Visual discrimination and attention after bilateral temporal-lobe lesions: A case study
Janine D. Mendola*, Suzanne Corkin

Department of Brain and Cognitive Sciences, and the Clinical Research Center, Massachusetts Institute of Technology, Cambridge, MA 02139, USA

Received 27 October 1997; accepted 20 March 1998

Abstract

We studied a woman (Case 1) who acquired achromatopsia, prosopagnosia, and memory loss after sustaining bilateral temporal-lobe lesions. Given her symptoms and locus of lesion, the affected area may be related to the monkey visual area IT. In order to examine her deficits, we assessed her basic discrimination capacities in several domains. She performed normally when stimuli differed in contrast, size, or motion. Her performance was abnormal for patterned targets, and was markedly impaired when the patterned targets were less prominent than distractors. This impairment decreased with practice. These symptoms partially resemble the deficits that have been found in monkeys with lesions in visual cortical area V4.

Keywords: Pattern; Perception; IT; Achromatopsia; Prosopagnosia; Attention

1. Introduction

It is well known that lesions in the temporal lobe adversely affect visual perception and memory [e.g. 14]. Here we study a patient (Case 1) whose bilateral temporal-lobe lesions resulted in achromatopsia, prosopagnosia, and memory loss. Case 1’s memory loss and prosopagnosia have been studied in detail in other experiments [36, unpublished observations]. In this study we chose to examine her visual abilities at a more basic level, with simple stimuli which were not confounded with semantic content. We used tests similar to those that have been used extensively to document the effects of lesions in the monkey visual cortex [48, 49]. One goal was to relate Case 1’s lesions and resulting deficits to the relatively well-understood monkey visual system. Humans and monkeys obviously differ with respect to abilities and brain organization. However, the evidence for similarities between the visual system is impressive [e.g. 10, 27, 54] (and is the basis for our working assumptions), but strict homologies should be considered hypotheses which future studies may or may not support.

Physiological and behavioral studies in monkeys indicate that visual area V4 and the anteriorly adjacent inferior temporal cortex are part of a relatively discrete visual stream that is particularly crucial for normal “object vision,” i.e. discrimination and mnemonic tasks with visually presented 3D objects or 2D patterns [55]. The physiological responses of neurons in this temporal (ventral) stream commonly vary with static form information such as the size, color, and shape of stimuli. These neurons are less sensitive to motion or position of stimuli [18].

Removal of visual area V4 is reported to cause mild difficulties with color and contrast discrimination, and striking deficits with form discrimination [23]. In studies of monkeys with incomplete V4 lesions [48, 49] Schiller found mild color, contrast, and form, deficits within the “scotoma.” Also, these monkeys were selectively impaired on oddball-out discrimination tasks when the oddball target was less prominent than the distractors, i.e. dimmer, smaller, or more slowly moving (but not when brighter, larger, or faster) than the respective distractors. Neural activity in area V4 is known to be modulated by selective visual attention [16, 39, 41, 53] and by expectancy with respect to an imminent stimulus [21, 22, 38].

Cytoarchitectonic experiments have demonstrated that the inferotemporal cortical area (IT) of macaque monkeys can be subdivided into a posterior area TEO and a more anterior area TE [5]. Removal of each of these areas has distinct and predictable results. Lesions confined to area TEO cause deficits in discrimination of patterns and
objects; TE lesions cause impairment in object recognition memory [13, 31, 34]. Many 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 [4, 17, 37, 47]. However, there is also evidence that lesions to the middle temporal gyrus (TE) (but not lesions to more posterior visual area V4, or more ventral rhinal cortex) causes striking deficits in color discrimination [7, 23, 24, 26].

The invariance of the deficit for L discriminations across the different visual domains of size, contrast, and motion is a striking aspect of the results of V4 lesions in monkeys. No studies have investigated whether lesions at stages other than V4 in the monkey ventral stream cause a similar difficulty discriminating less prominent targets. In particular, an inferior temporal (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. Lesions of IT might therefore be expected to result in more specific impairments of pattern or object perception.

