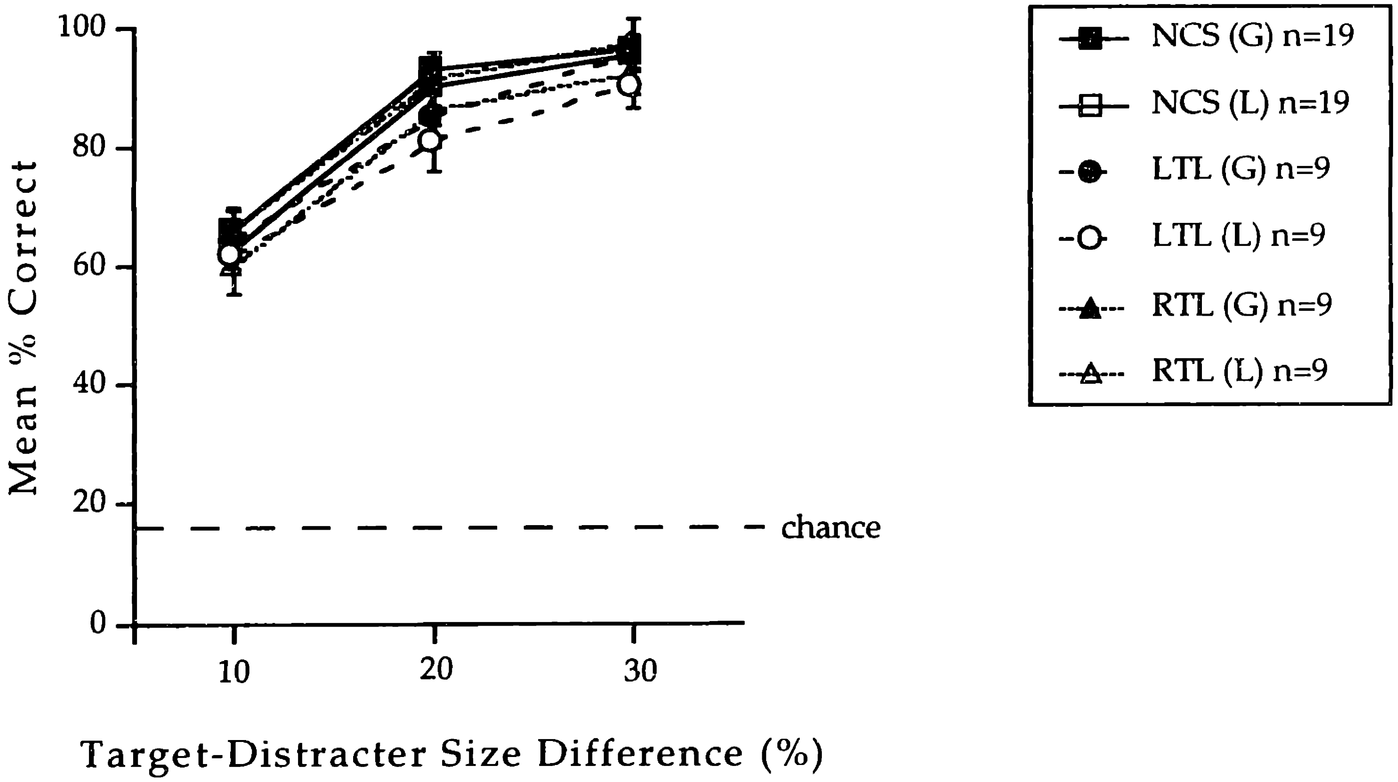


Figure 6. Experiment 1. Size discrimination is normal after left and right anterior temporal lobectomy. Results are shown for the greater-than (G) and lesser-than (L) condition.

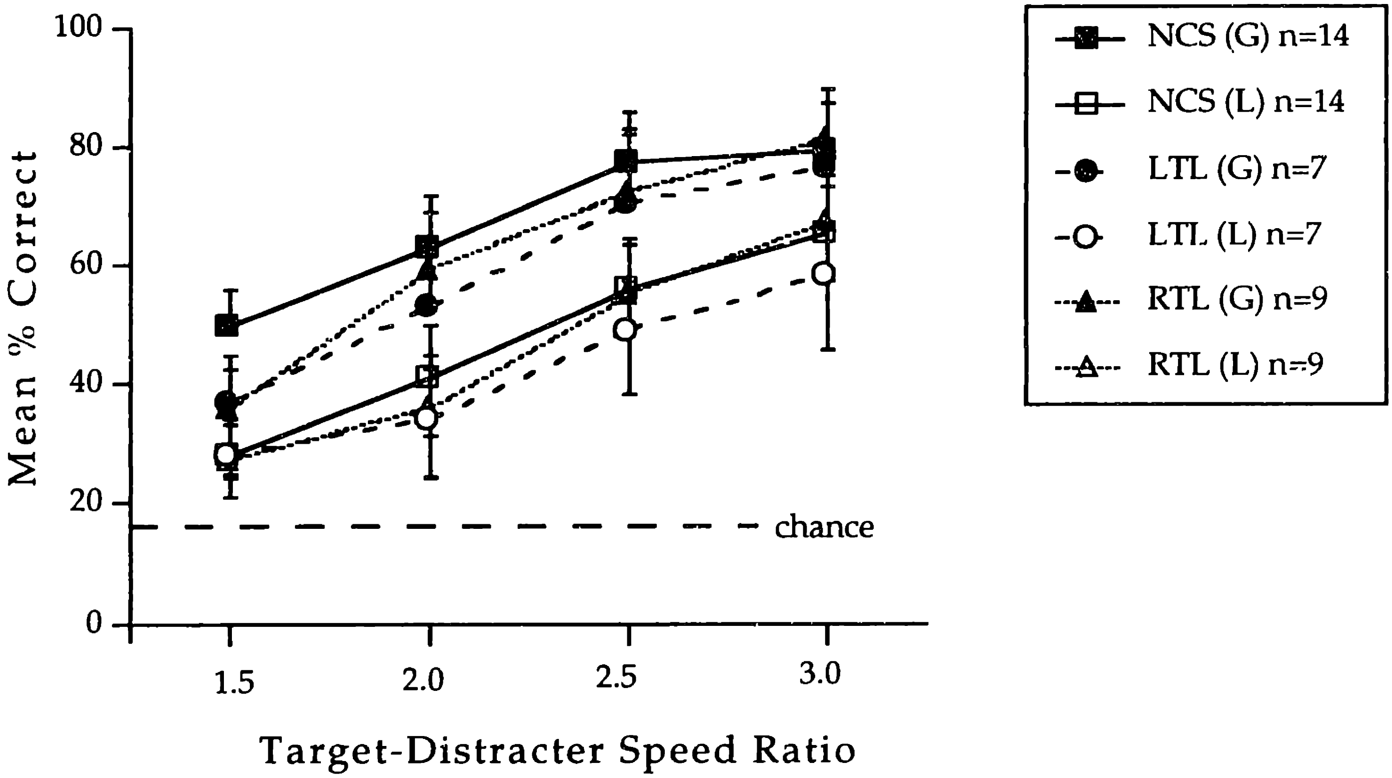


Figure 7. Experiment 1. Motion discrimination is normal after left or right anterior temporal lobectomy. Results are shown for the greater-than (G) and lesser-than (L) condition.

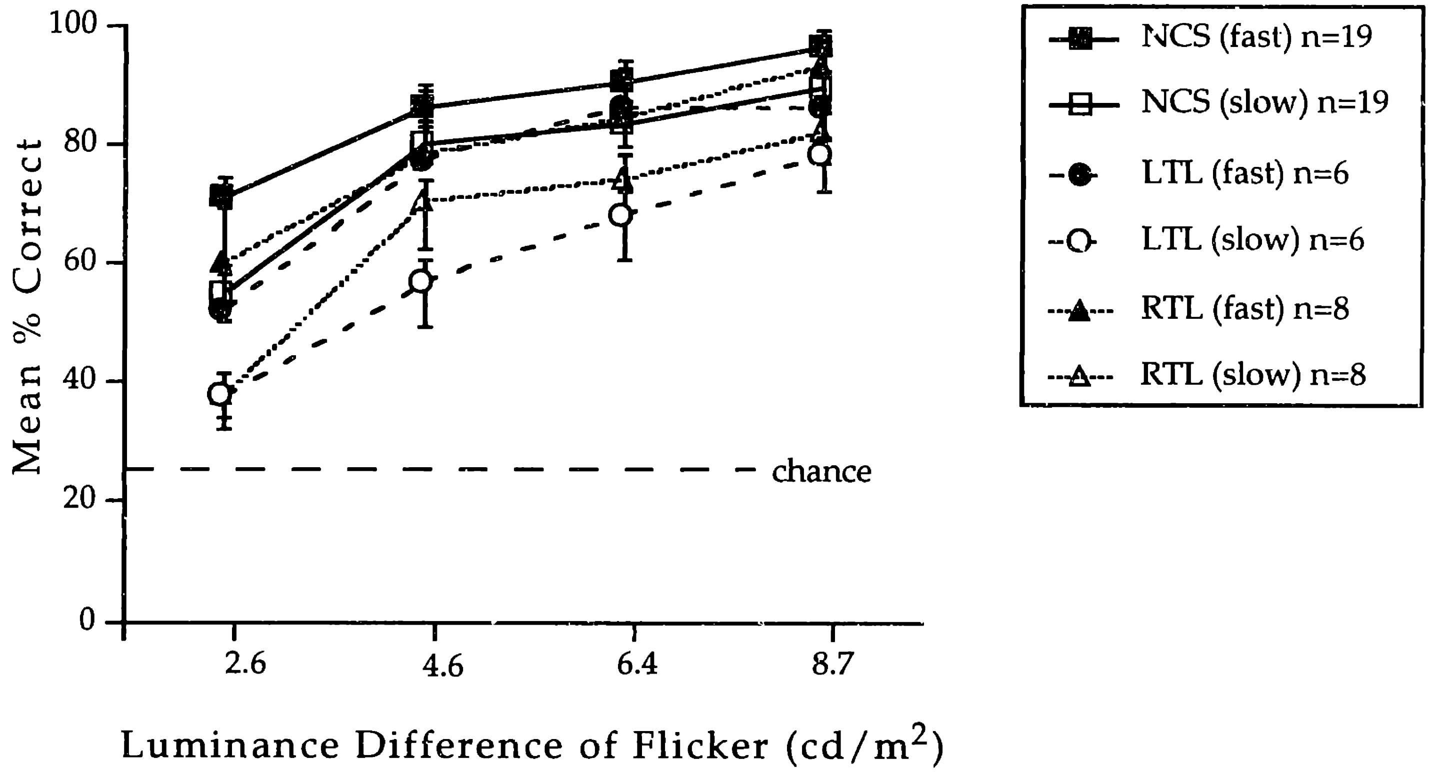


Figure 8. Experiment 1. Flicker discrimination is normal after left or right anterior temporal lobectomy. Results are shown for the slow and fast flicker condition.

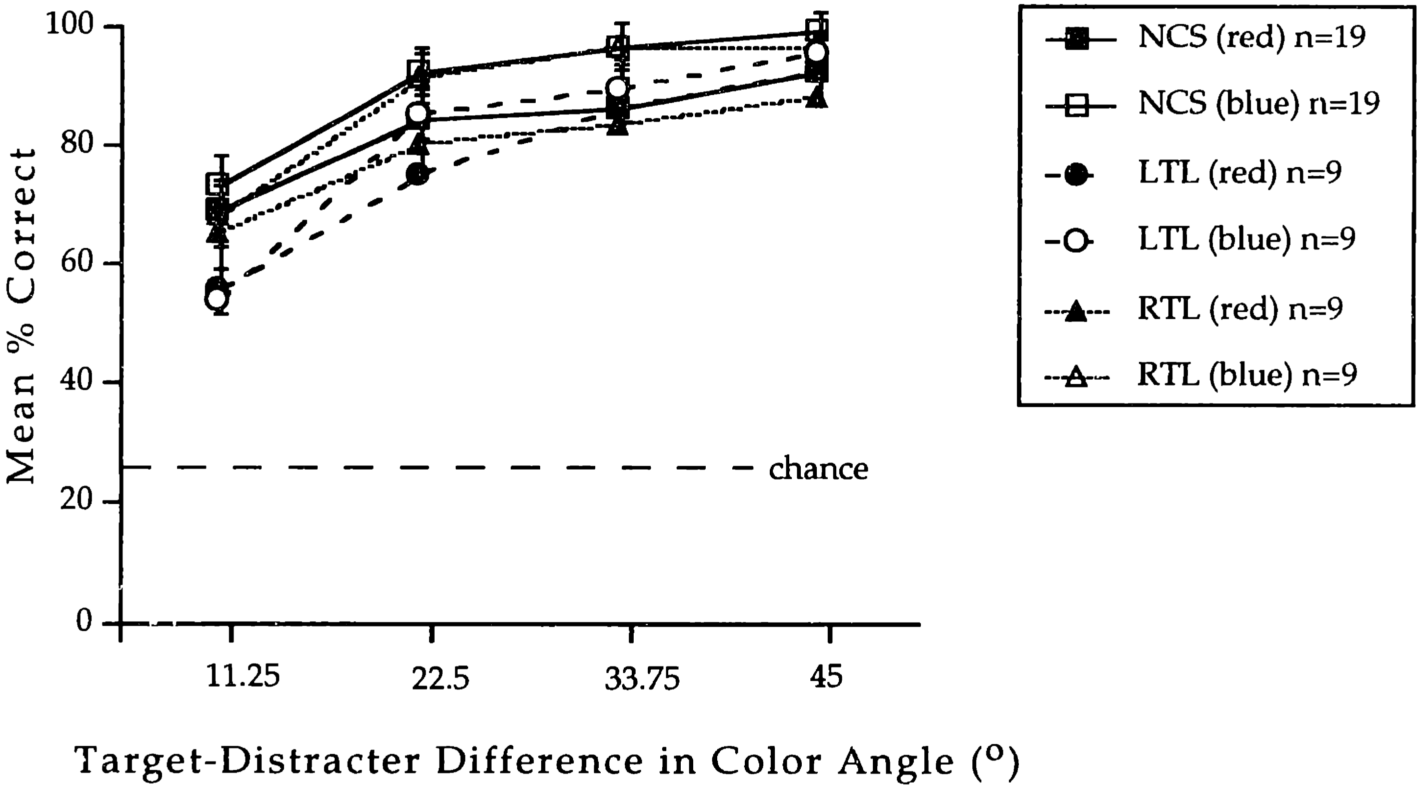


Figure 9. Experiment 1. Red and blue hue discrimination is normal after left or right anterior temporal lobectomy. Results are shown for the red color axis and the blue color axis.

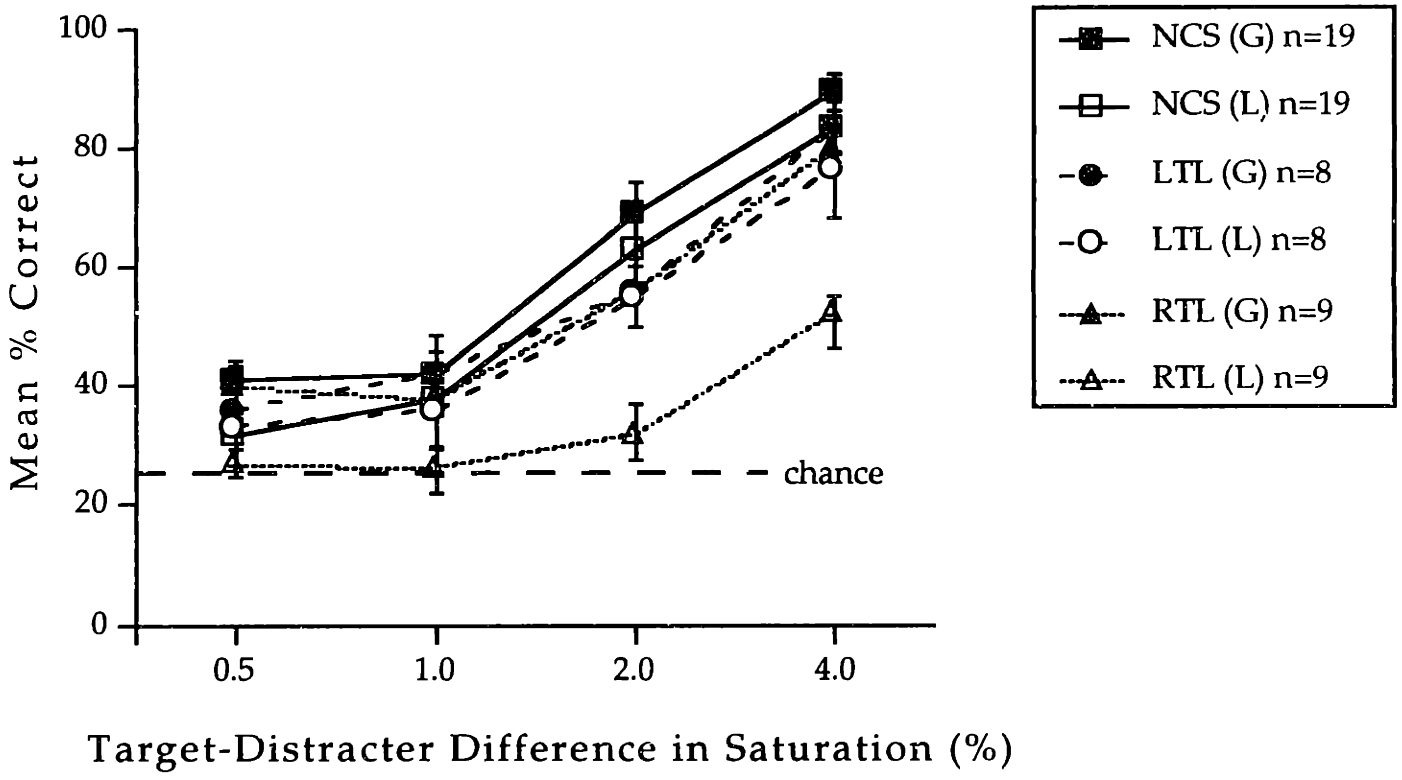


Figure 10. Experiment 1. Blue saturation discrimination is impaired after right but not left anterior temporal lobectomy. Results are shown for the greater-than (G) and lesser-than (L) condition.

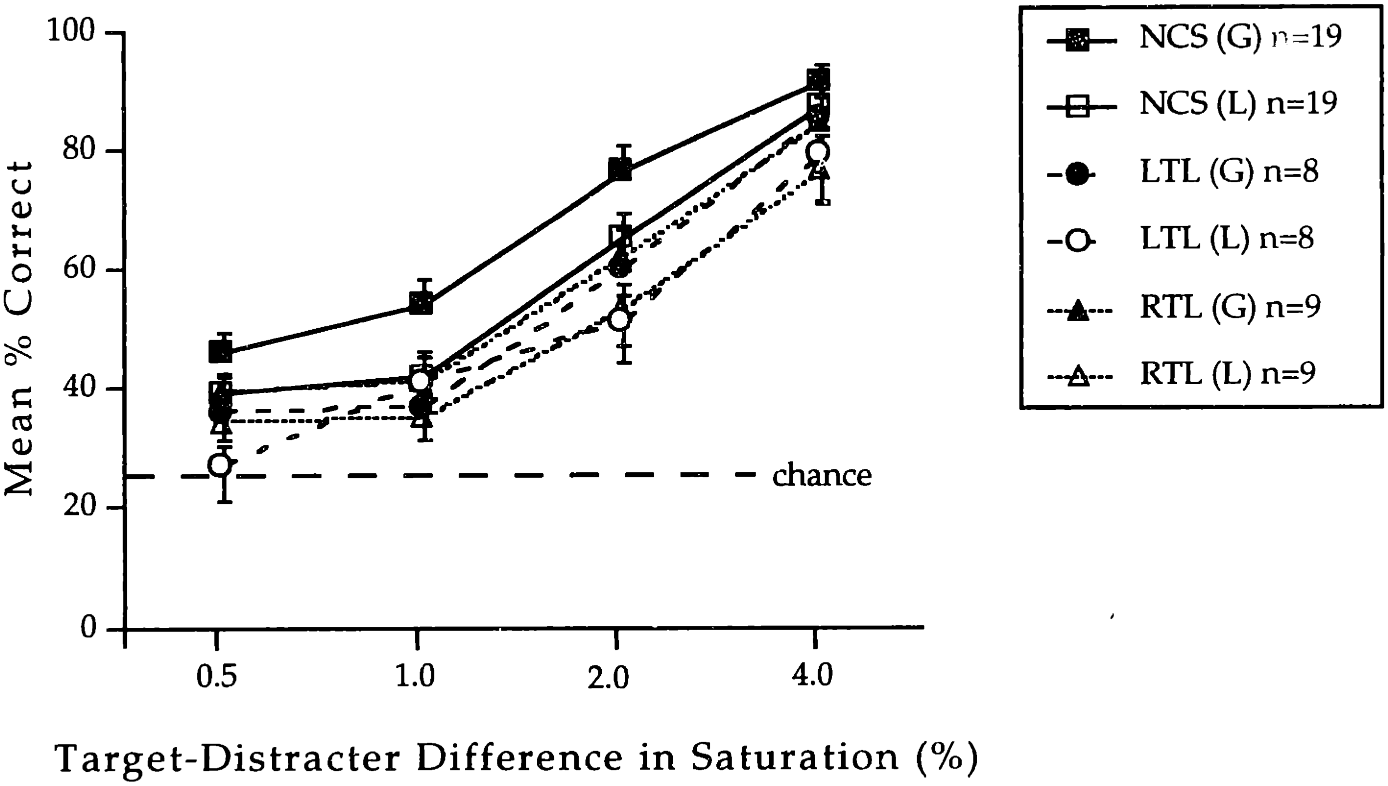


Figure 11. Experiment 1. Red saturation discrimination is normal after left or right anterior temporal lobectomy. Results are shown for the greater-than (G) and lesser-than (L) condition.