One barrier in the quest to relate the results of monkey experiments to studies of patients with visual agnosia is the nature of stimuli and tasks typically employed. Often, the stimuli used with humans are more conceptually complex than those used with monkeys. However, examples suggest that impressive similarities between the two species exist when care is taken to keep experimental paradigms equivalent [42]. One study by Rizzo et al. [46] directly compared the abilities of a patient, with cortical lesions that included bilateral inferior medial visual areas 18 and 19, to the abilities of monkeys with V4 lesions. The patient’s 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. The ability to discriminate less prominent targets was not assessed.

The available evidence suggests that Case 1’s lesion site may be related to the monkey visual area IT. This supposition is supported by the gross anatomical location of her lesions, and the fact that her achromatopsia, agnosia and memory loss are all consistent with the effects of removal of monkey areas TEO and/or TE. In order to further examine her deficits, we constructed tests to assess a wide spectrum of basic visual discrimination abilities, e.g. discrimination of contrast, size, motion, and pattern. In addition, we designed the tests to allow for comparison of discrimination of targets that were more prominent than their distractors (“greater than” their context [G]) versus targets that were less prominent (“less than” their context [L]). Here we investigate the hypothesis that Case 1 shows selective impairments in pattern perception with tests designed to be similar to those employed by Schiller [49]. We also created three additional tests of pattern discrimination (texture, striped, and +/L pattern) that could accommodate the G versus L design.

2. 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.

2.1. Subjects

The subjects in this experiment were Case 1 and 8 normal control subjects (NCS) recruited from the MIT community. The NCS group (3 men and 5 women) had a mean age of 28.1 (range 25–32) and mean years of education of 13.3 (range 12–15). All NCS reported no history of ocular, neural, psychiatric or other major disease. 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 amблиopía. Her visual acuity was OD: 16/13 +; OS: 5/200. Bilateral acuity was 20/30. 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, [57]), 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, [58]) 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, with 2 tritanomalous errors and 1 deutanomalous error (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 [15]. With OS she scored more poorly, beyond the normal range in the blue region. She had little depth perception due to poor acuity in one eye. Her stereoaucity was worse than 400 s of arc as measured by the Randot Stereoaucity Test. Her contrast sensitivity was normal as measured by PGCONSEN, (Vision Metrics, Berkeley, CA) [25]. 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 [56]. She scored in the severely impaired range on the Benton Facial Recognition Test (27/54 correct) [2]. She scored in the normal range on the Mooney Clos-
ure Faces test (35 correct), but was very slow [40]. Finally, Case 1 scored very low on a verbal (12/60) and a non-verbal (23/56) version of the Recurring Figures Test [35]. In summary, Case 1 demonstrated moderate achromatopsia, prosopagnosia, and memory loss.

Clinical MRI brain scans were consulted to determine the locus and extent of her lesions (Fig. 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 (Fig. 1B, C). The lesion was larger on the right side extending into the temporal pole, and including the anterior amygdala (Fig. 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 (Fig. 1D).

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

2.2. Apparatus and stimuli

All tests were administered with a Macintosh computer with color monitor using software developed in our laboratory. For all discrimination tests, the stimuli consisted of six elements arranged at the corners of a hexagon (Fig. 2). One element was always different (an “oddball”) from the five distractors. A fixation cross was placed in the center of the virtual hexagon. The stimuli appeared equidistant from the fixation cross between 6 and 8° eccentricity on a polar coordinate system.

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: G and L (Fig. 2A, B). 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. For all tests except the striped and +/L patterns, the absolute difference between targets and distractors 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 distractors by 1 of 3 or 4 difficulty levels, and appeared at 1 of 6 target locations to yield a randomized 2 × 3 × 6 or 2 × 4 × 6 design. Performance was also assessed using greater or lesser contrast, faster or slower stimulus motion, and more or less salient patterns (Fig. 2C–I). For the striped and +/L patterned stimuli we could not incorporate multiple levels of difficulty, so that the design was simply 2 prominence conditions × 6 target locations. It was unclear whether the correct definition of G and L stimuli included only stimuli that varied along a continuous dimension. Given such a situation, we created striped and +/L patterned stimuli that either had or lacked a certain feature, so that the issue could be examined empirically.