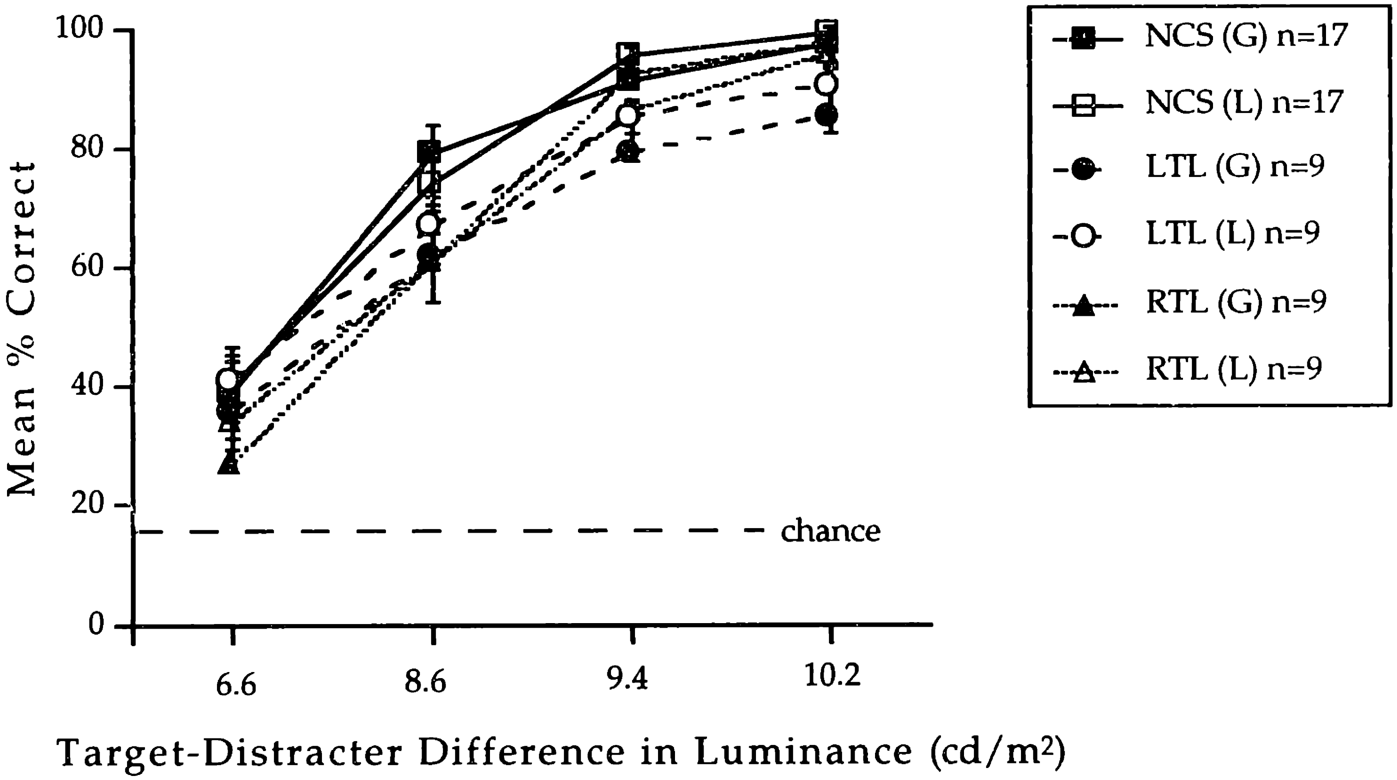
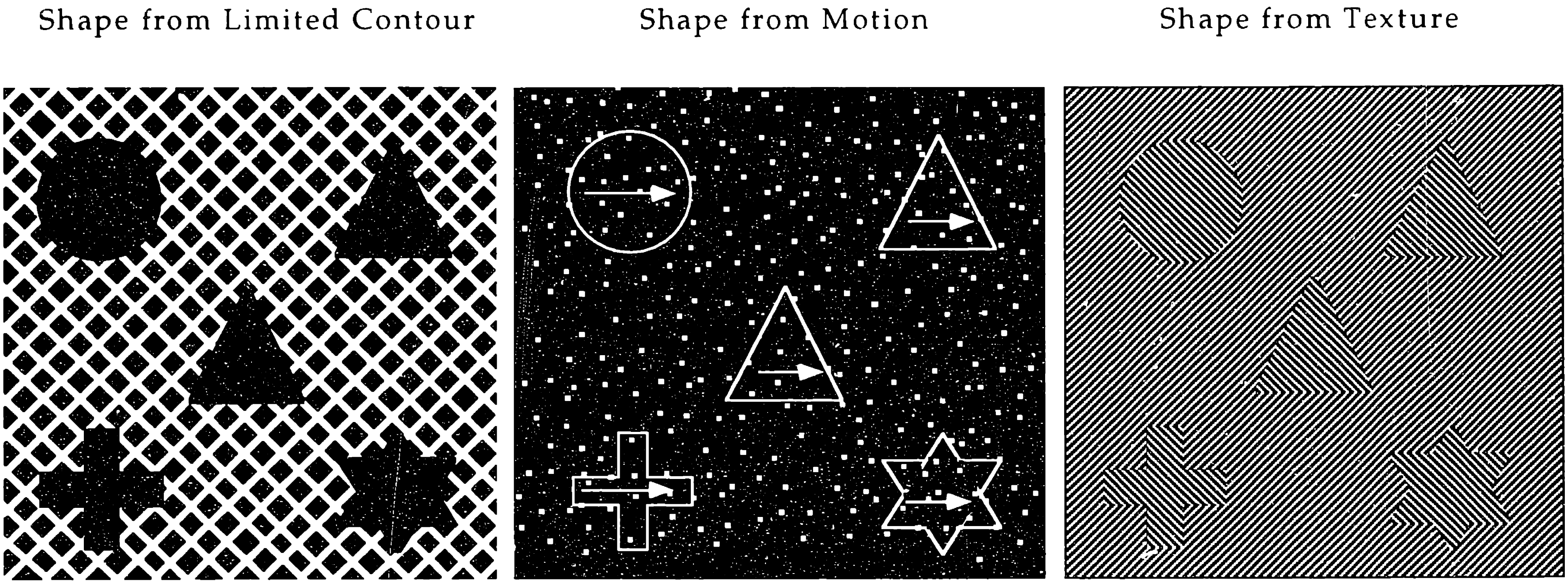


Figure 12. Experiment 1. Contrast discrimination is normal after left and right anterior temporal lobectomy. Results are shown for the greater-than (G) and lesser-than (L) condition.



Shape from Limited Contour

Shape from Motion

Shape from Texture

Figure 13. Experiment 2. Sample stimuli are depicted for the match-to-sample tests. In the Shape from Motion version, the dots inside the border of the shapes (which are not shown) are set in motion.

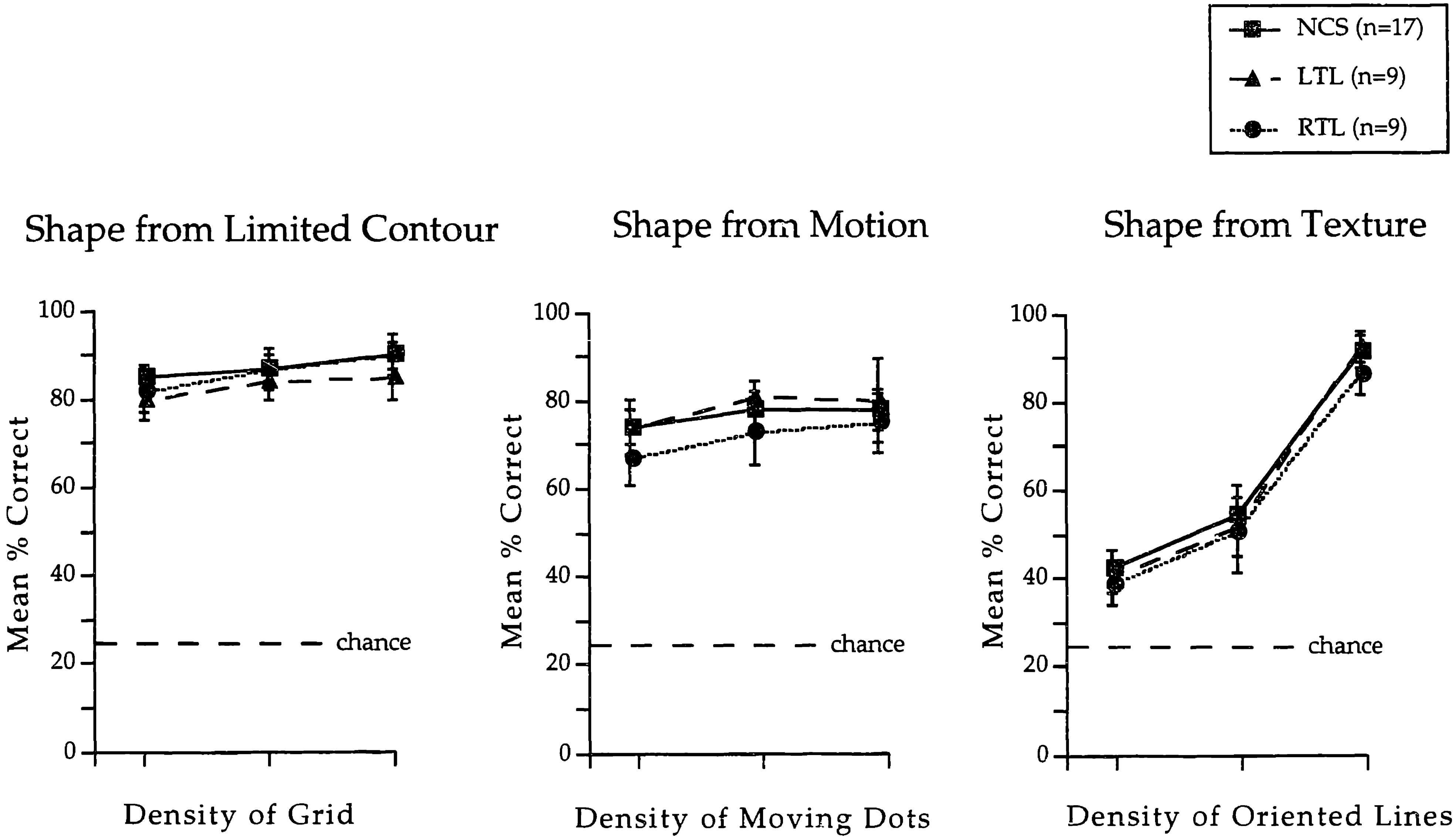


Figure 14. Experiment 2. Matching shape based on selective cues is normal after left or right anterior temporal lobectomy.

Visual Discrimination and Attention After Bilateral Temporal-Lobe Lesions: A Case Study

The ability to focus visual attention upon elements of a visual scene that are relatively small, dim, or slow, is clearly adaptive, but may pose a greater challenge to the visual system than the converse situation (e.g., a big, bright red speeding sports car). In many visual domains, stimuli that are physically more prominent ("greater than" their context) elicit more neural activity than those that are less prominent ("lesser than" their context). Attending to less prominent stimuli may require a special mechanism to override this more fundamental, perhaps automatic, means of directing attention. Support for this hypothesis comes from Schiller's studies of monkeys with incomplete V4 lesions. In addition to mild color, contrast, and form, deficits within the "scotoma," these monkeys were selectively impaired on oddball-out discrimination tasks when the oddball target was dimmer, smaller, or more slowly moving (but not when brighter, larger, or faster) than the respective distracters (Schiller and Lee, 1991; Schiller, 1993). Neural activity in area V4 is known to be modulated by selective visual attention (Fischer & Boch 1981; Moran & Desimone, 1985; Mountcastle et al. 1987; Spitzer et al., 1988) and by expectancy with respect to an imminent stimulus (Haenny & Schiller, 1988; Heanny et al. 1988; Maunsell et al. 1991)

Physiological and behavioral studies in monkeys indicate that V4 is part of a relatively discrete visual stream, extending from V1 to inferior temporal cortex (Ungerleider & Mishkin, 1982). The temporal (ventral) stream is particularly crucial for normal "object vision," specifically, discrimination and memorial tasks with visually presented 3D common objects or 2D patterns. The physiological responses of neurons in the ventral stream commonly vary with static form information such as size, color, and shape of stimuli. These neurons are less sensitive to motion or position of stimuli.

The invariance of the deficit for lesser-than discriminations across the different visual domains of size, brightness, and motion is a striking aspect of the results of V4 lesion. No studies have investigated whether lesions at stages other than V4 in the ventral stream cause a similar difficulty discriminating less prominent targets. In particular, an IT lesion may not have the same consequence as a V4 lesion, given that IT cortex is closer than V4 to the end of the stream of processing devoted to pattern and object vision. There is considerable evidence that bilateral IT lesions leave monkeys impaired in visual discrimination learning (Gross, 1973), but little is known about the role of IT in visual attention. One study found that monkeys with IT lesions showed only transient difficulties relearning an oddball-out task, but persistent difficulties making form discriminations, but not discriminations of luminance, color, and size (Iversen & Humphrey, 1971). According to Iversen (1973), color, size, and brightness are more easily discriminated than patterns under similar conditions. These investigators did not specifically contrast discrimination of greater-than versus lesser-than targets.

We sought to determine whether the symptoms obtained by Schiller and Lee in monkeys with focal lesions could be demonstrated in human subjects. One study (Rizzo et al., 1992) directly compared the abilities of a patient with peristriate lesions to the abilities of monkeys with V4 lesions. The resulting impairments were similar to those displayed by monkeys with V4 lesions. The patient displayed abnormal color and pattern discrimination, with relatively spared luminance contrast detection thresholds, and normal spatial contrast sensitivity, stereopsis, motion, and flicker perception. It is not known how Rizzo's patient or other patients with visual cortex lesions would perform on a task similar to Schiller and Lee's. In order to address this issue, we gave "greater-than" and "lesser-than" discrimination tests to a patient with bilateral temporal-lobe lesions.

Methods

All of the experiments reported in this paper had the approval of a human subjects committee, and all participants gave their informed consent to participate.

Subjects

The subjects in this experiment were Case 1 and 8 normal control subjects (NCS) recruited from the MIT community. The NCS group (3 males and 5 females) had a mean age of 28.1 (range 25-32) and mean years of education of 13.3 (range 12-15). At the time of testing Case 1 was a 27-year-old woman with 14 years of education. She sustained a head injury at age 25 after falling from a swing. She manifested untreated childhood amblyopia. Her visual acuity was OD: 16/13+ ; OS: 5/200. Her visual fields were full. She described her visual perception as "like waking from a dream, where things do not look real." Interestingly, she now enjoys photography, and teaches a photography class to children with learning disabilities.

On the Wechsler Adult Intelligence Scale - Revised (WAIS-R; Wechsler, 1981), Case 1 had a Verbal IQ of 98, a Performance IQ of 121, and a Full Scale IQ of 107. On the Wechsler Memory Scale - Revised (WMS-R; Wechsler, 1987) her Verbal Memory Index was 100, Visual Memory Index 101, General Memory Index 98, Attention/Concentration Index 94, and Delayed Memory Index 103.

Case 1's color vision was defective as measured with several tests. On the City University Colour Test she scored 7/10 correct (10 is normal). On the Farnsworth 100 Hue Test she scored poorly. With OD her discrimination profile resembled the *low discrimination profile* (with her errors not grouped in any region) seen in 10% of the normal males studied by Farnsworth (Farnsworth, 1943). With OS she scored even worse, out of the normal range in the blue region. She had little depth perception due to poor acuity in one eye. Her stereoacuity was worse than 400 sec. of arc as measured by the Randot Stereoacuity Test. Her contrast sensitivity was normal as measured by PGCONSEN, (Vision Metrics, Berkeley, CA). Case 1's face recognition ability was notably poor. She scored 21/50 correct on the face version of Warrington's Immediate Recognition Test, placing her below the 5th percentile (Warrington, 1984). She scored in the severely impaired range on the Benton Facial Recognition Test (27/54 correct). She scored in the normal range on the Mooney Closure Faces test (35), but was very slow. Finally, Case 1 scored very low on a verbal (12) and a nonverbal (23) version of the Recurring Figures Test (Kimura, 1963). In summary, Case 1 demonstrated moderate achromatopsia, prospagnosia, and memory loss.

Clinical MRI brain scans were consulted to determine the locus and extent of her lesions (Figure 1). The inferior and middle temporal gyri were missing bilaterally from the uncal hippocampal level to the posterior hippocampal level with encroachment into the temporal stem (Figure 1B, 1C). The lesion was larger on the right side extending into the temporal pole, and including the anterior amygdala (Figure 1A). Medial temporal-lobe structures appeared to be spared, except for a portion of the right amygdala. The inferior horn of the lateral ventricle was moderately enlarged on the right, and slightly enlarged on the left. Lacunar lesions were noted in the nucleus basalis/basal forebrain area. Finally, a small lesion was seen in left orbital frontal and ventrolateral frontal cortex, and a small lesion in the right temporoparietal white matter (Figure 1D).

At the time of testing Case 1 was taking 200mg of Tegratol 3 times per day to control seizures.

Apparatus and Stimuli

All tests were administered with a Macintosh IIci computer with color monitor using software developed in our laboratory. In all cases the stimuli consisted of six elements arranged at the corners of a hexagon (Figure 2). One element was always different (an "oddball") from the five distracters. A fixation cross was placed in the center of the virtual hexagon. Although this test used simple stimuli that assessed basic visual capacities, it also tapped a visual function of a higher level when the prominence of the target was varied. We used two prominence conditions: "greater than" (G) and "less than" (L) (Figure 2). For example, in the case of size discrimination, the G condition corresponded to a larger oddball target while the L condition corresponded to a smaller oddball target. The absolute difference between targets and distracters was varied in order to create several levels of difficulty (independent of prominence). On a given trial, a G or L target differed from the distracters by 1 of 3 difficulty levels, and appeared at 1 of 6 target locations to yield a randomized 2 x 3 x 6 design. Performance was also assessed using greater or lesser contrast, faster or slower stimulus motion, and more or less salient patterns.

Size. Following presentation of the fixation cross, six squares in a hexagonal arrangement were flashed for 250 msec. The size difference between the target and comparison stimuli was varied. Three difficulty levels corresponded to size differences of 30%, 20%, and 10%. Absolute size of the squares was 1.6, 1.76, 1.92, and $2.08^{\circ 2}$. The target was either larger (G) or smaller (L) than the distracters. The test comprised 288 trials.

Contrast. Following presentation of the fixation cross, six squares ($1.8^{\circ 2}$) in a hexagonal arrangement were flashed for 250 msec. The luminance difference between the target and comparison stimuli was varied. Four levels of difficulty were used. The absolute luminance values used were 1.41, 2.20, 4.18, and 10.81 cd/m^2 with background luminance at 84.04 cd/m^2. The target was either darker (G) or lighter (L) than the distracters. The test comprised 192 trials.

Motion. Following presentation of a fixation cross, six windows, each containing 50 moving dots, were displayed on the screen for 1000 msec. One window contained dots moving at a different speed than the other 5 identical windows. The speed was varied systematically, and corresponded to 4 difficulty levels with speed ratios between target and distracters of 1.5, 2, 2.5 , and 3 (^{o}/sec). The absolute speed of the dots was 1.5, 2.25, 3, 3.75, or 4.5 ^{o}/sec. The target moved either faster (G) or slower (L) than the distracters. In this test, each individual moving dot had a limited lifetime, that is, it traveled a particular course for just 100 msec before it disappeared and was randomly repositioned to a new location to move for 100 msec, disappear, and so forth. The result was a pure motion signal not confounded by position cues. The correct response could not be determined by following a particular dot. Instead, a global motion field was perceived by integrating the motions of all the dots in the field. The test comprised 192 trials.

Pattern. Following presentation of a fixation spot, six squares (2.1^{o2}) in a hexagonal arrangement were flashed for 250 msec. The squares contained high-contrast checkerboard patterns, with the target pattern having a different spatial frequency from the other identical comparison stimuli. The checkered patterns were 3 x 3, 4 x 4, 5 x 5, or 6 x 6, with check size 40, 30, 24, or 20 min. respectively. The check pattern size was either larger (G) or smaller (L) than the distracters. The test comprised 288 trials.

Texture. In this case, following presentation of a fixation cross, an array of vertical lines filled the screen for 250 msec. In six small areas (3.0^{o2}),the lines were tilted along the diagonal. Difficulty was varied by systematically increasing the amount of tilt difference between the target and distracters. In the G condition, the target area lines were more tilted, and the distracters blended easily into the background of vertical lines. Conversely, in the L condition the target area contained lines less tilted than the distracters. The test comprised 192 trials.

Procedure

The subjects sat 14 in. in front of the monitor in a dimly lit room. Before each test, subjects were shown sample G and L trials printed on a piece of paper.

They were always instructed to find the location of the oddball target, i.e., "the one that was different." They were always reminded that the oddball target could differ in two directions (e.g., it could be larger or smaller; it could be dimmer or brighter). Additionally, subjects were told that the difficulty level was mixed randomly, that they should to try to fixate the cross at the center of the screen, and that they should guess when unsure of the correct choice. Before the onset of the stimuli, a warning tone was given and a central fixation cross was presented for 2 sec. The subjects indicated their response by pressing 1 of 6 keys that corresponded to the hexagonal arrangement of stimuli. The subjects rested at several points during the test, indicated by a "please rest" screen. A block of trials ranged from 96 - 144 trials, and always contained stimuli of the same basic domain (e.g., size or contrast). There was no practice set. Subjects required 10 - 15 minutes to complete a block of trials.

Results

Size, Contrast, and Motion

Case 1 performed normally for G and L discriminations of size, contrast, and speed of motion for the entire range of difficulty (Figures 3, 4, and 5).

Texture

The results obtained when the oddball target was defined by texture differences clearly contrasted with the normal performance described above. In this situation, Case 1 displayed a striking discrepancy in performance between G and L conditions (Figure 6). Case 1's ability to discriminate the oddball target was normal when it was more salient than the distracters. The range of difficulty levels chosen here elicited a complete psychometric curve from near chance to near perfection for control subjects, and for Case 1, if the targets were relatively salient. When the oddball target was less salient than the distracters, however, Case 1's performance remained near chance at all levels.

Patterned Stimuli and Effects of Practice

After discovering Case 1's striking impairment with less prominent texture displays we proceeded to administer additional sessions of texture discrimination as well as sessions with two other patterned stimuli. In all cases, Case 1's impairment dissipated with practice. For the checkered stimuli shown in Figure 7, Case 1's performance on L discriminations steadily improved until no discrepancy relative to NCS was evident. Results are now plotted with abscissa representing increased training, trials were grouped into 4 sessions of 96 trials, administered in the same day (Figure 7).

Case 1's performance for the last patterned stimuli we used was different in that even greater-than discrimination was poor (Figure 8). In Case 1, pattern perception was impaired and in some cases this deficit went beyond the G vs. L discrepancy. This result is in agreement with many studies of the behavioral effects of IT lesions in monkeys (Gross, 1973). Results are again plotted with abscissa representing increased training, with trials grouped into 4 sessions of 96 trials, administered in the same day.

Discussion

We have shown that discrimination of less prominent patterns (impaired in Case 1) is dissociable from the discrimination of less prominent stimuli in other domains (normal in Case 1). Our findings support the hypothesis that the visual system of humans and monkeys is similar in that discrimination of less prominent targets can be selectively impaired after lesions. The deficits observed in Case 1 are more specific than would be predicted by explanations based on a supramodal reduction in visual attention. The following sections discuss our results, review the effects of temporal-lobe lesions in monkeys and humans, and relate our results to theories of visual attention.

Discrimination of greater-than and lesser-than targets

An important factor in the discrimination tasks used in this study is that distracters were present. Case 1 was not impaired at target detection in the absence of distracters. Her difficulties were revealed only when the target was competing with distracters. In this regard, the impairment was related to the extinction phenomenon classically observed after parietal-lobe lesions. In the present case, however, the distracters were patterned, and physically more prominent than the target.

One consideration is whether Case 1's performance represents a deficit that is selective to L conditions. The evidence that we obtained is equivocal on this point. In some cases, such as with the textured and checkered stimuli, Case 1 showed a dramatic impairment in the L condition along with normal discrimination of G targets. On the other pattern task, however, Case 1's performance for G discriminations was clearly depressed, suggesting difficulties with pattern discrimination in general. We believe that the balance of evidence suggests that discrimination of L targets is particularly sensitive to the effects of visual cortex lesions. Yet, we make this conclusion cautiously given Case 1's occasional difficulty with G discriminations combined with our observations in other experiments that L discriminations are often slightly harder in general for normal subjects.

The evidence for the selectivity of Case 1's impairment for patterned stimuli is strong. We dissociated Case 1's difficulties with pattern discrimination from normal discrimination of size, contrast, and speed of motion. Fortuitously, we tested Case 1 on the patterned discriminations after testing her with discriminations of size, contrast and, motion (all on the same day). Thus, we are not concerned that Case 1 failed to understand the task, or simply needed practice to execute the task. Case 1's difficulties with pattern perception are predictable given her temporal-lobe lesions. The exact computational role of the inferotemporal cortex is not clearly known, but much evidence suggests that IT cortex is critical for pattern discrimination (Iwai, 1985). A common assumption is that different stages of processing in visual cortex are needed to make various aspects (e.g., pattern, motion) of visual stimuli explicit (Desimone & Ungerleider, 1989). It would be reasonable if these levels of processing were the same levels that the visual system relied upon for judgments of saliency. The results of this study and that of Schiller's (1993) work with monkeys suggests that the normal visual system has a mechanism for quickly noticing less salient elements in a scene when necessary, and that the mechanism may be localized in areas that are relatively dedicated to processing the relevant visual cues.

Case 1's pattern discrimination performance improved with practice. Interestingly, similar practice effects were described after V4 lesion in monkeys by Schiller and Lee (1991). One possible interpretation of these results is that Case 1 showed slow learning of visual discriminations, particularly with less prominent targets. A large body of literature describes deficits in visual discrimination learning after bilateral temporal-lobe lesions in monkeys. This deficit in learning is sometimes thought to exist with relatively spared discrimination thresholds (Blake, Jarvis & Mishkin 1977). We do not believe, however, that such a learning deficit exists in Case 1 without some loss of pattern discrimination in general. On several of the pattern discriminations, Case 1's performance started well below the NCS.

Finally, the factor of lesion size must be considered when comparing the present results with monkey studies. In the experiments of Schiller and Lee, the V4 lesions were made intentionally "incomplete," affecting just a portion of the visual field. The deficit that the monkeys displayed when the target was less salient could have been caused by two factors: (a) the targets were physically less salient than the distracters, and (b) targets were processed in disturbed retinotopic space, whereas the distracters were processed in intact retinotopic space. In contrast, Case 1 had no local field losses, and her lesions were large. Thus, the deficit she displayed was in spite of the fact that the more prominent distracters were also subjected to abnormal processing.

Effect of Temporal-Lobe Lesions in Monkeys

As mentioned in the previous section, many studies have found that bilateral IT lesions leave monkeys with difficulties in learning pattern discriminations (reviewed in Gross, 1973). Some experimenters have focused on visual attention in explaining the effects of bilateral IT removal. Blake and colleagues (1977) concluded that "the common impairment in all the studies quoted seems to be a retardation in noticing the details or identifying the features of visual stimuli. Once these have been picked out and attended to, however, the impaired animals are about as capable as normal animals in resolving very fine differences along that dimension" (Blake, Jarvis & Mishkin, 1977, p. 219). Butter (Butter, 1968; Butter & Gekoski, 1966) performed several inventive experiments assessing stimulus generalization and pattern equivalence in normal and lesioned monkeys. He suggested that the underlying impairment is essentially one of noting the less salient features of visual stimuli, although IT monkeys are capable of doing so with enough training. There are three concerns with this interpretation, however: First, the IT monkey's deficits can often simply be attributed to slow learning; second, the evidence that IT monkeys did eventually perceive stimuli normally is weak; and third, there is no justification as to why some aspects of the stimuli deserve to be called "less salient."

Other experimenters manipulated the combinations of cues present in stimuli, as well as cue redundancy (the relevance each cue has to determining the correct response) (Gross, et al., 1971; Iversen & Weiskrantz, 1967; Manning, 1971a; Wilson, Kaufman, Zieler, & Lieb, 1972). The interpretation has been that monkeys with IT lesions have trouble focusing attention on the relevant cues. These studies, however, invariably find that "attention" is not focused on configural pattern cues when luminance, color, or size information is present. It is more parsimonious to assume that the monkeys have a true loss of pattern perception. They succeed in pattern discriminations (after prolonged learning) by finding unintended features, such as local size or flux cues (Iwai, 1985).

Effect of Temporal-lobe Lesions in Humans

Neuropsychological studies have demonstrated that unilateral damage to the temporal lobes in humans results in impaired visual perception and memory. The deficits in visuospatial processing of nonverbal material are more pronounced after unilateral right anterior temporal resections than after such resections on the left side. The stimuli used to elicit impairments are usually made challenging by ambiguity, reduced information, or brief exposure times (e.g., Milner, 1980; Kimura, 1963). One disadvantage of the stimuli that have been typically used is that they are conceptually rich as well as perceptually complex (classification of faces, identification of incomplete objects, discrimination of anomalous scenes). Few studies report deficits for perception of figures with no semantic content. We are aware of no studies that assessed simple visual discrimination ability in patients like Case 1 with bilateral temporal-lobe lesions.

Visual attention as a strategy selection process

Most experiments on visual attention view attention as a spatially restricted entity that can be allocated to different degrees in a visual task. Visual search experiments (Treisman & Gelade, 1980) focus on which types of visual data can grab attention and which cannot. For example, a C among O 's will 'pop out' because the broken contour in the C represents a feature. However, when an O is placed among C's, the O will not be readily detected because it lacks a unique feature. Dual task experiments (e.g., Braun, 1994) address this issue by forcing subjects to perform a standard attention-intensive task (such as a visual search) at the same time as they perform a probe task. If performance of the probe task is compromised by concurrent execution of the attention-intensive task, then both tasks are assumed to require common attentional resources. An example of a task that requires attention is perceptual grouping of some types of texture elements.

The experiments described in the previous paragraph try to dissociate tasks by the degree to which they require attention. A problem with this approach is that virtually all visual tasks can be made to require attention if they are simply made difficult enough. Conversely, Treisman originally proposed that conjunctive visual search (e.g., a red horizontal line target among green horizontal lines and red vertical lines), requires attention in order to 'co-join' the features. However, Wolfe (1989) showed that conjunctive visual search can be done pre-attentively (i.e. in parallel) if the stimuli are made more salient (i.e. if the colors are brighter and the lines crisper). Other experiments challenge the view that attention is predominantly a space-limited resource. Wilson and Richards (1990) showed that when attention is directed to a single figure, such as a vernier offset display, it is not possible to analyze two aspects (vernier alignment and judgment of relative brightness) of the figure at the same time without a great loss in sensitivity for both tasks. Thus, two tasks interfere, even though attention is focused in the same spatial location.

A better explanation of attention is as a particular strategy used to solve a given task. Visual attention is limited by the number of strategies that can be performed concurrently. For example, according to Rossi and Paradiso (1993), after subjects attend to the orientation or spatial frequency of a gabor patch at fixation, they are more sensitive to low-contrast gratings presented in the periphery if the gratings match either the attended orientation or the attended spatial frequency.

Thus, this experiment dissociates attention from spatial location and can best be viewed as evidence for selective enhancement of strategies for analyzing the gabor patch. In physiological experiments on the macaque monkey, Richmond and Sato (1987) recorded the responses of IT cells during tasks that required attention either to different parts of space, irrespective of what was located there, or attention to a pattern discrimination. IT cells, which are believed to analyze pattern information, became more responsive when the monkey performed pattern discrimination tasks than when the monkey performed spatial attention tasks, even if the spatial locus of attention was the same. This result provides evidence that visual neurons can be modulated by the strategy needed for the task independently of the spatial location of stimuli.

In our experiment, subjects were required to perform concurrently two visual strategies, namely discrimination of G and L targets. Case 1 was not impaired when we separated the G and L conditions into separate blocks. However, at that time she had considerable practice with the mixed G and L condition, so we can not dissociate the effects of practice. Under the mixed conditions, which stress visual attentional resources, finding L targets is especially demanding given their low salience. There is evidence that the saliency of a particular target depends greatly upon its surrounding context. Braun (1994) (using stimuli similar to the ones used here) has provided evidence that the discrimination of L but not G targets is severely disrupted in a dual-task situation that is intended to reduce or eliminate selective attention from the task. We conclude from the present study that when focal brain lesions disrupt visual information processing of certain visual cues, judgments of saliency are also disturbed. Discrimination of less prominent targets demands a high degree of processing, and perhaps a specialized mechanism to make them salient enough to guide action. Thus, L discrimination tasks are particularly sensitive to the effects of visual cortex lesions, and may indicate the visual cues that are predominately processed by different visual cortical areas.

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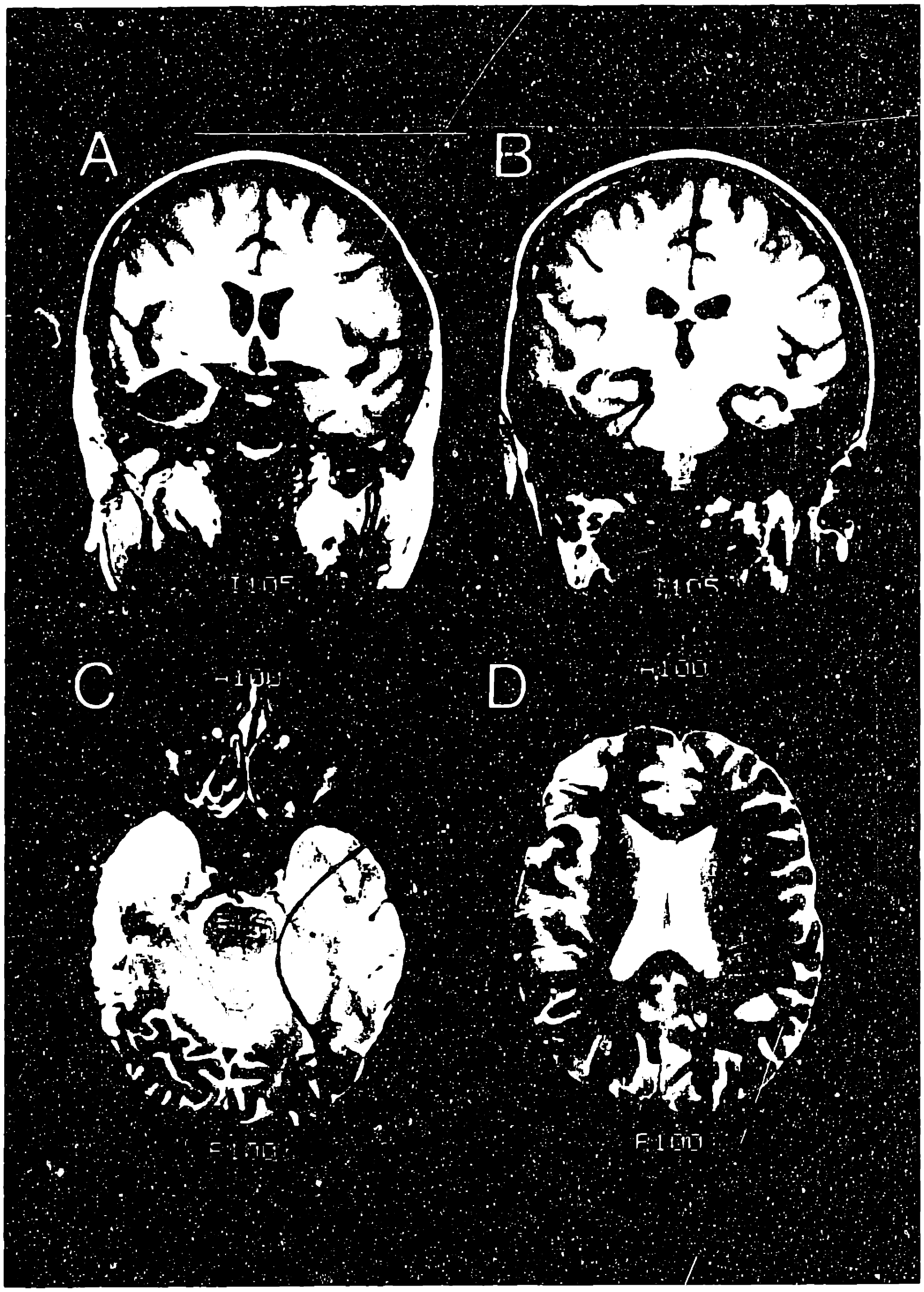

Figure 1. Representative images from Case 1's MRI brain scan. The lesions included inferior and middle temporal gyri bilaterally (A, B). The lesion was larger on the right side, including the anterior amygdala (C). Other medial temporal lobe structures appeared spared. A small lesion was noted in left orbital frontal cortex and in the right temporoparietal white matter (D).

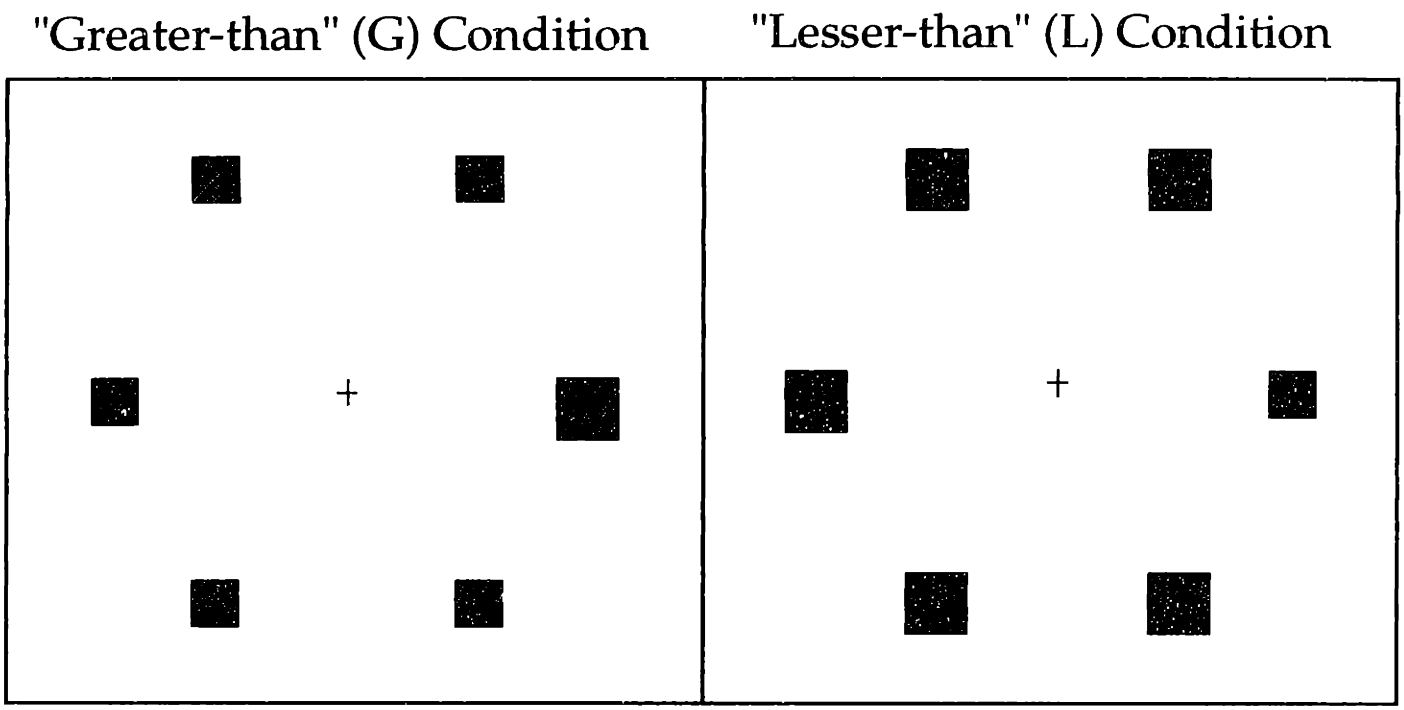

Figure 2. Depiction of stimulus array for the greater-than and lesser-than condition. Size discrimination is shown as an example.

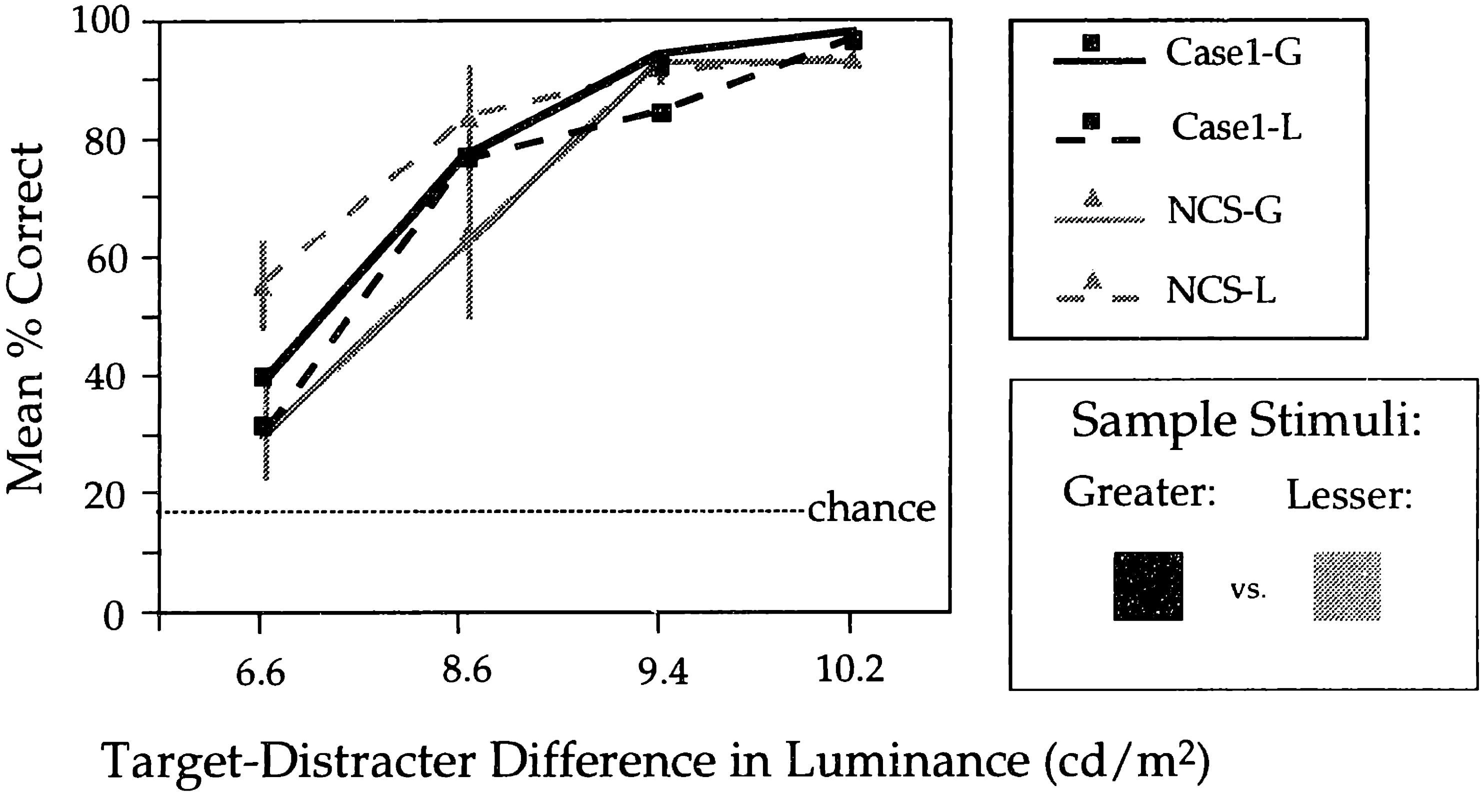

Figure 3. Case 1 shows normal performance on G and L discriminations of contrast. The performance of Case 1 is compared with that of NCS (with standard error bars).

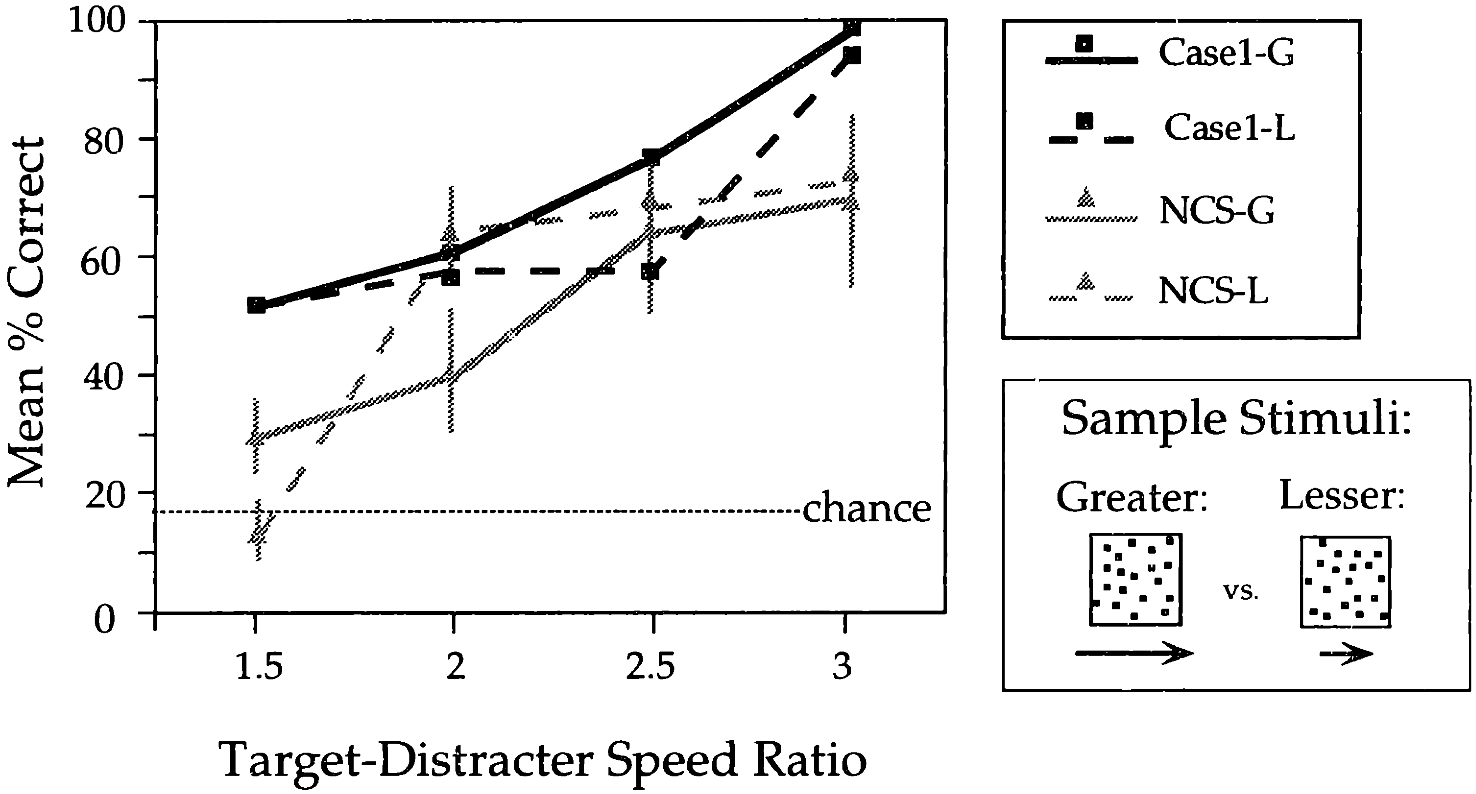

Figure 4. Case 1 shows normal performance on G and L discriminations of speed of motion. The performance of Case 1 is compared to NCS (with standard error bars).