In the case of size, contrast, and checked pattern the tests were designed to be qualitatively similar to those used by Schiller [49]. The exact parameters we used were determined after initial pilot studies to ensure that we would obtain orderly psychometric curves from human subjects that spanned the possible range of percent correct. The texture discrimination test was an original creation for this study, but was inspired by a detection version used by Schiller. A speed of motion discrimination task was also used in Schiller’s studies, but we employed a modification in which moving dots had limited lifetimes so that a purer motion signal was required. Finally, the striped pattern and +/L patterns were created de novo for this study.

2.2.1. Size

Following presentation of the fixation cross, six squares in a hexagonal arrangement were flashed for 250 ms.

Fig. 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).
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’ sides was 1.6, 1.76, 1.92, and 2.08", respectively. The target was either larger (G) or smaller (L) than the distractors. The target and distractors were 6.7" distant from the fixation point. The test comprised 288 trials.

2.2.2. Contrast
Following presentation of the fixation cross, six squares (1.8") in a hexagonal arrangement were flashed for 250 ms. The luminance difference between the target and comparison stimuli was varied. The absolute luminance values were 1.41, 2.20, 4.18 and 10.81 cd/m² with background luminance at 84.04 cd/m². The target was either darker (G) or lighter (L) than the distractors. The target and distractors were 6.7" distant from the fixation point. The test comprised 288 trials.

2.2.3. Motion
Following presentation of a fixation cross, six windows (3.2" × 3.2"), each containing 50 moving dots (2 × 2 pixels), were displayed on the screen for 1000 ms. The center of each window was 7.2" distant from the fixation point. One window contained dots moving at a different speed than the other five identical windows. The speed was varied systematically, and corresponded to four
difficulty levels with speed ratios between target and distractors 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°/s. The target moved either faster (G) or slower (L) than the distractors. In this test, each individual moving dot had a limited lifetime, that is, it traveled a particular course for just 100 ms before it disappeared and was randomly repositioned to a new location to move for 100 ms, disappear, and so forth. The result was a pure motion signal not confused 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 [43]. The test comprised 384 trials.

2.2.4. Texture

Following presentation of a fixation cross, an array of vertical lines filled the screen for 300 ms. The array contained 14×14 line elements which subtended 19.2°×19.2° overall. Each line was 38 arcmin long and 3 arcmin wide. In six small areas (1.9°×1.9°), a 2×2 array of lines were tilted towards the diagonal. Difficulty was varied by systematically increasing the amount of tilt difference between the target and distractors (10, 20, 30, and 40°). The absolute tilt of the target and distractor elements was 5, 15, 25, 35, or 45°. In the G condition, the target area lines were more tilted, and the distractors blended easily into the background of vertical lines. Conversely, in the L condition, the target area contained lines less tilted than the distractors. The target and distractors were 6.5° distant from the fixation point. The test comprised 384 trials.

We also used a detection version of this task in which a target appeared at one of six locations only. The remaining field was covered with the homogeneous background of vertical lines. Targets differed in orientation by 20, 30, or 40° from the background. Other aspects were similar to the discrimination version. The test comprised 144 trials.

2.2.5. Checked pattern

Following presentation of a fixation spot, six squares (2.1×2.1°) in a hexagonal arrangement were flashed for 250 ms. 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 3×3, 4×4, 5×5, or 6×6, with check size 40, 30, 24, or 20 arcmin respectively. The check pattern size was either larger (G) or smaller (L) than the distractors. The target and distractors were 6.7° distant from the fixation point. The test comprised 384 trials.

A more simple version of this checked pattern discrimination test which contained only one difficulty level was also used. In this case, the 4×4 and 6×6 patterns were used. The check pattern size was either larger (G) or smaller (L) than the distractors. Otherwise the test was identical to the multiple difficulty level described above. The test comprised 144 trials.