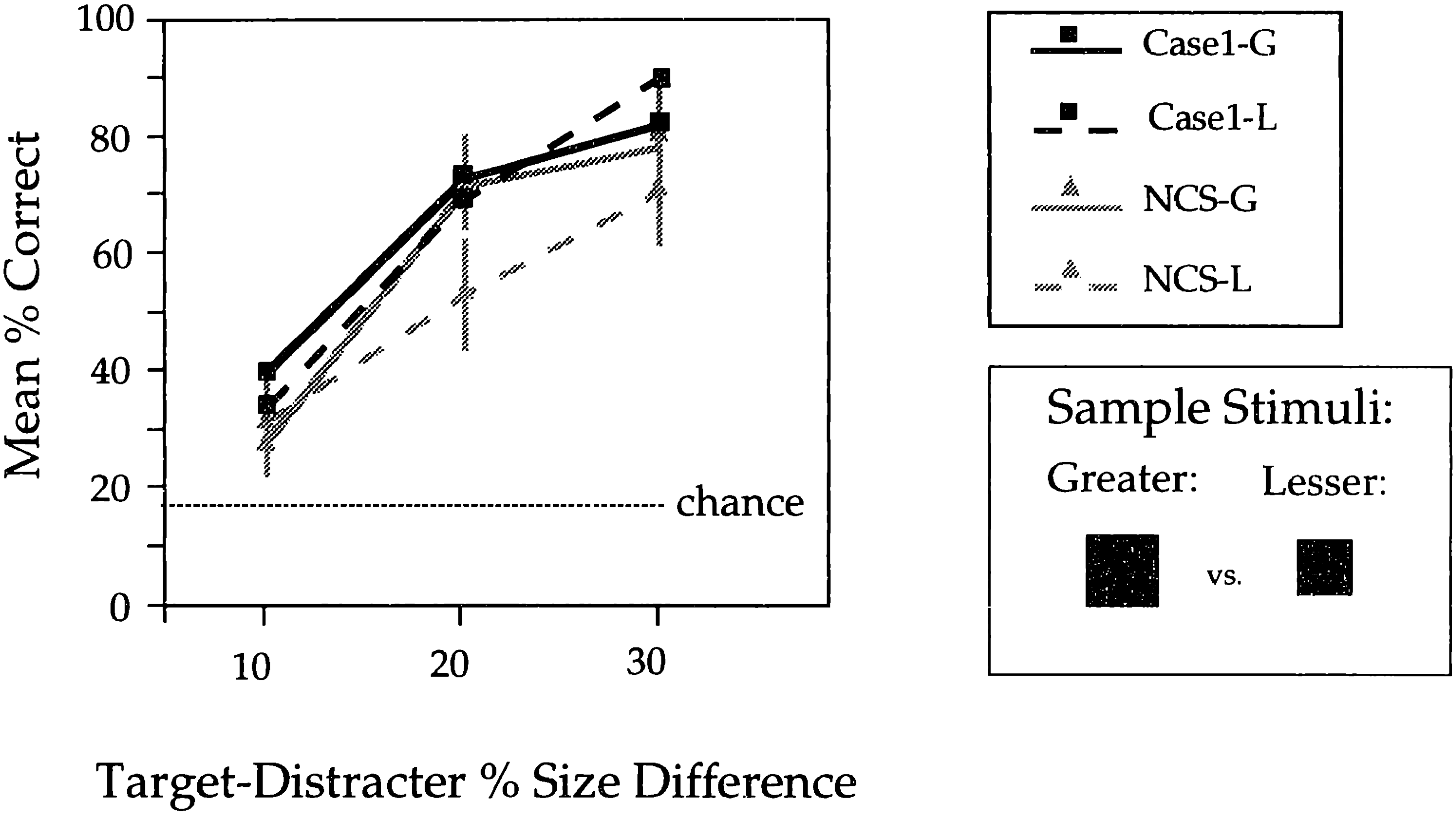

Figure 5. Case 1 shows normal performance on G and L discriminations of size. The performance of Case 1 is shown is compared to NCS (with standard error bars).

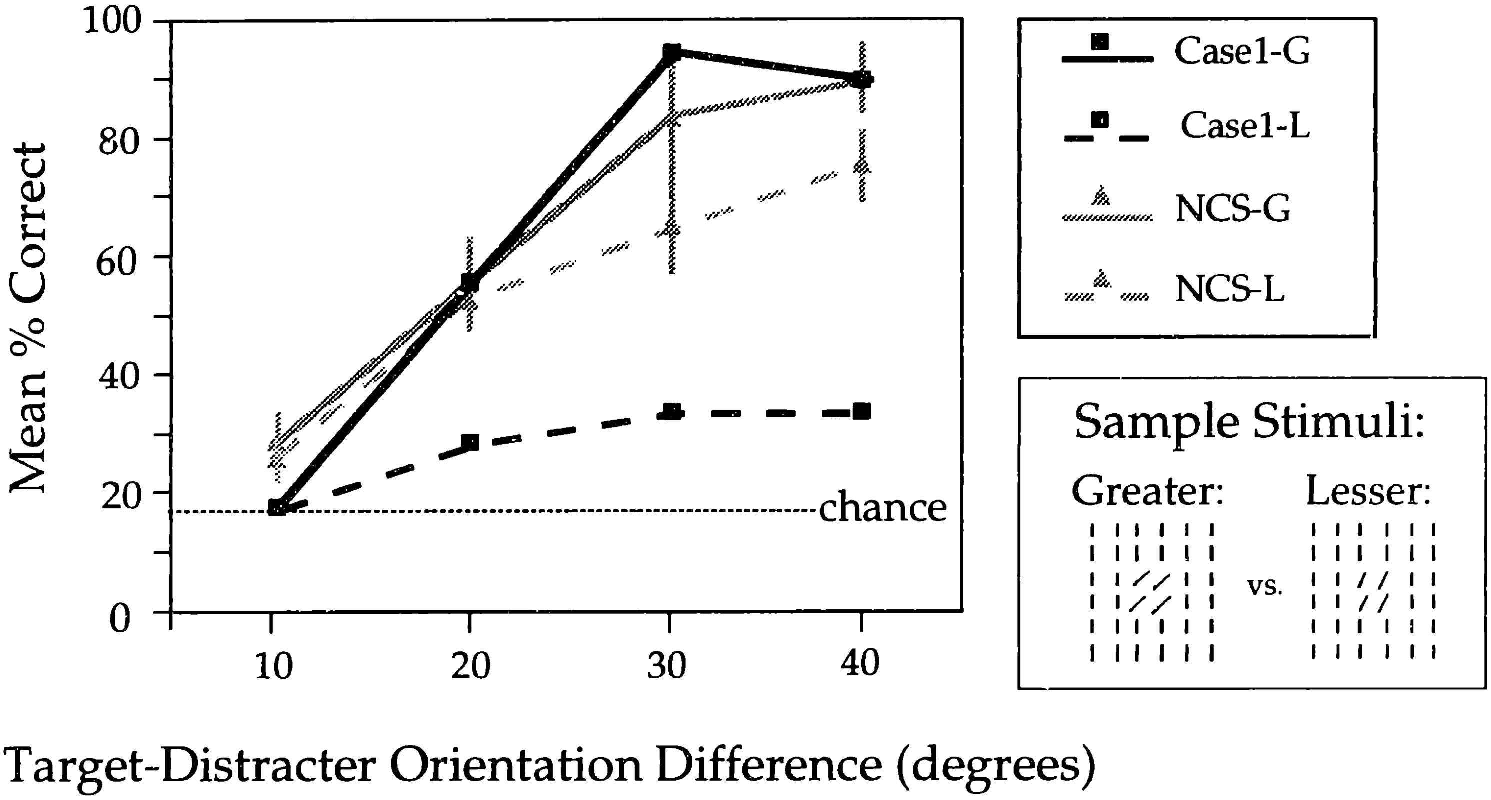

Figure 6. Case 1 shows impaired performance on L (but not G) discriminations of oriented texture. The performance of Case 1 is compared to NCS (with standard error bars).

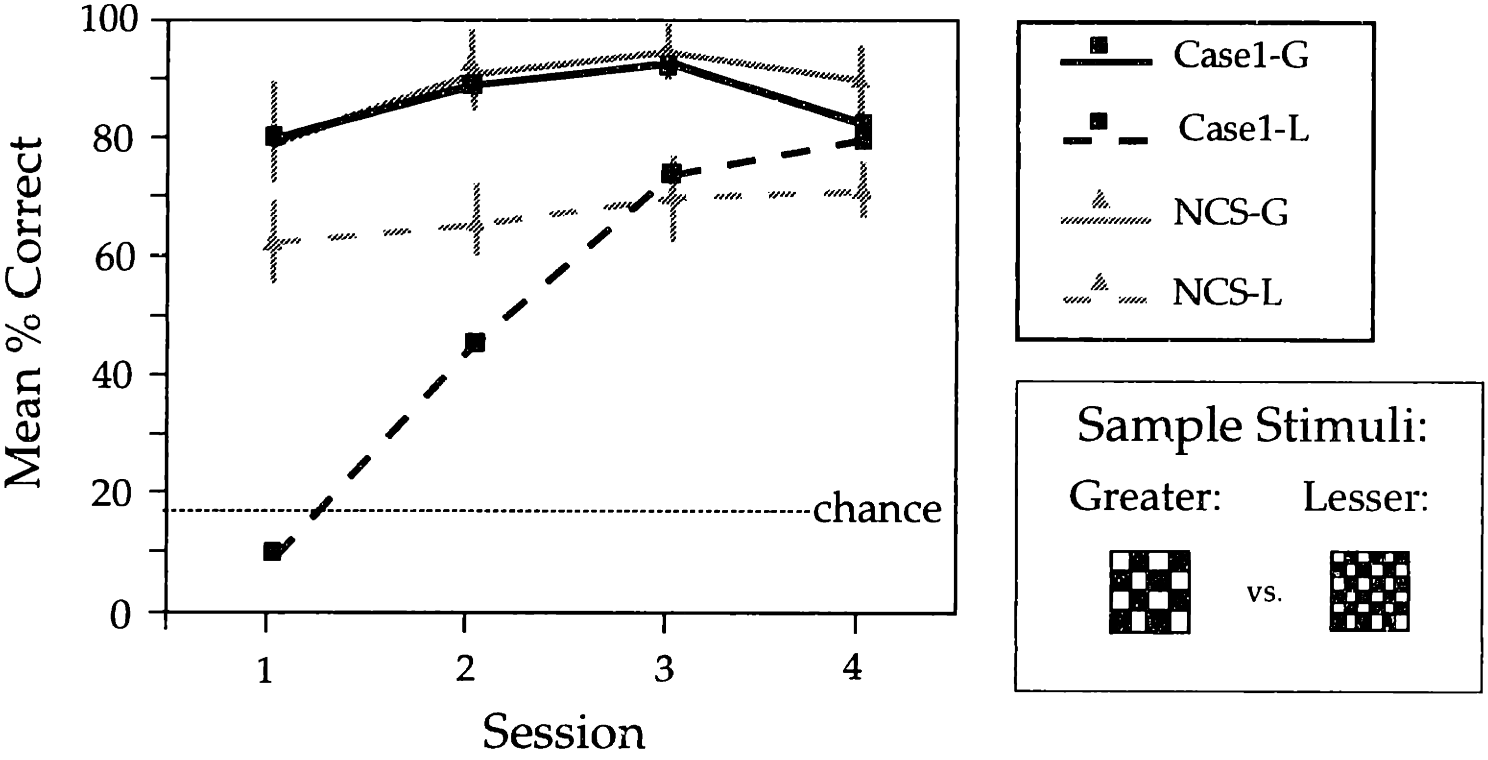

Figure 7. Case 1 shows improvement with practice for discriminations of L patterned targets. The performance of Case 1 is compared to NCS in gray (with standard error bars). Each session consisted of 96 trials, all administered on the same day.

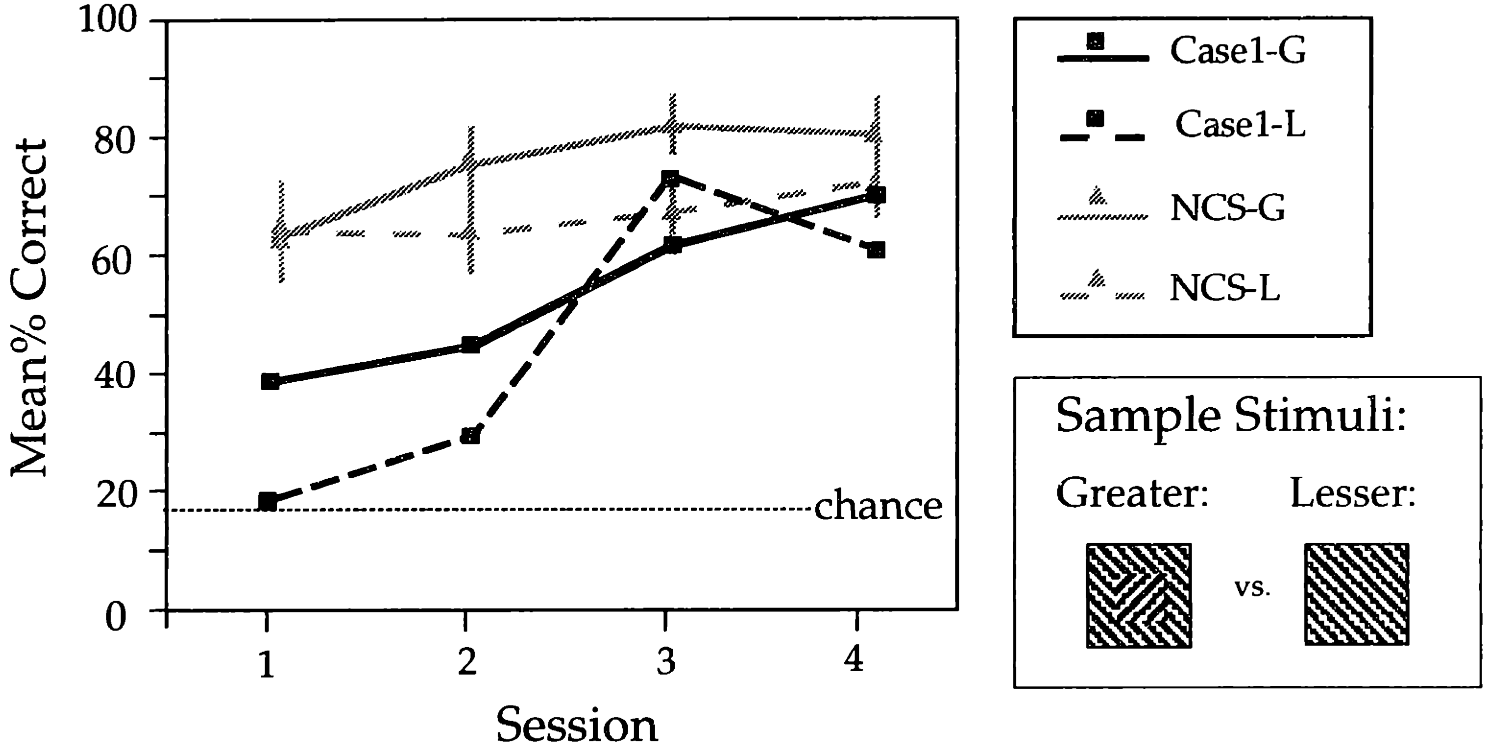

Figure 8. Case 1 shows improvement with practice for discriminations of L and G patterned targets. The performance of Case 1 is compared to NCS (with standard error bars). Each session consisted of 96 trials, all administered on the same day.

Recognition Memory After Anterior Temporal Lobectomy

The deficit in visual recognition and recall memory for complex visual patterns after right anterior temporal lobectomy (ATL) is well established (Jones-Gotman, 1986b; Kimura, 1963; Milner, 1960; Milner, 1968). The influential studies of Brenda Milner and her colleagues have taken advantage of the fact that their patients typically undergo an operation that resects anterior temporal neocortex, the amygdala, and the perirhinal cortex, but varies in the extent of hippocampal removal. A consensus that has emerged over the past 30 years is that some deficits are related to the extent of hippocampal removal while others are not (Smith, 1989a). No perfect system exists for predicting which abilities are hippocampus dependent and which are not. It is evident, however, that the hippocampus is important in tasks with a strong spatial component (Corkin, 1965; Corsi, 1972; Jones-Gotman, 1986a; Milner, 1965; Petrides, 1985). Smith and Milner showed that patients with right anterior temporal lobectomy (RTL) (but not patients with left temporal lobectomy [LTL], right frontal lobectomy [RFL], or left frontal lobectomy [LFL] lesions) are impaired at recollection of the spatial position of an array of objects after a delay, and the impairment depends upon hippocampal removal (Smith & Milner, 1981). A follow-up study, which did not employ a delay period, did not find an impairment for RTL patients, indicating that the deficit was in retrieval not encoding.

A different group of tests has proven to be sensitive to RTL irrespective of the amount of hippocampus removed. It has been proposed that the patterned nature of visual stimuli is important, although this variable has not been explored systematically. One study found that patients with RTL (but not those with LTL, RFL, or LFL) were impaired on a sequential, delayed same/different judgment of nonsense patterns but not colors (Prisko, 1963) cited in (Milner, 1968). Another study assessed recognition memory for different aspects of complex figural scenes (Pigott & Milner, 1993). RTL patients (but not LTL, RFL, or LFL) showed impaired memory for figural detail and spatial composition (arrangement of filled and unfilled space) of a scene. Only RTL patients whose lesions included extensive hippocampal removal displayed a deficit in the spatial location of specific objects. These results are consistent with many reports that have emphasized the important role of the hippocampus in spatial memory in humans (Smith & Milner, 1981) and monkeys (Parkinson, Murray, & Mishkin, 1988). The impaired memory for visual patterns is usually interpreted to result from the neocortical removal because of the lack of correlation with the extent of hippocampal removal, and because of the striking loss of visual recognition memory after bilateral IT lesions in monkeys. Further, a recent report describes complementary pattern and verbal memory loss after right or left neocorticectomy, respectively (Burke & Nolan, 1988).

RTL is known to result in impaired memory for nonverbal stimuli, such as abstract designs, but typically the impairment is seen only when there is a delay between study and test phases of the task (Smith, 1989). Yet, mild perceptual deficits have been reported to occur after RTL, suggesting encoding problems. This finding raises the possibility that an immediate recognition impairment would emerge if stimuli were made more challenging perceptually.

A study by Doyon and Milner (1991b) contrasted "local" and "global" perception. They employed hierarchically structured letter or geometric pattern stimuli, in which a global pattern is made up of many local elements. When asked to identify the local elements, normal subjects are hindered by an inconsistent global pattern. Patients with RTL, however, are less affected by this interference, irrespective of the extent of hippocampal removal. Patients with RTL apparently do not possess an automatic sensitivity to the global aspect of the stimulus as do other groups. These deficits in patients with RTL were interpreted to reflect difficulty in forming a meaningful whole out of discrete parts.

Rock (Rock, 1972) has demonstrated that normal subjects show better recognition memory for subtle changes in the contour of an open line segment than for the same contour when it is part of a closed figure. Presumably, the subtle contour change is rendered less salient when global aspects (such as inside/outside relations, concavities, and convexities) are created by connecting the ends of the line segment. Other studies have indicated that the temporal lobe may be critical for abstracting global and closure properties from patterned stimuli (Mooney, 1956; Doyon, 1991b).

In Experiment 1, we administered a recognition memory test inspired by Rock's 1972 study. Given that previous studies suggest that subjects with RTL lack a normal sensitivity to the global features of abstract nonverbal figures, we predicted that subjects with RTL would show less interference from global features, and thus a smaller decrement in memory for open versus closed figures. Such stimuli seemed like good candidates to create a test of immediate recognition memory for subjects with RTL that had high encoding demands. Additionally, we constructed the test such that it was challenging even for normal subjects. As a reference point, we also administered two tests that have been used to dissociate the memory deficits resulting from left and right ATL in previous studies (Kimura, 1963, Warrington, 1984). In Experiment 2, we administered another test of recognition memory for nonverbal figures that allowed (a) the use of a large number of precisely controlled abstract figures, and (b) comparison between simultaneous, immediate, and delayed recognition memory performance.

EXPERIMENT 1

Methods

Subjects

The subjects were 18 patients with unilateral anterior temporal-lobe resection to treat intractable epilepsy. Normal control subjects (NCS) who did not differ with respect to age ($p = 0.994$; $F[1,32] = 0.1$) or education ($p = 0.720$; $F[1,32] = 0.3$) from the resection patients were also tested for comparison (Table 1). Nine patients underwent surgery on the left side (LTL), while 9 patients had surgery performed on the right side (RTL). The operation included removal of anterior temporal neocortex, peri- and entorhinal archicortex, amygdala, and part of the hippocampus. Resection size was documented in operative reports for lateral neocortex and for mesial structures (Table 2). T-tests showed that the size of the medial excision did not differ between the LTL and RTL groups ($p = 0.2$), whereas the lateral excisions in the RTL were significantly larger than in the LTL group ($p = 0.002$). At the time of testing, the patients varied in time elapsed since operation with a range of 1 to 7 years. The LTL and RTL groups did not differ with respect to time elapsed since operation ($p = 0.7$). All patients were seizure free, or experiencing only rare seizures, and most were taking therapeutic doses of anticonvulsant medication.

In addition to the subjects with ATL, two other amnesic subjects with temporal-lobe lesions were tested for comparison. H.M. was a 69-year-old amnesic patient, with 12 years of education, who has been well described in previous publications (e.g., Corkin, 1984). He underwent a bilateral medial temporal-lobe resection to treat a seizure disorder in 1953. Since that time, he has manifested a remarkably dense global anterograde amnesia. Case 1 was a 27-year-old women with 14 years of education. She suffered a head injury at the age of 25 after falling from a swing. She had untreated childhood amblyopia. Visual acuity was OD: 16/13+ ; OS: 5/200. Her visual fields were full, but she manifested moderate achromatopsia and prospagnosia. Case 1's memory impairment was mild in comparison with H.M. Unlike H.M. she lived alone, and had a job (teaching photography to children). Like H.M., however, Case 1's amnesia is global and extends to both verbal and nonverbal material . On the Wechsler Adult Intelligence Scale - Revised (WAIS-R; Wechsler, 1981), H.M. had a Verbal IQ (VIQ) of 91, a Performance IQ (PIQ) of 103, and a Full

Scale IQ (FSIQ) of 94[1]. On the Wechsler Memory Scale - Revised (WMS-R; Wechsler, 1987) H.M. had a General Memory Index (GMI) of 69. Case 1's VIQ was 98, her PIQ was 121, her FSIQ was 107, and her GMI was 98. A measure of memory loss is obtained by calculating the difference between subjects' FSIQ and GMI. H.M.'s FSIQ - GMI = 25, whereas Case 1's FSIQ - GMI = 9.

Recent MRI scans indicated that H.M.'s temporal-lobe lesion included the medial temporal pole, most of the amygdaloid complex, and all of the entorhinal cortex bilaterally. In addition, the uncal hippocampus and the anterior 2 cm, approximately, of the dendate gyrus, body of the hippocampus, and subicular complex were removed. The posterior 2 cm, approximately, of these fields were spared, but appeared atrophic. The rostral, temporal polar portion of the perirhinal cortex was removed, but some of the ventral perirhinal cortex appeared to be intact. The parahippocampal gyrus appeared to be only slightly damaged, and only at the rostral level.

In contrast to H.M., clinical MRI brain scans in Case 1 indicated that the inferior and middle temporal neocortical gyri were missing bilaterally from the uncal hippocampal level to the posterior hippocampal level with encroachment into the temporal stem. The lesion was larger on the right side extending into the temporal pole, and including the anterior amygdala. Unlike H.M., medial temporal-lobe structures appeared to be spared, except for a portion of the right amygdala. The inferior horn of the lateral ventricle was moderately enlarged on the right, and slightly enlarged on the left. Lacunar lesions were noted in the nucleus basalis/basal forebrain area Finally, a small lesion was seen in left orbital frontal and ventrolateral frontal cortex, and a small lesion in the right temporoparietal white matter.

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[1] It should be noted that previous publications (e.g., Corkin, 1984) have reported H.M.'s IQ scores for an older version of the Wechsler Adult Intelligence Scale, which is known to be easier than the revised version reported here. We wish to make clear that H.M.'s IQ has not decreased since previous reports.

All testing was conducted at the MIT Clinical Research Center (CRC). All subjects gave informed consent to the testing. Concurrent with the vision testing, all patients and control subjects received a physical examination in order to ensure that they met the inclusion and exclusion criteria, and to document retino-calcarine abnormalities. The physical examination included funduscopy, evaluation of fixation, pupillary function, extraocular movement, and visual fields by response to confrontation.

Five of the LTL subjects and 4 of the RTL subjects also received a neuro-ophthalmological examination performed at the Massachusetts Eye and Ear Infirmary by Dr. Joseph F. Rizzo. It included applanation tonometry to detect glaucoma and nonglaucomatous ocular hypertension; examination of the anterior segment and lens to detect and describe cataract and other lens opacities; determination of refractive error to ensure appropriate correction; funduscopy to inspect the retina and optic nerve; evaluation of fixation; pupillary function; extraocular motility; and Snellen acuity. Formal Goldman perimetry was performed to detect and delineate field defects on confrontation testing. Patients judged to have significant ocular disease, such as glaucoma, cataracts, and macular degeneration, or a corrected Snellen acuity of worse than 20/50 were excluded from the study. All subjects demonstrated a corrected near Snellen acuity of 20/30 or 20/20.

Of the 4 subjects with RTL, 2 subjects demonstrated a history of "lazy left eye" or amblyopia. Accordingly, visual acuity was reduced unilaterally, and stereopsis was poor or absent. The amblyopia was not judged to be related directly to the surgical procedure. The other 2 subjects with RTL had a normal neuro-ophthalmological examination. Of the 5 subjects with LTL, 2 had a normal examination. One subject was judged to have a "monofixation syndrome" in the left eye, which is a subtle form of strabismus with subsequent loss of stereopsis.

Finally, the 2 other subjects with LTL displayed some optic neuopathy (moderate constriction and pallor of optic nerves) thought to be related to a period of high intracranial pressure early in life. One of these 2 subjects also had a history of "lazy right eye" that lead to strabismic surgery at age eight. We considered the optic abnormalities found in the subjects with ATL a possible confound in the attribution of visual deficits to ATL. The results of this study are interpreted with this consideration in mind.

Test Materials and Procedures

Rock Figures. Stimuli consisted of 2-dimensional abstract designs of two types. One category of figures consisted of curved line segments resembling 'squiggles.' The second category of figures was created by connecting the ends of the squiggles to create a closed figure (Figure 1). There were 16 sets of these 2 categories, which comprised the set of 32 "base objects" (Figure 2). Each of these base figures was used to construct three comparison figures. For each figure, in each category, one local concavity or convexity was enlarged either a small, medium, or large amount, corresponding to difficulty levels of hard, medium, and easy. Each of the three comparison objects was paired with its corresponding base object, so that in the total of 96 comparisons, each base object appeared 3 times and each of the three comparison objects appeared once. It was randomly determined whether the base object or one of its comparison objects would appear as the initially presented target (Figure 3). For each of the 16 stimulus sets, six comparisons (two categories x three difficulty levels) were made, making it theoretically possible for subjects to learn which local contour was critical for any given test object.

Subjects' immediate recognition memory was assessed with a two-alternative match-to-sample procedure. Images were presented on the screen of an Apple Macintosh II computer, using software developed in our laboratory. Subjects sat 14 in. in front of the computer screen in a dimly lit room. They were told that they would be presented with a complex figure, that would appear for 4 sec. They were asked to study and try to remember the figure. When the target stimulus disappeared, after a delay of 2 seconds, two figures appeared on the screen side by side. One of them was the figure they had just seen, and the other was different from, but similar to, the first. They indicated the one they had just seen by pressing either a key on the left if it was the one on the left, or a key on the right if it was the one on the right. There was no time limit to decide; subjects were instructed to make their best guess when unsure. They rested at several points during the test, indicated by a "please rest" screen. The test was administered in two parts, each of which used eight base-figures in 48 different comparisons. Trials were pseudorandomly organized so that the same figure was not presented twice in succession. There was no practice set. Subjects usually required 1 hr. to complete the entire procedure.

Warrington's Immediate Recognition Test. This test was administered twice, first with nonverbal, and then with verbal materials. The study materials consisted of two booklets, one with 50 black and white photographs of Caucasian men, one with 50 common four letter words. Each page contained either a face or a word. The experimenter displayed each page in the study booklet for 3 sec. Subject were instructed to say "yes" if they thought that the face (or word) was pleasant, or "no" if the face (or word) was not so pleasant. Subjects were told that there were no right or wrong answers, but that a judgment was needed for each face (or word). In the test phase, face recognition was tested with a test booklet in which each of 50 pages contained a pair of faces, one seen previously, one seen for the first time. For the word test, the test card contained 50 pairs of words, one seen previously, one seen for the first time. Immediately after viewing the study booklet, the subjects were given the recognition booklet or card and were asked to indicate, orally or by pointing, which face (or word) had been seen previously.

Recurring Figures Test. The stimuli consisted of two decks of index cards. For the verbal version, 144 cards (and 10 practice cards) contained either a four letter common word, a three digit number, or a three letter nonsense syllable. Twelve of the cards (4 words, 4 nonsense syllables, and 4 digits) from the first 24 cards reappear with 12 new cards in each of five blocks. In the nonverbal version 160 cards (and 10 practice cards) contained either an regular geometric figure or an irregular nonsense figure (squiggle). Four nonsense and 4 geometric designs from the first 20 cards in each of seven blocks. After a short practice series, subjects were presented with each card in the deck for 3 sec. each. Successive presentations of the same card were separated by 30 to 90 sec. To each card, subjects said "yes" if they thought the card had appeared previously in the deck, or "no" if they thought the card had not appeared previously.

Results and Discussion

Rock Figures. We performed a mixed within and between subjects ANOVA with the factors: group (LTL, RTL, NCS), difficulty (3 levels), and condition (open vs. closed figure). We found significant main effects for difficulty ($p = 0.0001$; $F[2,60] = 47.2$) and condition ($p = 0.0003$; $F[1,30] = 16.53$), but not group ($p = 0.467$; $F[2,30] = 0.8$). No interactions were significant. Thus, we did not to confirm that hypothesis that subjects with RTL would show impaired immediate recognition memory when encoding demands were particularly high. We did confirm our expectation that the open condition is easier than the closed condition. Interestingly, it is the easier levels of open condition that elicited the largest (although not significant) differences between the performance of the ATL and NCS groups. Similarly, H.M. showed a deficit for the open figures at the medium and easy levels of difficulty (>2

SD of the NCS); in all other conditions he was within 1 SD of NCS. Case 1's performance was within 1 SD of the NCS, except for a score which slightly exceeded 1 SD for the most difficult closed figures.
(Figure 3, 4).

Warrington's Immediate Recognition Test. A mixed within and between subjects ANOVA for subjects with LTL, RTL, and NCS showed a significant main effect of group (*p* = 0.002; *F*[2,34] = 11.18) and condition (faces versus words) (*p* = 0.001); *F*[1,34] = 29.0), as well as a significant interaction between diagnosis and condition (*p* = 0.001; *F*[2,34] = 13.3). Planned contrasts showed that LTL depressed word (*p* = 0.0001), but not face recognition, whereas RTL depressed face (*p* = 0.0001), but not word recognition. These results, therefore, replicate the well-documented double dissociation of verbal versus nonverbal memory loss after LTL and RTL respectively. In contrast to the subjects with unilateral lesions the performance of H.M. and Case 1 were depressed relative to NCS for word (> 17 and 2 SD of the NCS, respectively) and face (> 4 and 3 SD of the NCS, respectively) recognition (Figure 5). Unlike the Rock Figures Test this test elicited impairments in the RTL and LTL groups as well as Case 1. The critical difference is the presence of interference effects between stimuli studied during the same period. Such interference effects appear necessary to challenge the retention abilities of the subjects with mild memory loss sufficiently to demonstrate an impairment.

Recurring Figures Test. The mixed within and between subject ANOVA for subjects with LTL, RTL, and NCS indicated a significant effect of group (*p* = 0.035; *F*[2,35] = 3.7) and of condition (verbal versus nonverbal) (*p* = 0.0001; *F*[1,35] = 22.0). The interaction between condition and group just missed significance (*p* = 0.074); *F*[2,35] = 2.8). Planned contrasts showed that LTL depressed verbal (*p* = 0.043) and nonverbal (*p* = 0.048) recognition, while RTL depressed nonverbal recognition with borderline significance (*p* = 0.095), but not verbal recognition. The scores for H.M.

and Case 1 were inferior to both unilateral temporal-lobe groups for both verbal (> 6 and 5 SD of the NCS, respectively) and nonverbal (> 3 and 2 SD of the NCS, respectively) conditions (Figure 6). This test provided a dissociation between normal verbal and impaired nonverbal recognition for RTL, but did not provide the reverse dissociation for our LTL group. It is unclear why we did not find a dissociation for the LTL group, but it may be related to our modest group size. The global amnesia of H.M. and Case 1 were documented by their impairments for the verbal and nonverbal condition. Like Warrington's test the potential for interference between stimuli studied during the same period was probably critical for revealing the deficits that follow ATL. The results of Experiment 1 are discussed further in the General Discussion section.

EXPERIMENT 2

Methods

Subjects

The subjects in this experiment were the same as those in Experiment 1, except that there was 1 less subject with right anterior temporal lobectomy and 15 new NCS (Table 3, 4). The groups did not differ significantly with respect to age (p= 0.887; $F[1,32] = 0.1$) or education (p= 0.455; $F[1,32] = 0.8$).

Apparatus and Stimuli

Images were presented using a Iris Silicon Graphics computer with software developed at MIT (Bülthoff & Edelmann 1992). Stimuli consisted of 3-dimensional abstract designs resembling a paper clip unbent to make a meaningless sculpture, called 'wire figures' (Figure 7). These figures always contained 7 segments and were generated mathematically by selecting vertices in a 3-dimensional space, with constraints that excluded intersection of segments and extremely sharp angles between successive segments. Fifty such 'base figures' were created for each of 3 tests that differed in the length of delay between the study and test phases of the experiment.

Each of these base figures was used to construct three comparison figures (Figure 8). For each figure, noise was added to the x, y, or z, coordinate of the vertices. The amount of noise varied from 4% of the average segment length to 40% of the average segment length (in increments of 4) to create 10 levels of difficulty. For each of 50 trials, all of the three comparison objects were shown with their corresponding base object.

Procedure

Subjects' recognition memory was assessed with a four-alternative match-to-sample procedure. Subjects sat 52 in. in front of the computer screen in a dimly lit room. They were told that they would be presented with 5 wire figures. One figure appeared in the center of the screen, and 4 choices appeared in the corners of the monitor (which were numbered 1 -4). The subjects' task was to indicate the corner object that best matched the sample object in the center of the screen.

The test was administered 3 times with different stimuli. First, the sample and 4 choices were presented simultaneously. Second, version the sample stimulus appeared for 4 sec. and then disappeared. After a delay of 2 sec., the four choices were presented. Third, the delay between presentation of the sample and choices was increased to 15 sec. During the delay, the subject and experimenter simply waited silently in front of the blank computer screen. There was no time limit to respond, and subjects were instructed to make their best guess when unsure. They rested at several points during the test. There was no practice set. Subjects usually required 1 hour and 30 min. to complete the entire procedure.

Results and Discussion

We computed a mixed within and between subject ANOVA with factors of group (LTL, RTL, NCS); noise (with 10 levels); and delay (0 sec. versus 15 sec.). We found no main effect of group ($p = 0.801$; $F[2,47] = 0.223$), but we did find a significant effect of noise level ($p = 0.0001$; $F[9,47] = 15.5$) and delay ($p = 0.0001$; $F[2,47] = 49.5$). Predictably, performance decreased with increased noise and delay (Figure 9). The task demands were not sufficient to demonstrate deficits in the RTL group even with a delay period of 15 sec. and stimuli that were novel and very difficult to name verbally. Previous experiments that have employed comparable delay periods, found impaired memory for faces and complex scenes, but importantly those experiments required subjects to study many stimuli during the test phase before recognition was tested. Subjects with ATL were not sufficiently impaired for performance to be affected when stimuli are studied one at a time.

By contrast, the performance of Case 1 and H.M. did not follow the normal pattern (Figure 9). H.M., in particular, manifested a clear depression of accuracy when the delay was inserted between study and test phases, indicative of his striking amnesia. Case 1's performance provided an interesting contrast with that of H.M. In the case of simultaneous matching, her accuracy seemed particularly sensitive to the noise level of the distracters. With a 15 second delay, her performance is remarkably unstable, with little systematic relation to noise level, suggesting that she guessed randomly on many trials.

GENERAL DISCUSSION

This study compared recognition memory after left or right anterior temporal lobectomy. The results did not support our hypothesis that immediate recognition memory would be impaired in the RTL group when stimuli with presumably high encoding demands were used. Our negative results underscore the difficulty of eliciting encoding deficits after RTL, and the lack of any system to predict when such deficits should be apparent. We also tested 2 patients with bilateral lesions in the anterior temporal lobe, who were impaired on many of our tests; their performance provided an instructive comparison. The following discussion reviews our results and relevant past studies with monkey and humans subjects.

Recognition of Verbal and Nonverbal Stimuli

Although we did not find a significant effect of diagnosis for the Rock Figures test, the trends in the data were interesting. First, as predicted, the performance for the open figures was better than that for the closed figures. Second, the largest difference between subjects with right ATL and NCS emerged at the *easier* levels of the open condition. The Warrington Face test (the best discriminator of RTL and NCS groups) is also quite easy for control subjects. It may be the case the differences between subjects with ATL and NCS only emerge at moderate difficulty levels. In contrast, when the task is very difficult both patients and control subjects perform poorly. There may be an optimal level of difficulty where control subjects seem to perform the task relatively automatically and effortlessly, while patients lack this facile performance.

One question is why both left and right ATL subjects were impaired on the non-verbal Recurring Figures test. It seems likely that even for the 'non-verbal' condition subjects employed verbal labeling strategies when they were able to do so. Thus, subjects with LTL may have been at a disadvantage in using that supplemental strategy. The results of the Warrington Recognition test did manifest a typical dissociation between right and left ATL. The face stimuli used in Warrington's test probably elicit less fewer verbal labels than the simple geometric designs used in the Recurring Figures test.

Another question is why the Warrington and Kimura test elicited deficits while the current tests did not. A likely possibility is interference effects from intervening stimuli. For the Warrington test, 50 stimuli are studied, and then recognition of all 50 is tested. The situation is more complex for the Recurring Figures because study and test phases are not strictly separated. Stimuli repeat several times during the test with novel stimuli occurring throughout the test. Nevertheless, both of these older tests require the storage and retrieval of many stimuli concurrently. When we purposely excluded such potential for interference from the Rock Figures test, no significant impairment was found.

Finally the performance of Case 1 and H.M., subjects with bilateral anterior temporal lobe lesions needs to be discussed. Studies in monkeys have determined that bilateral temporal lobe lesions cause much more pronounced effects than unilateral lesions (Chow, 1951; Mishkin & Pribram, 1954). The primary reason for including these subjects in this study was to provide a reference point, and demonstrate that the tests we used were, in fact, sensitive to certain types of brain lesions. H.M. in particular provides a good estimate of the degree to which the tests tap explicit memory functions. He performed poorly on all tests in Experiment 1, and showed a dramatic effect of delay in Experiment 2 . H.M.'s perceptual abilities have always been good (e.g., normal performance on the Mooney Closure Faces test (Milner, 1990)). H.M.'s lesions largely spare the anterior temporal neocortex. Case 1 has demonstrated more perceptual impairments then any other subject in this study, and this is likely related to her bilateral anterior temporal neocortical lesions. Her performance does not provide a clear dissociation of perceptual and mnemonic capacities. Inclusion of her data in Experiment 2 is notable for the less systematic relationship between accuracy and delay, as well as the suggestion of a more dramatic relationship between accuracy and noise level.

Studies of Monkeys with Temporal Lobe Lesions

Cytoarchitectonic experiments have demonstrated that the inferotemporal area of macaque monkeys can be subdivided into a posterior area TEO and a more anterior area TE (Bonin and Bailey, 1947). Removal of one these areas has distinct and predictable results. Lesions confined to area TEO cause deficits in discrimination of patterns and objects (Iwai, 1969; Kikuchi, 1980). TE lesions cause impairment in object recognition memory (Iwai, 1969; Kikuchi, 1980). An influential set of experiments contrasted performance on a simple visual discrimination ("0" pattern versus "+" pattern, one of which is assigned positive reward value) with a concurrent object visual discrimination (20 visual discriminations learned in parallel) (Ettlinger, et al., 1968). The two tasks proved selectively sensitive to TEO versus TE lesions, respectively.

A less cited, but clever dissociation between TEO and TE lesions is provided by Sahgal and Iversen (1978). They used two color match-to-sample tasks that differed only in the number of possible matches and samples. Monkeys with TEO removal had more trouble with an 8 x 4 version. This condition used eight sample colors presented randomly one per trial. The task was to chose the sample from four alternatives (the correct match and three distracters randomly chosen from the set of eight colors). In contrast, TE lesions caused a deficit on a 4 x 8 task. In this case, the sample stimulus was randomly chosen from a smaller set of four colors. The task was to chose the sample from eight alternatives (the full set). The authors assumed that the 8 x 4 and 4 x 8 tasks strained encoding and retrieval components respectively. Finally, other experiments have shown that TEO lesions are more sensitive to stimulus parameters, while TE lesions are more sensitive to interpolated interference and reward/punishment contingencies (Bolster & Crowne, 1978; Gross, Cowey, & Manning, 1971; Manning, 1971a; Manning, 1971b). One particularly critical area for memory function may be anterior ventral TE. Perhaps even more critical is the cortex located anteroventrally from TE, perirhinal and parahippocampal cortex (Meunier, Bachevalier, Mishkin, & Murray, 1993). This cortex provides the major gateway for neural activity from temporal neocortex to the hippocampus.

Electrophysiology studies of memory processes in IT have found that neuronal response reflects both sensory features of a given stimulus as well as stimulus familiarity (Li, Miller, & Desimone, 1993; Miller, Li, & Desimone, 1991). Miller and colleagues have described two parallel memory mechanisms in IT. Many neurons show diminished activity in response to stimulus repetition, regardless of behavioral task. Some neurons display a specific enhancement of activity when presented with a picture that matches one held in memory. Another neural correlate of memory found in IT is activity associated with periods of delay between stimulus presentation and retention assessment in tasks such as delayed match-to sample (Colombo & Gross, 1994; Fuster & Jervey, 1982; Miyashita & Chang, 1988). Although investigators often do not relate the locations of memory sensitive neurons to the border between area TEO and TE, a survey of the literature clearly shows that such neurons have been located in anterior IT (TE).

Studies of Humans with Unilateral Anterior Temporal Lobectomy

A question that still remains embedded in the human literature is whether the impairments observed in memory and perception after right ATL represent one or two underlying deficits. It was originally suggested that these impairments may map on to damage to the medial limbic structures versus neocortex, respectively (Milner, 1968). There is now ample evidence, however, of recall and recognition deficits that do not depend on removal of the hippocampus and surrounding tissue. Yet, the original question still remains, particularly given that RTL patients are said to have a severe loss of visual memory and a milder one in perception. It has been implied that the perceptual difficulties are separate or even secondary to the memory loss. The hypothesis that motivated this study was that the so-called perceptual and mnemonic deficits after ATL are likely to represent the same underlying disruption of brain function, and that their manifestation depends on task demands. However, we actually provided a rather strong dissociation between normal encoding and abnormal retention after ATL. We suggest that human temporal neocortex is organized in a manner analogous to the organization previously discussed in monkey temporal lobe, namely, that the weighting of memory functions to perceptual functions increases as one progresses anteriorly in the visual temporal lobe. The neocortical lesions that result from ATL may not remove cortex that commonly subserves encoding functions. Fortunately for the subjects who undergo the procedure, unilateral ATL seems to disrupt retention moderately and selectively.