2.2.6. Striped pattern

Following presentation of a fixation spot, six squares (2.4×2.4°) in a hexagonal arrangement were flashed for 250 ms. The squares contained a high-contrast diagonal striped pattern, with black stripes (8 arcmin wide) separated by 14 arcmin wide white space (13 stripes per square). In the G condition the squares contained a smaller square in which the orientation of the diagonal stripes was rotated 90°. The L condition lacked this central orientation change. The target and distractors were 6.7° distant from the fixation point. The test comprised 144 trials.

2.2.7. (+/L) pattern

Following presentation of a fixation spot, six squares (2.9×2.9°) in a hexagonal arrangement were flashed for 250 ms. The squares contained a high-contrast pattern, with black line segments arranged in “L”-shapes on a white background. Each square contained a 4×4 array of “L”-shapes, each 24 arcmin in width and height. In the G condition a subset of the “L”-shapes (the central 2×2 array) were replaced by “+”-shapes of the same size and contrast as the “L”-shapes [31]. The L condition lacked this central change. The target and distractors were 6° distant from the fixation point. The test comprised 144 trials.

2.3. Procedure

The subjects sat 14 inches 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 fixate the cross at the center of the screen, that moving their eyes would only hinder performance, 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 s. 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 min to complete a block of trials.
3. Results

3.1. Contrast, size and motion

Case 1 performed normally on G and L discriminations of contrast, size, and speed of motion for the entire range of difficulty (Fig. 3A, B, C).

3.2. Texture

The results obtained when the oddball target was defined by texture differences (Fig. 3D) clearly contrasted with the normal performance described above. Case 1’s ability to discriminate the oddball target was normal when it was more salient than the distractors. Across four difficulty levels in the G condition, the performance of Case 1 and NCS ranged from near chance to near perfection. In contrast, when the oddball target was less salient than the distractors, Case 1’s performance remained near chance at all difficulty levels.

3.3. Effects of practice

After discovering Case 1’s striking impairment with less prominent texture displays, we proceeded to administer additional sessions of texture discrimination. Case 1’s performance improved over the 2 additional sessions of texture discrimination that we administered, most notably for the L condition (Fig. 3E, F).

3.4. Texture detection

We also tested Case 1 on a detection version of the texture task to ensure that her difficulties with the discrimination task were not simply due to inability to detect the targets and distractors. This is of particular concern given that the background of vertical lines in the texture stimuli could mask the targets and distractors. Case 1 performed normally for all 3 difficulty levels (Fig. 4). Her score in the hardest condition was below the mean score of control subjects, but she was comfortably within the normal range.

3.5. Checked pattern

Case 1’s performance with the first session of checked stimuli was similar to that seen with the texture discrimination. Her performance was in the normal range for the G condition and markedly poor for the L condition. However, her performance in the L condition steadily improved across additional sessions until no discrepancy relative to NCS was evident (Fig. 5A). Results are plotted with the abscissa representing increased training, and the trials grouped into four sessions of 96 trials, all administered in the same day (a different day from the tests of contrast, size, motion, texture, and checked pattern).

3.6. Striped pattern

The last two tests represent further efforts to generalize Case 1’s deficit to additional pattern discriminations. These tests were designed to be compatible with the G versus L condition, although we were not able to incorporate several levels of difficulty as we had in the other tests. In the case of the striped pattern, Case 1’s performance was poor in the G and L conditions, although discrimination was worse in the L condition (Fig. 5B). In G and L conditions, she improved over the 4 sessions we administered, all in the same day (a different day from the tests of contrast, size, motion, texture, and checked pattern).

3.7. (+/L) pattern

Lastly, we tested Case 1’s performance with the L versus + patterned stimuli (Fig. 4C). Once again her performance was poor in the G and L conditions, although discrimination was worse in the L condition (Fig. 5C). In G and L conditions, she once again improved over 4 sessions, all administered on the same day (the same day as the striped pattern).