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Table 1: Subject Characteristics for Experiment 1

Group	Number of Subjects [M, F]	Mean Age [SD]	Mean Education [SD]
L-ATL	[3, 6]	32.9 [11.9]	14.4 [2.8]
R-ATL	[2, 7]	32.7 [11.4]	14.0 [1.8]
Normal Control	[6, 9]	33.1 [8.3]	14.2 [1.3]

Table 2: Excision Characteristics for Experiment 1

Group	Number of Subjects	Lateral Cortex* [SD]	Mesial Structures* [SD]	Months Since Surgery
L-ATL	9	3.7 [1.2]	5.2 [1.1]	40.4 [27.7]
R-ATL	9	5.6 [0.6]	4.6 [1.3]	34.4 [30.7]

*Measured in cm

Table 3: Subject Characteristics for Experiment 2

Group	Number of Subjects [M, F]	Mean Age [SD]	Mean Education [SD]
L-ATL	[3, 6]	32.9 [11.9]	14.4 [2.8]
R-ATL	[2, 6]	33.5 [11.4]	14.1 [1.8]
Normal Control	[7, 8]	33.1 [9.8]	13.9 [1.1]

Table 4: Excision Characteristics for Experiment 2

Group	Number of Subjects	Lateral Cortex* [SD]	Mesial Structures* [SD]	Months Since Surgery
L-ATL	9	3.7 [1.2]	5.2 [1.1]	40.4 [27.7]
R-ATL	8	5.6 [0.6]	4.8 [1.4]	38.1 [31.2]

*Measured in cm

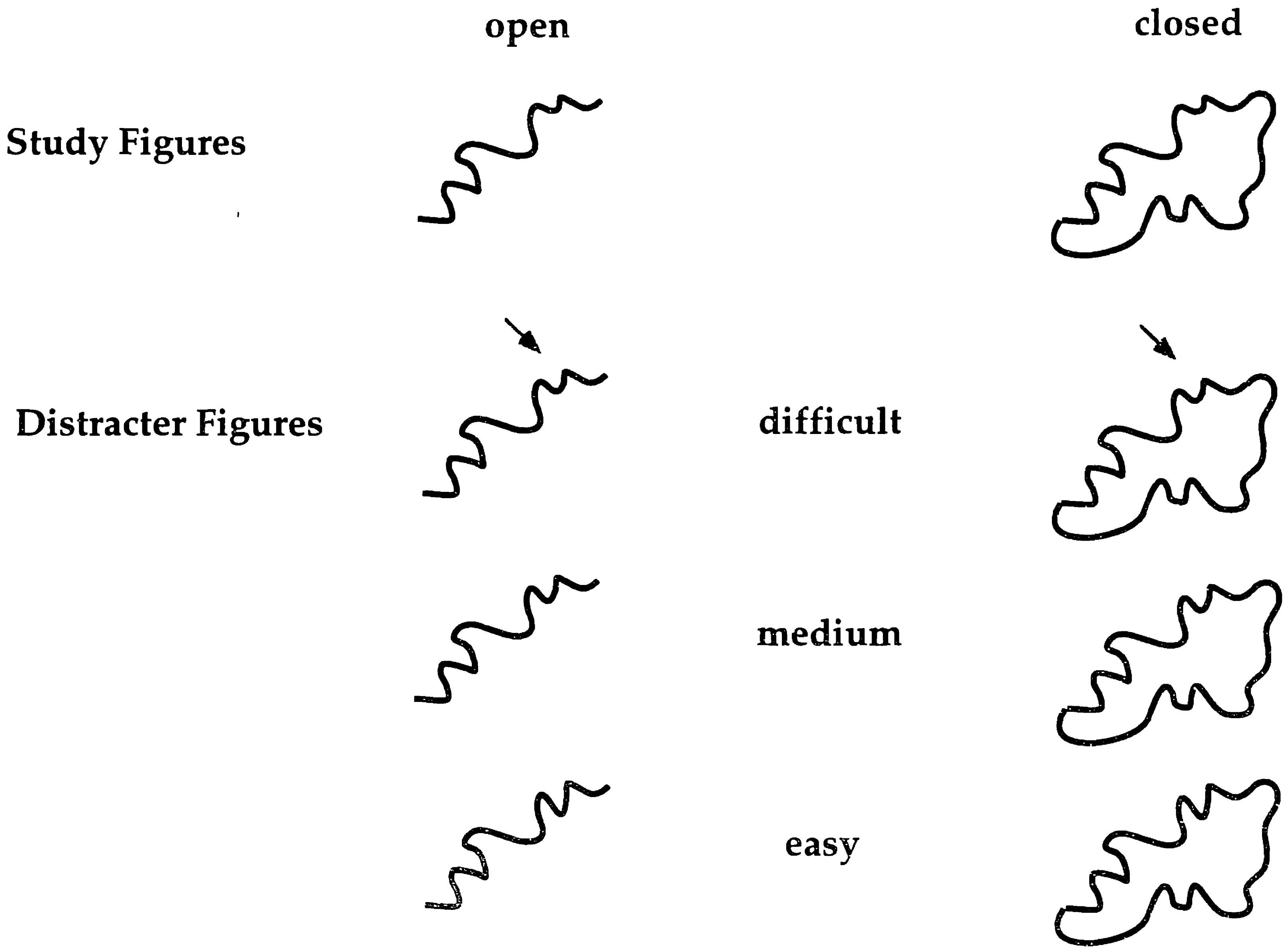

Figure 1. Experiment 1. An example of a set of study figures and corresponding distracter figures. The small-open figure is contained within the closed figure. Each study figure was paired once with each of the three corresponding distracter figures during the test. Arrow indicates area of local difference between study and distracter figures.

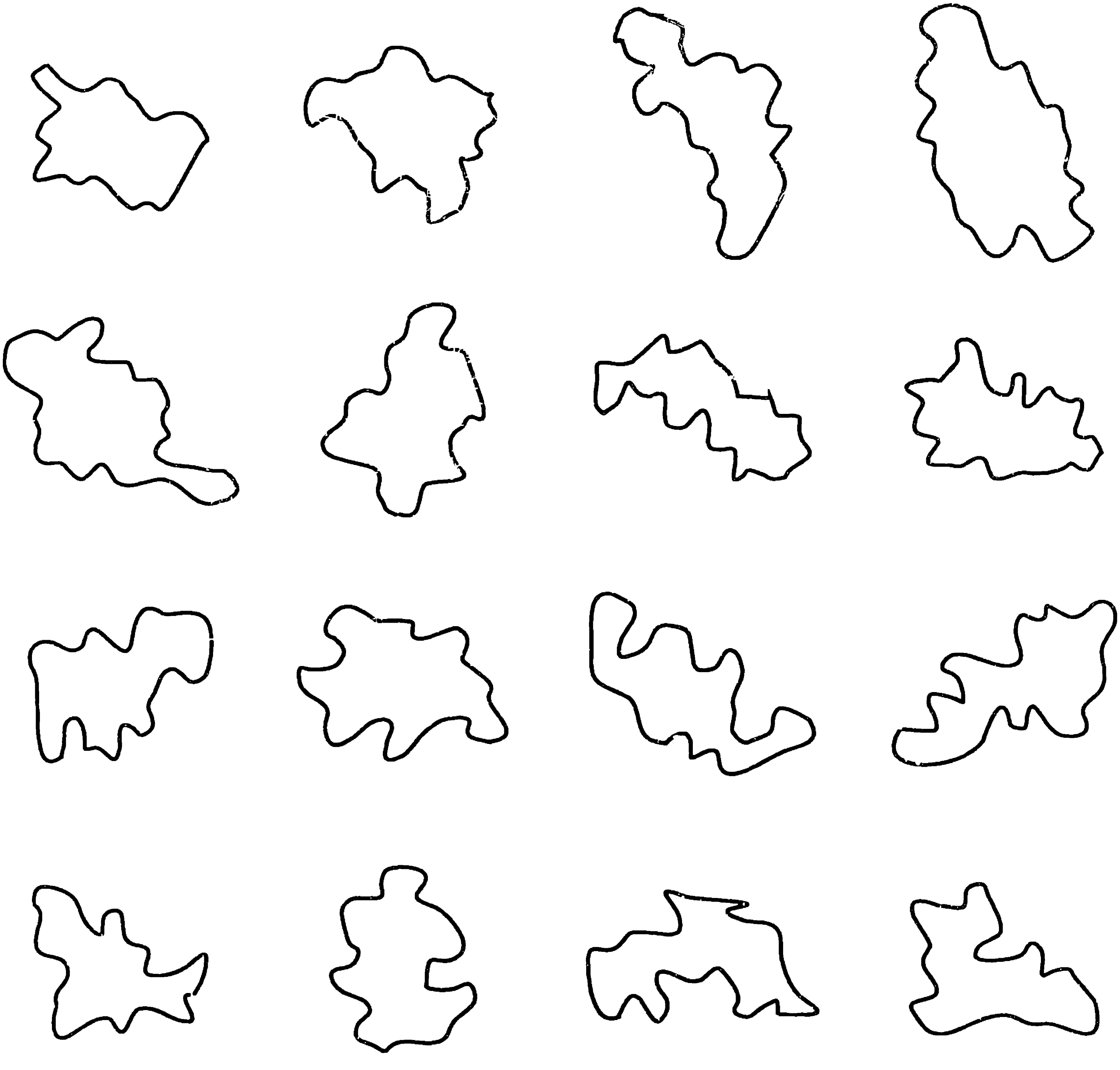

Figure 2. The large-closed category is shown for all 16 figure sets.

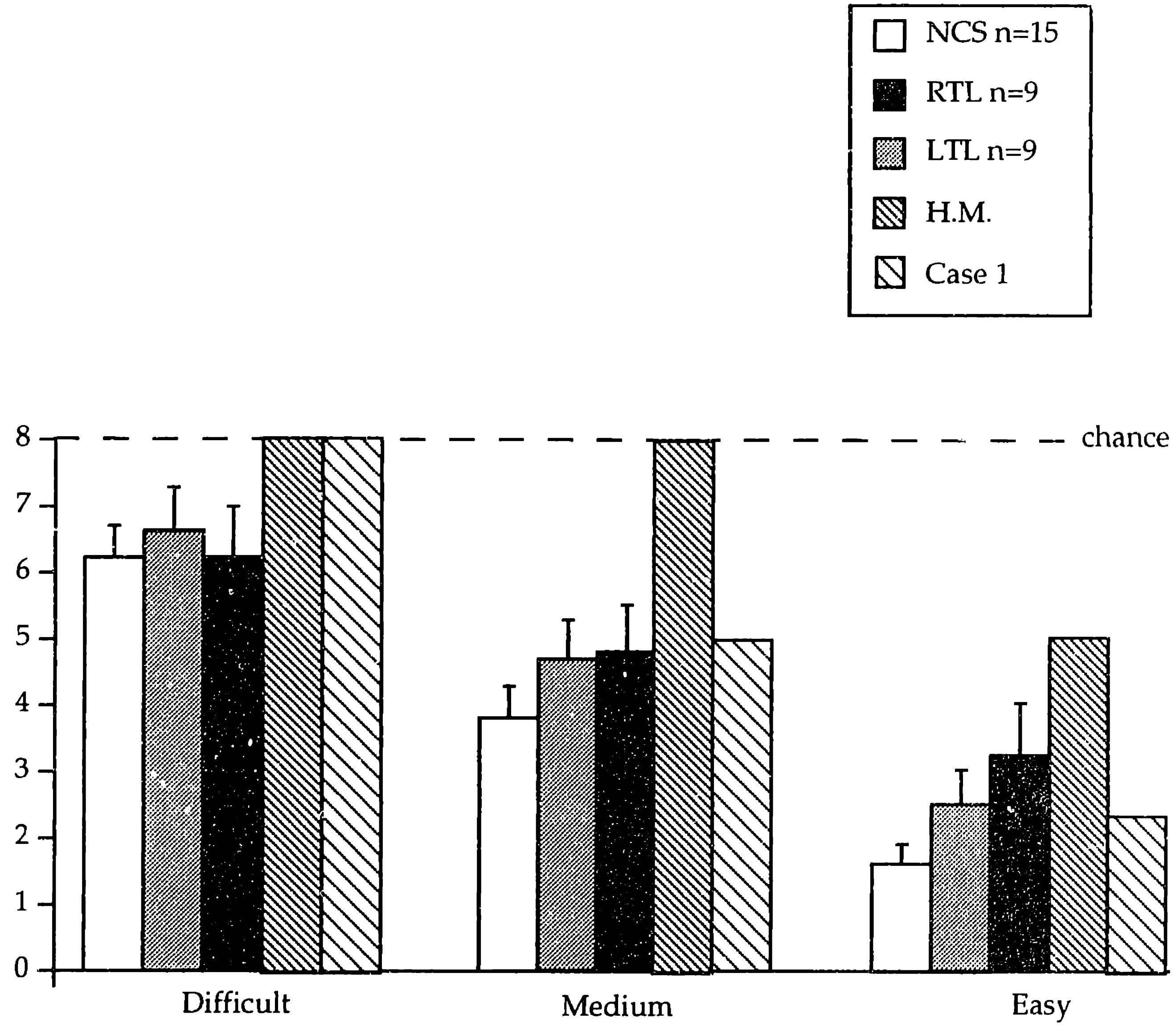

Figure 3. Experiment 1. Immediate recognition of abstract open figures is normal after left and right anterior temporal lobectomy. The scores for H.M. and Case 1 fall within 1 SD of the NCS group, except that the scores for H.M . are > 2 SD below the NCS group for the medium and easy level.

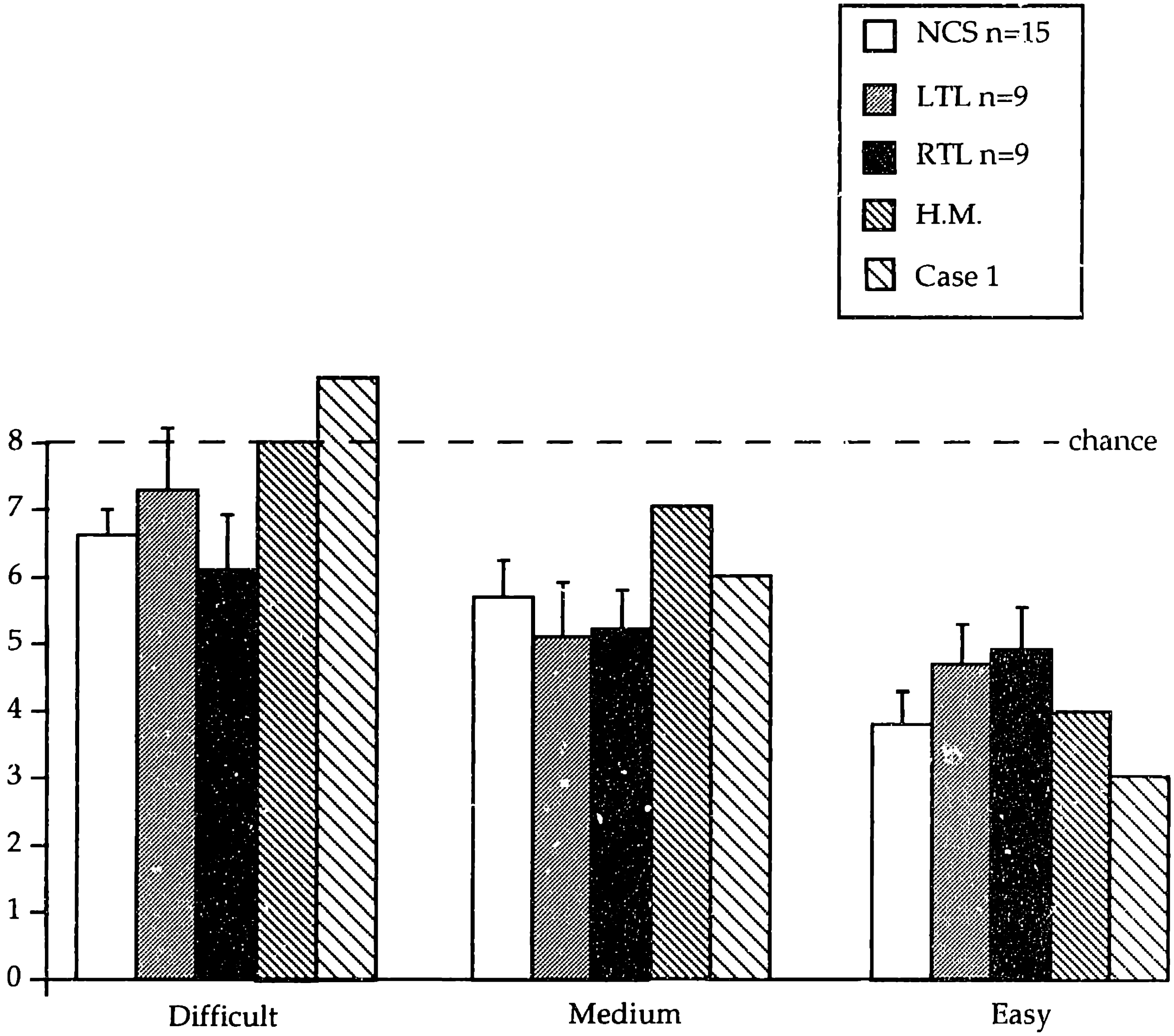

Figure 4. Experiment 1. Immediate recognition of abstract closed figures is normal after left and right anterior temporal lobectomy. The scores for H.M. and Case 1 fall within 1 SD of the NCS group, except that the score for Case 1 slightly exceeds 1 SD for the difficult level.

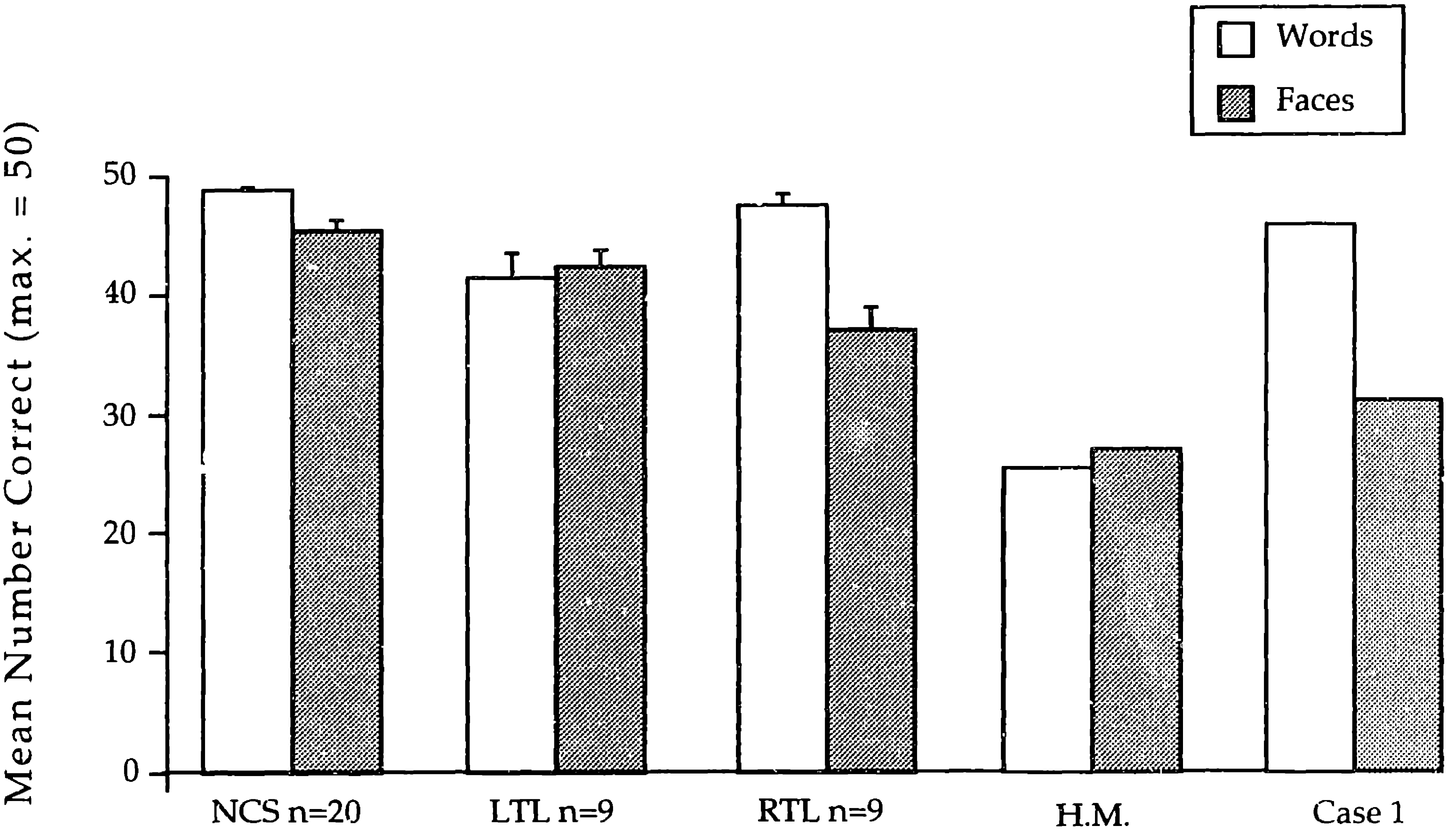

Figure 5. Experiment 1. Warrington's Immediate Recognition Test. Left anterior temporal lobectomy impairs word recognition but not face recognition relative to control subjects. Right anterior temporal lobectomy impairs face recognition but not word recognition relative to control subjects. The scores for H.M. and Case 1 are > 3 SD below the NCS group.

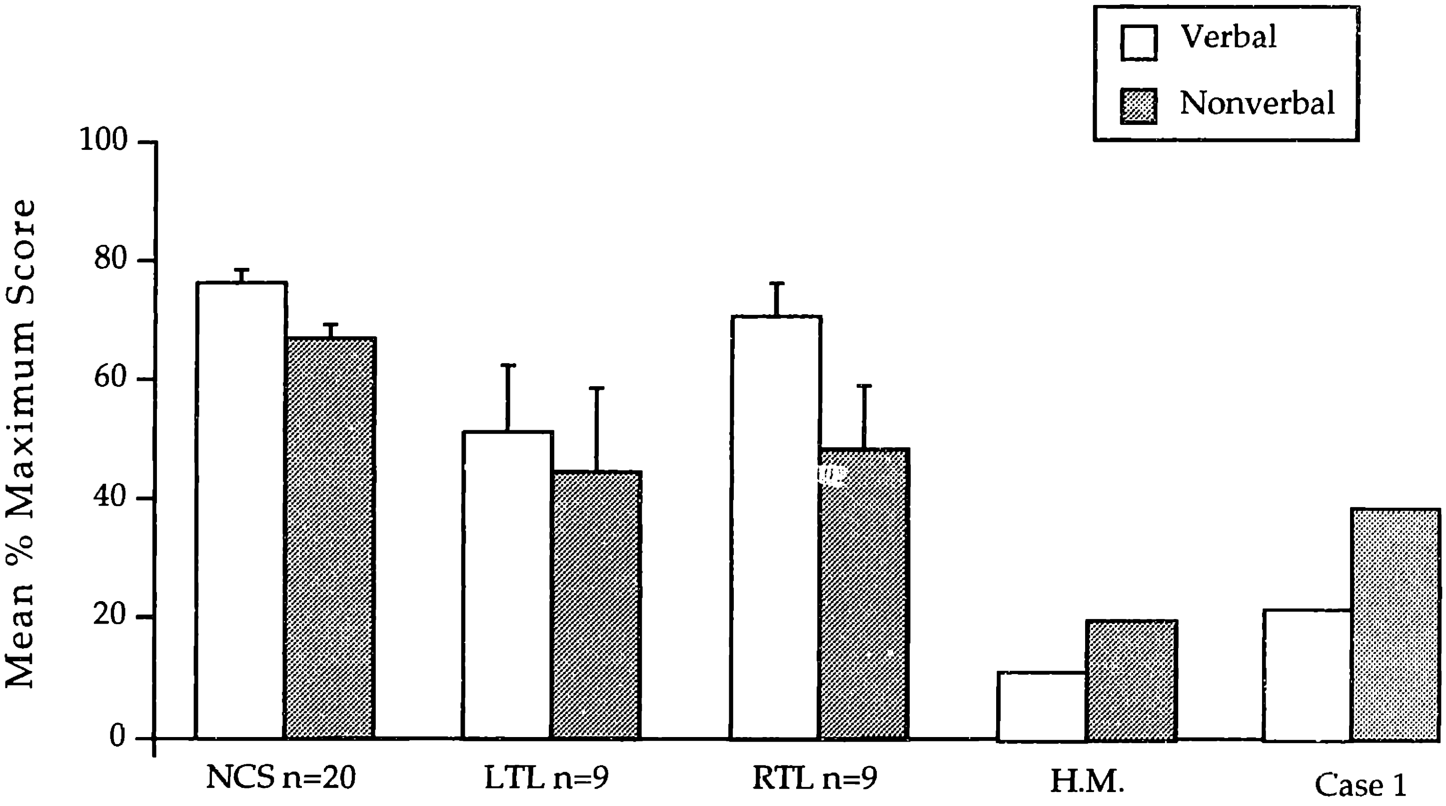

Figure 6. Experiment 1. Recurring Figures Test. Left anterior temporal lobectomy impairs word recognition and design recognition relative to control subjects. Right anterior temporal lobectomy impairs design recognition but not word recognition relative to control subjects. The scores for H.M. and Case 1 are > 2 SD below the NCS group.

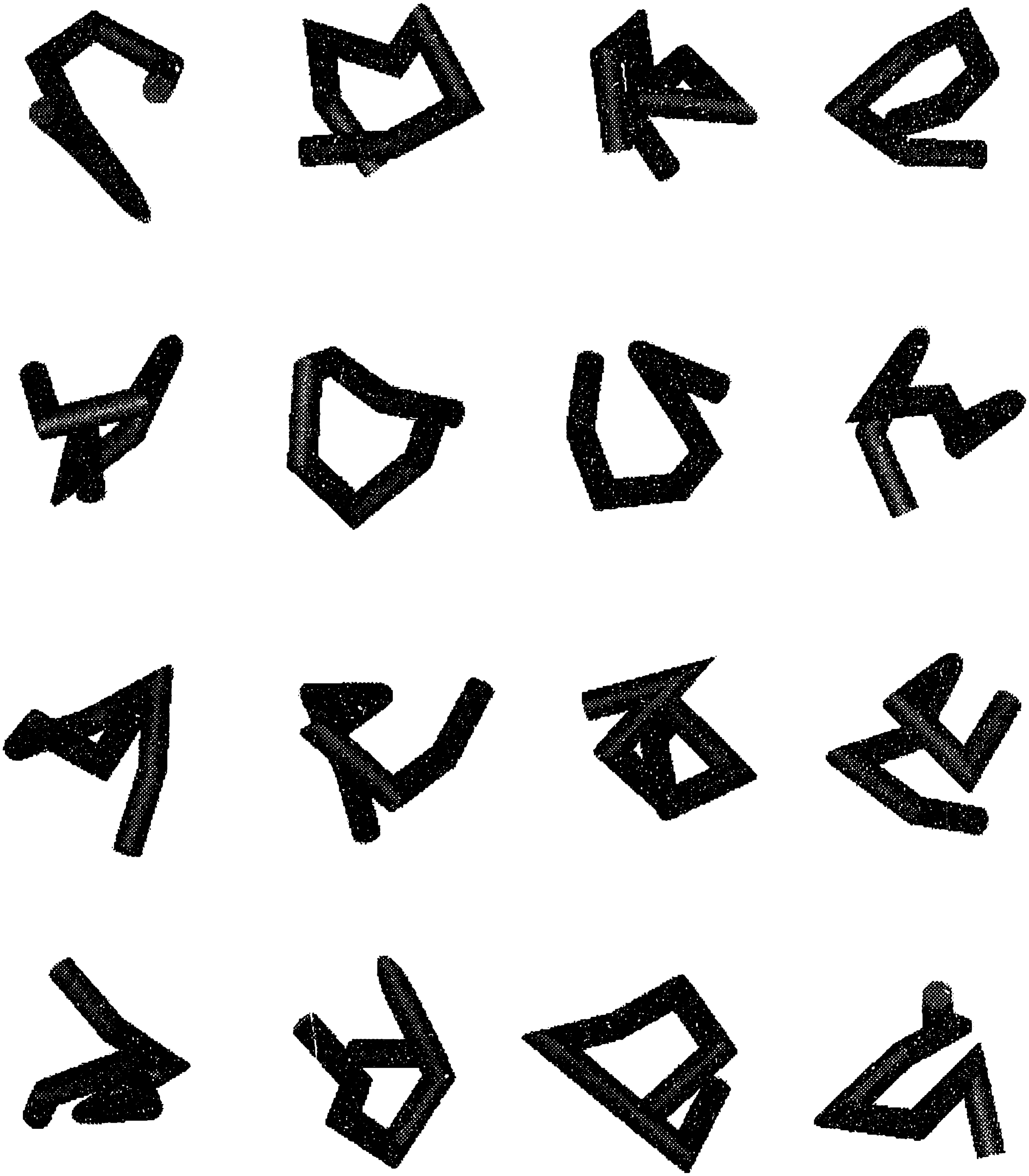

Figure 7. Experiment 2. Sixteen representative study figures selected from the 150 used in the experiment.

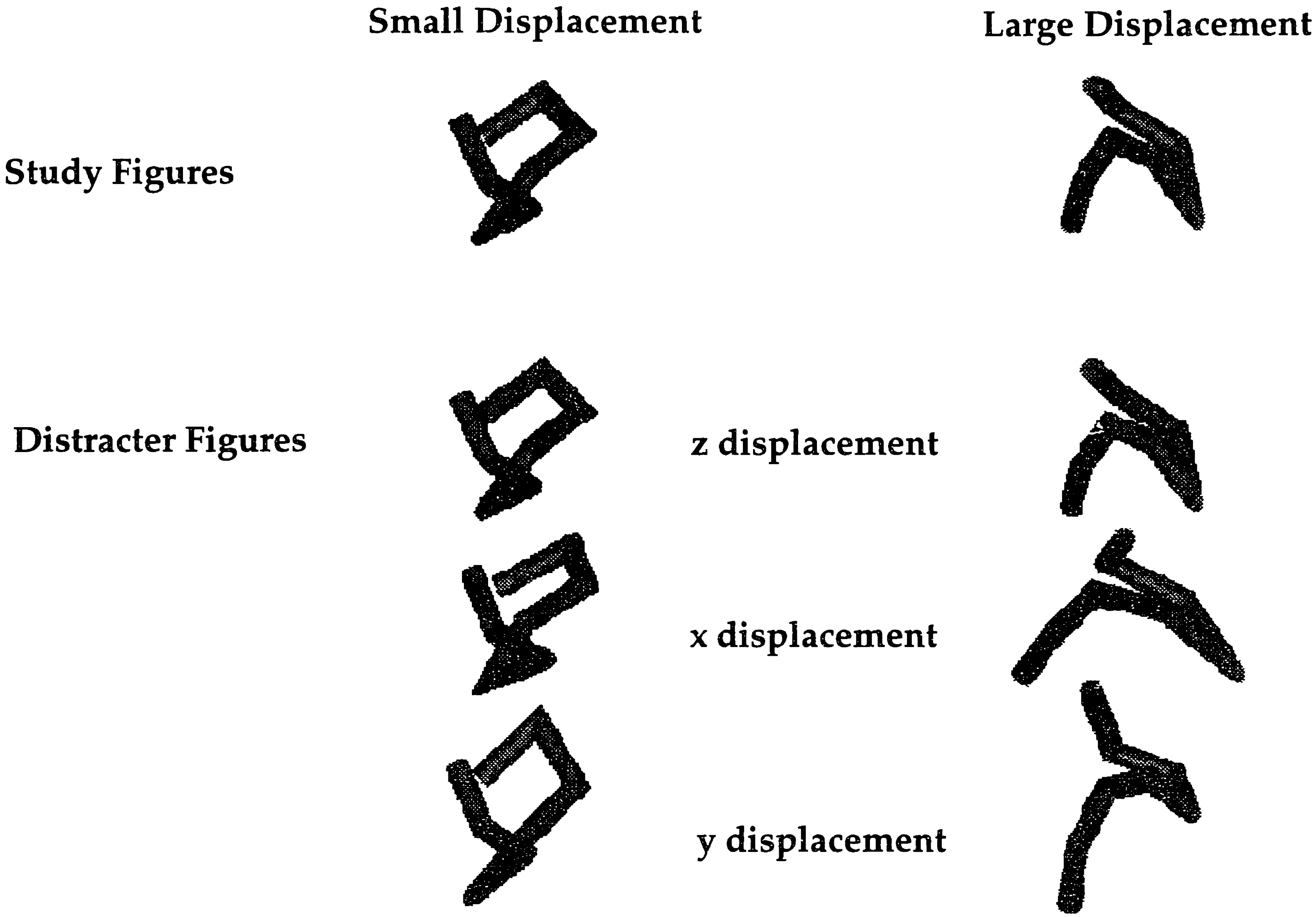

Figure 8. Experiment 2. An example of study figures and corresponding distracter figures for small and for large displacement. Each study figure was paired once with all three corresponding distracter figures.

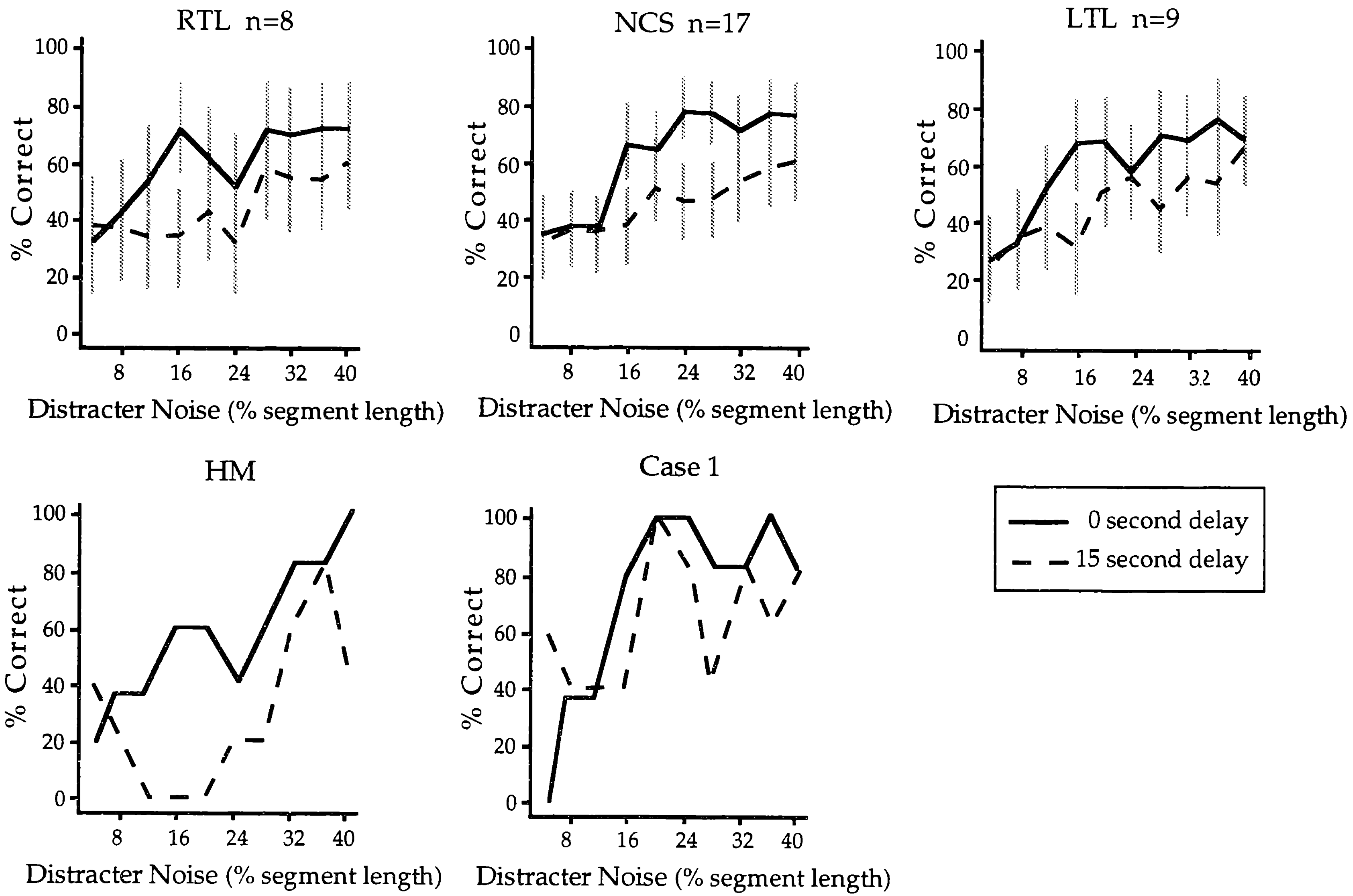

Figure 9. Experiment 2. Simultaneous and delayed recognition of abstract wire figures is normal after left and right anterior temporal lobectomy. Percentage correct is plotted on the ordinate, noise level on the abscissa. Neither H.M. or Case 1 showed the normal pattern of performance.

The Role of Global Features and Stimulus Complexity in Immediate Recognition Memory for Abstract Designs

Gestalt psychologists in the early part of this century proposed that a fundamental distinction exists between the local and the global properties of visual objects (Koffka, 1963; Kohler, 1971; Wertheimer, 1967)(cited in Kimchi (1992)). Local properties consist of the small details or component parts of larger objects or images. The perception of these larger objects is not necessarily a linear sum of its local features, but may also have emergent properties that arise out of the interrelations among those features. Faces, for example, are not perceived as simple collections of eyes, noses, and mouths, but have distinct, global characteristics that depend on the spatial arrangement, size, and shape of these components relative to each other.

Studies of patients with lateralized brain lesions have found that the processing of global and local information is lateralized, with the left hemisphere more specialized for local processing and the right for processing of global features (Delis, Robertson, & Efron, 1986; Doyon & Milner, 1991b). Robertson and Lamb (1991) reviewed the neuropsychological evidence in this area and proposed a model in which four separate neuroanatomical subsystems are responsible for the processing of visual objects: the left and right superior temporoparietal regions, responsible for global and local processing, respectively; an attentional control module that coordinates the distribution of attention to local and global information, localized in the lateral parietal lobes bilaterally; and a circuit that combines the two types of information that depends on interconnecting posterior right temporal-lobe with left temporal-lobe pathways. Hemispheric specialization has also been described in terms of a right-sided advantage for Gestalt organization, and for categorical as opposed to coordinate spatial relations (Laeng, 1994; Van Kleeck & Kosslyn, 1989).

Global and local analysis can interact differently, depending on the perceptual circumstances. A study by Rock, Halper, and Clayton (1972) found that it is much more difficult to distinguish between figures that have one local contour changed when that contour is a part of a whole, closed figure than when it is a part of a smaller, open line segment. Incidental memory of the shapes was assessed because the subjects believed they were being tested for perception of afterimages. Subjects were briefly shown figures like those in Figure 1 (the small-open and large-closed base-figures) and immediately asked to distinguish between two such figures, one of which differed from the target by only a very small change in one local feature. Performance was no better than chance for the closed figures, while that for the open segments was very good. Rock interpreted this result to mean that the details of a complex Gestalt figure that do not significantly affect its overall shape are not remembered and are perhaps not even fully perceived. These results, however, could also be explained by a difference in the size and complexity of the figures. Attentional and mnemonic resources may simply be more taxed and less able to form representations of as many local features (in the same short amount of time) when there are more local features to process.

Closing a figure increases the amounts of local and global information differently. The increase in local information is directly proportional to the size of the segment used to close the curve. There are also additional global features that emerge from the closure: a distinction between "in" and "out," and a greater degree of relational information between the local features, making it possible to represent the figure's characteristics *relative to each other* in terms of distance, shape, and size. If this emergent global information takes additional time to process, it may be expected that closure would adversely affect performance to a greater degree than a linear relation to size would predict. Alternatively, global and local information could be processed in parallel without interference. If a representation based on emergent relations is formed in addition to one based on individual features, more information would be available that could enhance recognition memory.

A study by Navon (1977) demonstrated the effects that global and local information processing can have on each other. Subjects were shown figures in the shape of capital letters that were composed of smaller capital letters. The large and small letters could be consistent with one another (e.g., an S composed of small Ss) or inconsistent (e.g., an S composed of small Hs). Subjects were presented with such composite figures and asked to attend to, and identify, either the smaller local letter or the larger global letter. Global identifications were generally faster and more accurate than local. Reaction times for consistent and inconsistent conditions were about the same when attention was directed to the global letter. When trying to identify the smaller composite letters, however, subjects were significantly slower when the large and small letters were inconsistent. These results were interpreted to indicate that global processing takes precedence over local processing in two ways; encoding and retrieval are faster, and global representations actively interfere with local representations when the two are inconsistent with each other. Another possibility is that local-level processing is facilitated by global processing when the two levels are consistent with each other.

Navon's results do not directly predict how global and local processing interact when the two levels are neither consistent nor inconsistent with each other, as in the Rock study. Because laterality studies have found that the two processing systems are, to some extent, separate and independent from each other, it is possible that global processing does not significantly detract from local processing resources, and may in fact augment the ability to make a local discrimination rather than interfere with it. Nevertheless, the results of the Rock study suggest that there is interference with local processing when the global information present in the stimulus is increased.

The present study was designed to clarify whether Rock's results represent "global interference" or simply the effect of size-related information content. We designed stimuli similar to Rock's, including short stretches of open contours and the same contours contained in closed figures. In addition, the degree of globality for both kinds of stimuli was varied without varying their overall sizes. This effect was accomplished with the closed figures by reorienting the same complex curve segments so that they formed a long, unclosed line. The original short, open segments were closed with simple, smooth curves. It was then possible to compare local discrimination performance with global and less-global figures without the confound of differences in size and complexity.

Methods

Subjects

The 31 subjects were right-handed male and female MIT students and affiliates, aged 20 to 30 years. They were paid standard subject fees to participate in this study. All had normal or corrected to normal vision, and none had a history neurological or psychiatric disorders.

Apparatus and Stimuli

A total of 256 different figures were used in 192 comparison trials. There were four categories of figures: small-open, large-closed, small-closed, and large-open (Figure 1). The small-open figures were used to construct each of the other three categories: small-closed figures were created from small-open figures by connecting the endpoints of the line with a short, smooth arc; large-closed figures contained another complex, detailed line to make the closure; and large-open figures contained both line segments from the large-closed figures connected end-to-end to form a longer, unclosed, complex line. Therefore, the amount of information in the two "large" categories was equivalent, and that in the two "small" categories was roughly equivalent.

There were 16 sets of these four categories, which comprised the 64 "base figures" (Figure 2).

Each of these base figures was used to construct three comparison figures. For each figure, in each category, one local concavity or convexity was enlarged by either a small, medium, or large amount, corresponding to difficulty levels of hard, medium, and easy. Each of the three comparison figures was paired with its corresponding base figure, so that in the total of 192 comparisons, each base figure appeared 3 times and each of the three comparison figures appeared once. It was randomly determined whether the base figure or one of its comparison figures would appear as the initially presented target (Figure 3). It should be noted that for each of the 16 stimulus sets, 12 comparisons (4 figure categories x 3 difficulty levels) were made, making it theoretically possible for subjects to learn which local contour was critical for any given test figure. Images were presented on the screen of an Apple Macintosh II computer, using software developed in our laboratory.

Procedure

Subjects' immediate recognition memory was assessed with a two-alternative match-to-sample procedure. Subjects were told that they would be presented with a series of complex figures, each of which would appear for 4 seconds. They were asked to study and remember them. When the target stimulus disappeared, subjects pressed a key, whereupon two figures appeared on the screen side by side. One of them was the figure they had just seen, and the other was different from but similar to the first. They indicated the one they had just seen by pressing either a key on the left if it was the figure on the left, or a key on the right if it was the figure on the right. There was no time limit to decide; subjects were instructed to make their best guess when unsure. They rested at several points during the test, indicated by a "please rest" screen. The test was administered in two parts, each of which used 8 base-figures in 96 different comparisons. Trials were organized pseudorandomly so that the same figure was not presented twice in succession. There was no practice set. Subjects usually required 45 minutes to 1 hour to complete the entire procedure.

Results

A within-subjects ANOVA with difficulty level and category of figure (small-closed, small-open, large-closed, large-open) as dependent variables indicated main effects of difficulty level ($F(2, 60) = 51.8$, $p < 0.0001$) and category ($F(3, 90) = 30.1$, $p <0 .0001$) (Figure 4). The interaction between difficulty level and category was significant ($F(6,180) = 2.38$, $p = 0.047$). T-tests comparing the percentage of correct responses for the two small categories with that for the two large categories showed that responses to the smaller stimuli were more accurate than those to the larger stimuli at difficulty levels medium ($t = 4.90$, $p < 0.0001$) and easy ($t = -6.26$, $p < 0.0001$). There were no other significant effects at these difficulty levels. At the most difficult level, an effect of globality emerged. Average percentage correct for small-closed and large-closed figures was higher than that for open-large figures ($t = 2.68$, $p = 0.012$).

An item analysis was performed to determine whether the 16 different base figures and their derivatives were equally difficult. There was a significant main effect of item for Block 1 $F(7, 210) = 15.0$ and Block 2 $F(7,210) = 12.0$, ($p < 0.0001$), indicating that some figures were easier to remember than others, averaging over all difficulty levels and figure categories.

There was no main effect of block (i.e., test half), $F(1, 30) = 2.09$, $p = 0.16$, suggesting that subjects' overall performance did not improve over the course of the test. In addition, an order analysis was performed by splitting the test into fourths. The main effect of order was not significant $F(3,90) = 2.48$, $p = 0.067$.

The interactions between block and difficulty level and block and category were significant (_F_(2,60) = 4.04, _p_ = 0.023 and _F_(3,90) = 3.15, _p_ = 0.029 respectively). Inspection of the data indicated that the source of this interaction was performance at the hardest difficulty level (Figure 5). For Block 1 post hoc _t_ tests confirmed that performance in the small-closed condition was significantly better than in the small-open condition (_t_ = 2.85; _p_ = 0.008). In Block 2 the accuracy for the large-closed condition was greater than that for the large-open condition (_t_ = 2.67; _p_ = 0.012).

Discussion

This study contrasted immediate recognition memory for stimuli in which global properties and information content were manipulated in an orthogonal comparison. We tested two hypotheses: (a) increasing information degrades performance, and (b) global context interferes with the processing of local detail. The first hypothesis was supported, while the second hypothesis was not. The following discussion reviews our results and compares them with past studies.

Effects of Difficulty Level and Figure Condition

These results did not replicate the findings of Rock et al. (1972). The degree of globality in the figures did not have an adverse effect on the accuracy of discriminations at the local level. Instead, performance was highly dictated by figure size (amount of information). Further, there was an indication that, under challenging circumstances, global information enhanced the ability to make local discriminations. Although other differences between the task used here and that of Rock probably contributed to this discrepancy (discussed in the next section), it is possible that his results may be explained, in part, as an effect of overall size, and not of interference of local representations by global processing.

At the most difficult level, where the local contour was altered by only a very small amount, performance was somewhat better (overall and within each size condition) for figures with more global properties. It may be that in the easier conditions, local information was sufficient to make local distinctions, but at the most difficult level subjects could make greater use of the additional relational information contained in global figures.

The interaction between block and difficulty and between block and figure category indicated that when the task became very challenging, closed figures elicited superior performance. This result is consistent with the literature describing similar advantages for processing figures with organized global properties (see next section). It is not clear why subjects appeared to shift, at the highest level of difficulty, from a global advantage for the small figures in Block 1 to a global advantage for large figures in Block 2. Perhaps subjects paid more attention to the large figures in Block 2 because they learned in Block 1 that these stimuli were the most challenging. Performance for small-closed figures may have suffered due to this shift in strategy combined with fatigue. We cannot exclude the possibility that uncontrolled differences between the 8 figures used in the first block and the 8 figures used in the second block contributed to this difference (Figure 2). However, we have no reason to suspect that this is the case.

Subject's performance may have been helped if they realized that only one part of the line segments and closed figures was relevant for the task, and that closed figures contained the same line segments shown in isolation. It seems unlikely that subjects could guess at the construction of the stimuli until well into Block 1 at the earliest. By Block 2 some subjects may have acquired this general principle. However, given that a new set of stimuli were used in the Block 2, subjects would still have had to learn the specific forms and parts relevant for the task. Perhaps subjects paid particular attention to the larger figures in the second block given their improved performance in the difficult condition. Nevertheless, any principles the subjects might have acquired were not powerful enough to boost their performance at the medium and easy level of difficulty. Finally, the lack of a main effect of block or order argues against the development of effective strategies to take advantage of the experimental design.

Comparison with Past Studies

Previous studies have identified many factors and conditions that influence the relative advantages of either local or global processing, such as familiarity, size ratio of global and local features, retinal position, spatial uncertainty, and stimulus duration above threshold (Robertson & Lamb, 1991). The results of the present study indicate that task difficulty may also influence the relative advantages of each processing strategy.

In a thoughtful review, Kimchi (1992) pointed out that the documented global advantage does not necessarily prove the existence of a global precedence in the temporal development of the percept. Crucially, the assumption has never been proven that the logical distinction between the global and local levels in a hierarchical description of an image corresponds to analogous perceptual levels. In fact, Kimchi has shown that the perceptual analysis of global and local features depends strongly upon the number and relative size of the elements (Kimchi, 1983; Kimchi & Palmer, 1982). Briefly, when local elements are relatively small and numerous, they are perceived as texture and are perceived independently from the global shape. When the local elements are relatively large and few in number, they are perceived as component parts of the whole. In the later case, replacing the local elements with different elements would create a highly salient change in the figure. The global advantage may result simply from a processing advantage for relatively large size (independent of position in an hypothesized hierarchy). Independent evidence exists that stimuli that are 'greater than' others (in size, contrast, motion, depth, or pattern size) may be processed more easily (Braun, 1994; Schiller, 1993).

Kimchi (1992) reserved the terms global and local to refer to logical levels in an hierarchical description of an image. She uses the term wholistic to refer to properties such as closure, symmetry, intersection, and parallelism, which emerge as relations between parts (components) of an figure. Evidence exists that so-called component and wholistic properties are not perceived independently, and that there may be a wholistic dominance. For example, Kimchi reported that the difficulty of discrimination between stimuli such as an outline square, outline diamond, x, and +, is explained by the wholistic properties of closure and intersection, not by the baseline discriminability of the oriented line segments in isolation.

Other investigators have found similar effects. Pomerantz, Sager, & Stoever (1977) report that, for example, patterns: () vs.)) are more easily discriminated from each other than the patterns: (vs.) leading to a configural superiority effect. Weisstein and colleagues discovered a so-called object superiority effect (Lanze, Weisstein, & Harris, 1985; Weisstein & Harris, 1974; Williams & Weisstein, 1978). A line segment was more accurately discriminated when it was part of an organized object with a unitary 3-dimensional percept than when it was part of a flat, fragmented background. In addition, under some circumstances, line segments are identified better with an organized background than when presented alone. The effect is believed to depend upon 3-dimensional organization as well as emergent wholistic features.

Similar results have been described using memory paradigms. Ankrum and Palmer (1991) showed that immediate recognition (assessed with a same-different judgment and a forced-choice task) of whole abstract stick figures (as well as figure parts) was better when probed with the whole figures than with parts of the figures. This result does not obtain if the whole figures are presented in a fragmented arrangement that disrupts the form.

Ankrum and Palmer (1991) offered a clue as to why greater object superiority effects were not observed in the present experiment. Their results indicate that the object superiority effect is increasingly diminished to the extent that subjects perceptually dissociated the figures into parts. Several subjects reported that they had become familiar enough with the different figures to know where the local change would be in the figure, and could then pay particular attention to that region. This strategy may have confounded our results. However, subjects' performance did not improve over the course of the test, indicating that not all subjects were learning the figures well enough to guide attention. Nevertheless, this confound could be removed in future studies by presenting fewer repetitions of the same figure, and by testing only one difficulty level.

In hindsight, we have several reasons to expect that Rock's results would not be replicated here. It seems likely that the incidental, one trial memory paradigm employed by Rock was in fact critical to his results. In one condition (using stimuli different from those described in this paper), his subjects were instructed to "look at the figure carefully and pay particular attention to the lines inside the figure" (the local features). Not surprisingly, recognition performance for the local features improved markedly.

The relevance of Navon's (1977) global versus local paradigm and associated global interference effect to the stimuli used here is now seen as questionable. Rock's interpretation of his 1972 results states that local features that do not contribute to the global shape do not establish memory traces. However, in later papers (Rock & Gutman, 1981; Rock & Schauer, 1976), he states simply that without attention a perceptual (nonverbal) description of an object is not created. Apparently, his incidental memory task taxed attentional resources, and under such circumstances there is a recognition bias in favor of wholistic properties. Given Kimchi's analysis, the terms wholistic and component are much more appropriate than global and local for the stimuli used in this paper and in Rock's study. We conclude that the slightly better performance for closed figures in our study extends the conditions under which object or configural superiority can be manifest. Overall, the results presented here reinforce the idea that the interactions between different "levels" of object features are complex and dependent upon task instructions and demands.

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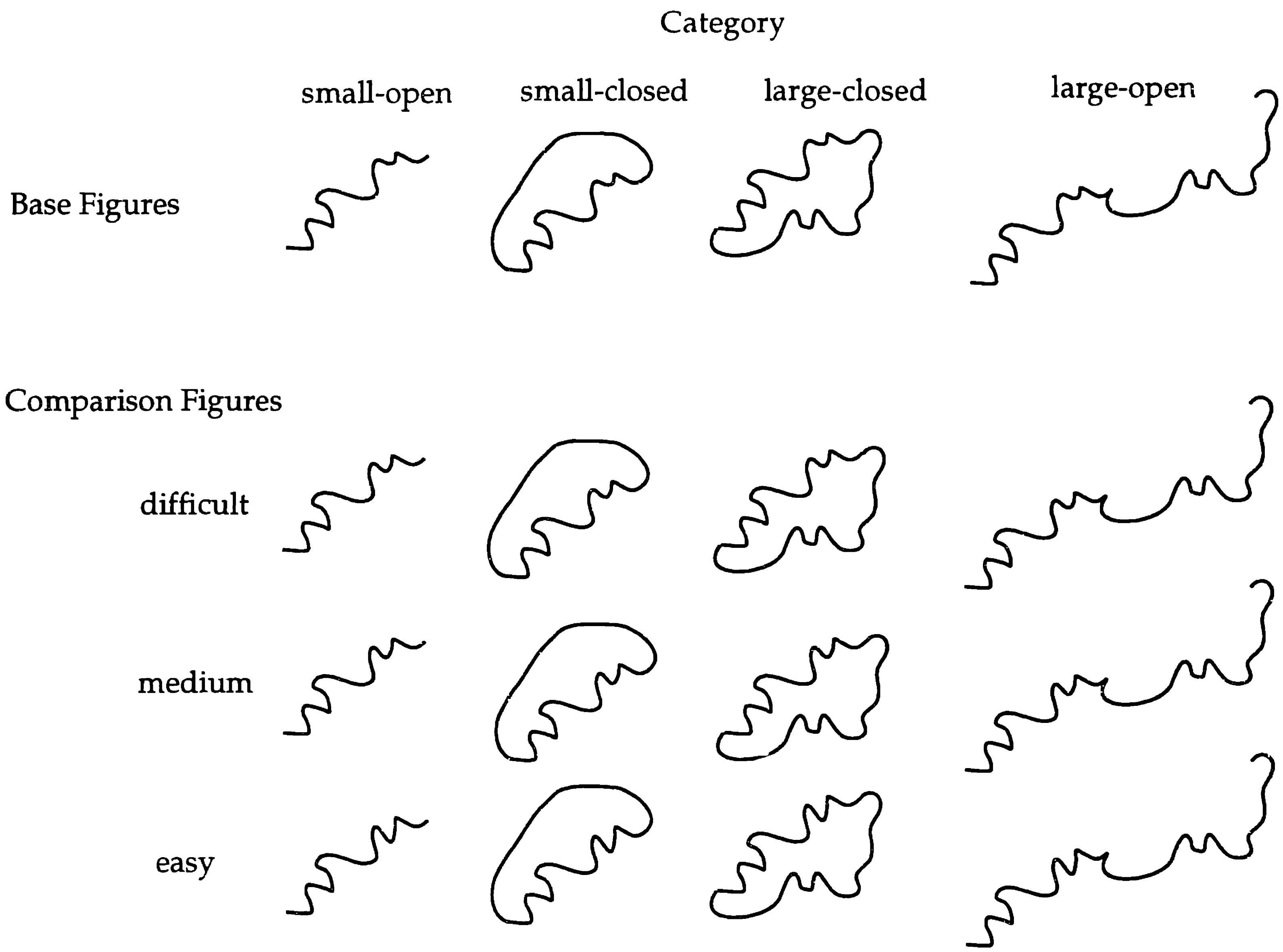

Figure 1. An example of a set of base-figures and the comparison figures derived from them. The small-open figure is contained within each of the other figure categories. Each base figure was paired once with each of the three corresponding comparison figures during the test.

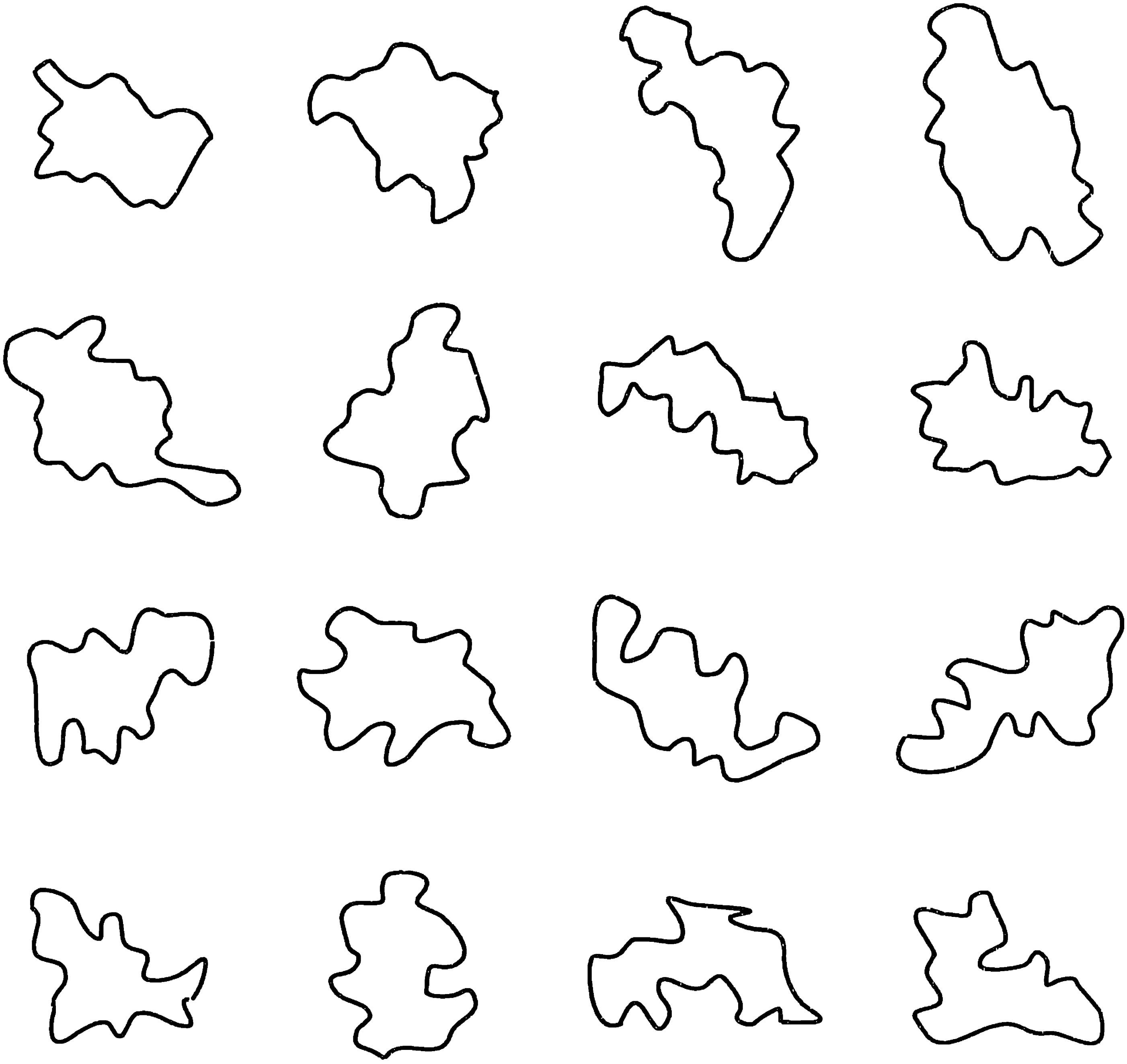

Figure 2. The large-closed category is shown for all 16 figure sets.

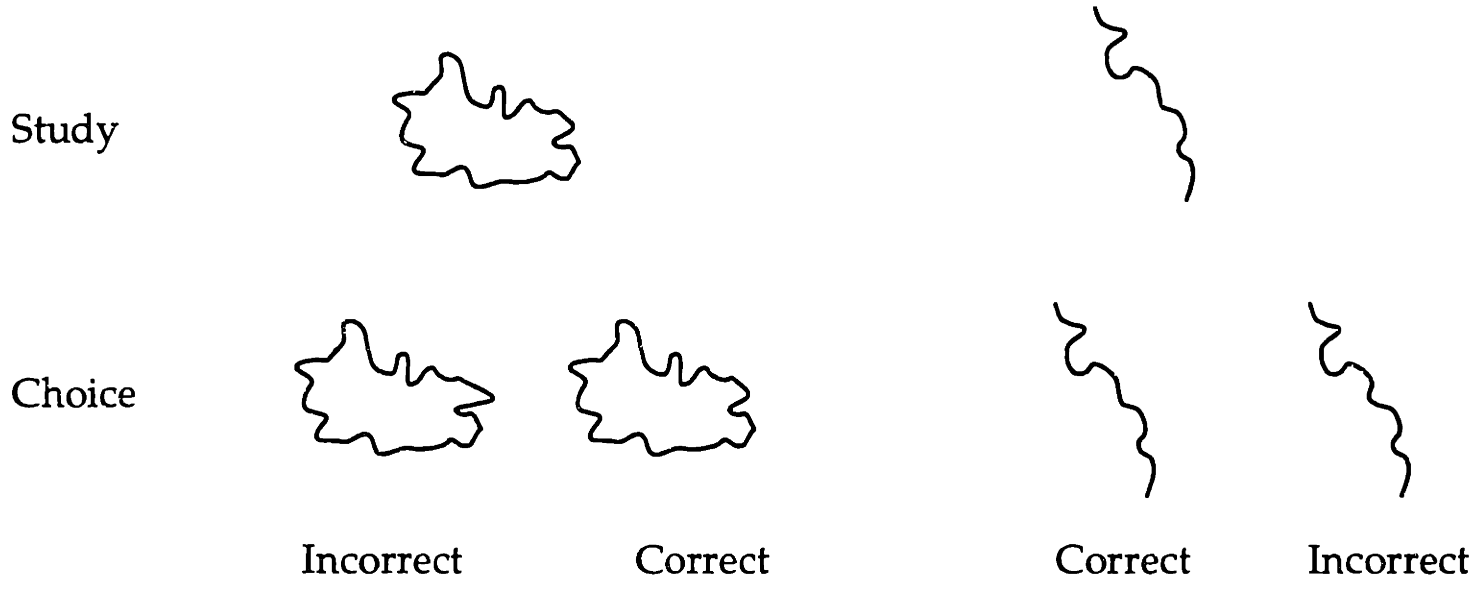

Figure 3. Two sample trials. Subjects were presented with the study figure for 4 seconds. They were then presented with the same figure and that same figure with a single local contour changed. The task was to choose the figure that matched the sample. There were 192 trials.

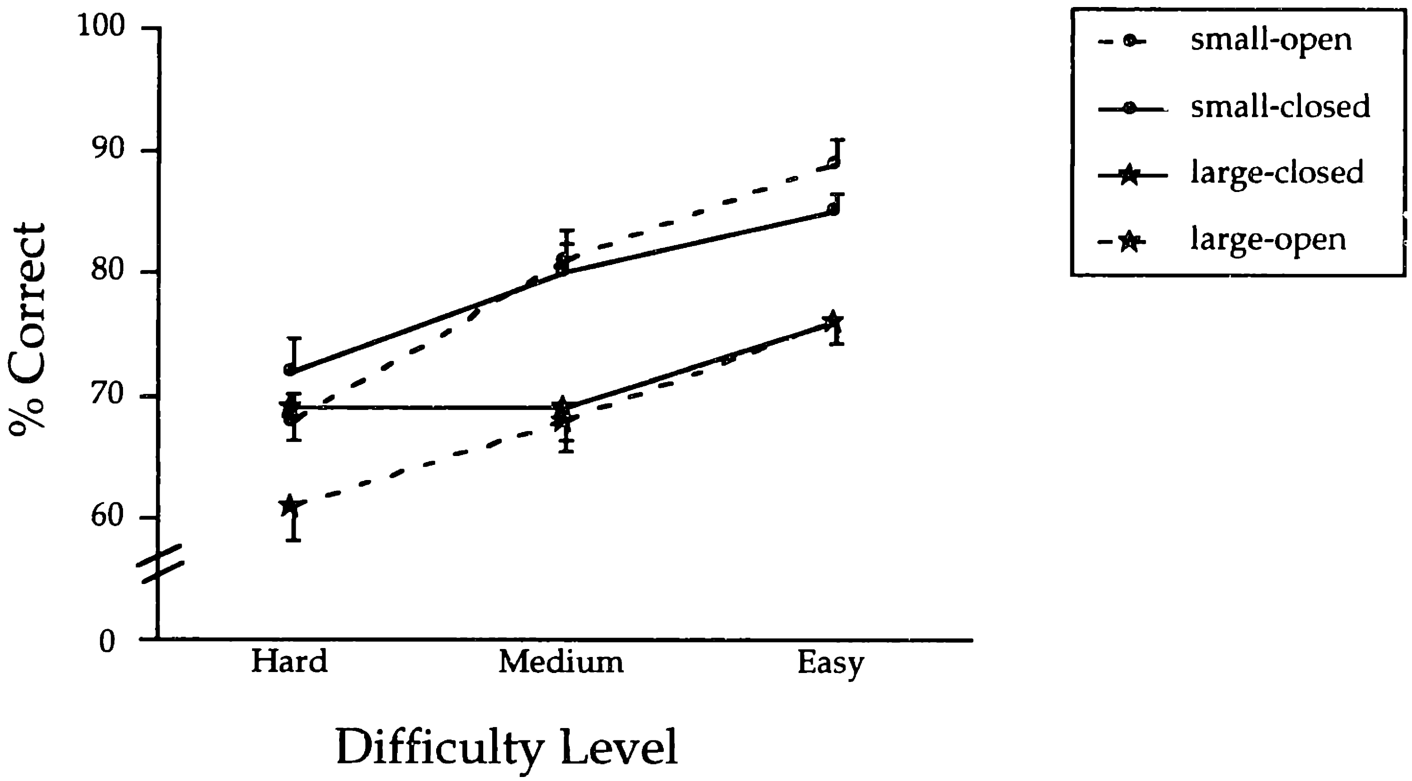

Figure 4. Performance for total number of trials in percentage correct is shown for the 4 figure categories and 3 levels of difficulty. Note: Ordinate axis begins at 50% correct performance, which is the score expected by chance.

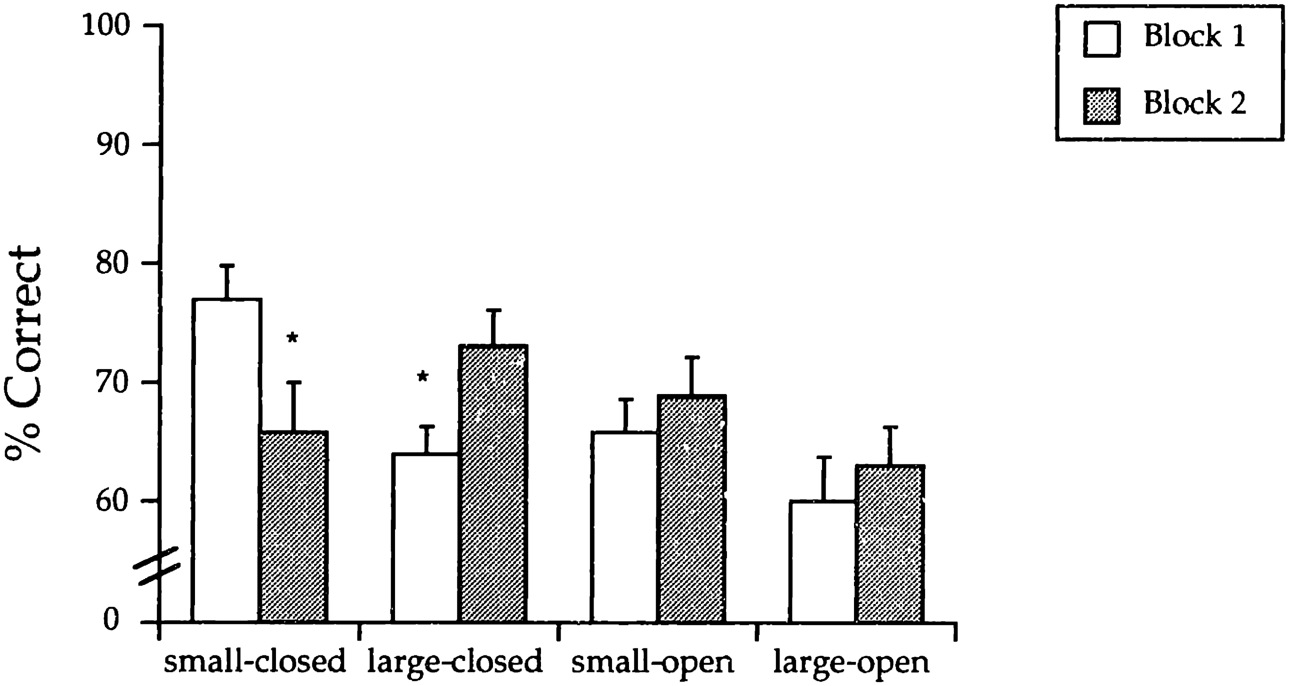

Figure 5. Performance in percentage correct is shown for the most difficult condition for Block 1 and Block 2 separately. Note: Ordinate axis begins at 50% correct performance, which is the score expected by chance.