3.8. Effects of target position

Our experimental design allowed us to determine if Case 1’s accuracy in pattern discriminations varied systematically with the 6 target positions. However, we saw no large systematic difference in accuracy for different locations. The largest differences were in the case of texture discrimination, so we performed a Fisher–Exact test for each of the three sessions and for data pooled across all sessions. There was not a significant difference in the percentage of correct discriminations across target locations for the first or third session, or for pooled data (P values = 0.163, 0.963, and 0.169 respectively). For the second session the difference (greater accuracy for middle left and lower left target position) was marginally significant at (P value = 0.019; P value = 0.076 after Bonferroni correction).

4. Discussion

We have shown that discrimination of patterns (impaired in Case 1) is dissociable from the discrimination of
Fig. 3. (A)-(F) The performance of Case 1 is compared to NCS (with standard error bars). (A) Case 1 shows normal performance on G and L discriminations of contrast; (B) Case 1 shows normal performance on G and L discriminations of size; (C) Case 1 shows normal performance on G and L discriminations of speed of motion; (D) Case 1 shows impaired performance for L (but not G) discriminations of oriented texture; (E) and (F) Case 1’s performance for L condition improves in the second and third repeated session of texture discrimination.
The performance of Case 0 is compared to normal control subjects (NCS) with standard error bars for texture detection. Case 0 performed within the normal range for 2 levels of difficulty.

Target Orientation Difference (degrees)

Fig. 4. The performance of Case 1 is compared to normal control subjects (NCS) with standard error bars for texture detection. Case 1 performed within the normal range for 3 levels of difficulty.

stimuli in other visual 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 cortical 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 and consider the role of visual attention.

4.1. Discrimination of greater-than and lesser-than targets

An important factor in the discrimination tasks used in this study is that distractors were present. Case 1 was not impaired at target detection in the absence of distractors. Her difficulties were revealed only when the target was competing with distractors. In this regard, the impairment is related to the extinction phenomenon classically observed after parietal-lobe lesions [1, 11]. In the present study, however, the distractors 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, she showed a dramatic impairment in the L condition along with normal discrimination of G targets. On the striped and (+/L) pattern task, however, her performance on G discriminations was clearly depressed, suggesting difficulties with pattern discrimination in general. This result is in agreement with many studies demonstrating a loss of pattern perception after IT lesions in monkeys [19]. Furthermore, in many studies of IT lesions in monkeys, the degree of impairment depends on the difficulty of the discrimination as measured by the performance of normal monkeys. Normal control subjects in the current study performed slightly more poorly in the L condition than in the G condition. It remains possible that Case 1’s deficit with L pattern discriminations is simply due to greater difficulty.

We believe, however, that the balance of evidence suggests that discrimination of L targets is particularly sensitive to the effects of visual cortex lesions. The difference between Case 1’s G and L discrimination is clearly larger than the corresponding difference for control subjects. Also, the striking improvement with practice that Case 1 demonstrated for L targets is not evident for control subjects. Furthermore, Case 1’s impairment was found only for patterned stimuli. In the case of size, contrast, and motion discrimination, she performs normally over the entire range of difficulty, despite the fact that for size discrimination, the L condition was clearly harder for control subjects than the G condition.

The evidence for the selectivity of Case 1’s impairment for patterned stimuli is strong. We dissociated her difficulties with pattern discrimination from normal discrimination of size, contrast, and speed of motion. Fortuitously, we tested her on the texture discriminations after testing her with discriminations of size, contrast, and motion (all on the same day). Thus, we are not concerned that she failed to understand the task, or simply needed practice to execute it. Furthermore, we tested her on additional patterned stimuli on other days, ruling out the possibility that her impairment on any particular day of testing was due to fatigue. The tests were administered without feedback, so Case 1 remained naive about her performance. When asked about the checked patterned test, for example, she did comment that the task became easier with practice, and that she could catch more of the small targets. Finally, we do not believe that her deficits are directly due to her medication (Tegretol) because we have tested other patients on similar or higher doses of medication who incurred unilateral anterior temporal lobe excisions to relieve intractable epilepsy. These 18 patients were not impaired in the G or L conditions on any of these tests.

The stimuli used in the texture discrimination were different from the other patterned stimuli in that the detectibility of individual targets was reduced due to the masking background of vertical lines. Nonetheless, Case 1 was not impaired on a detection version of this task. So, we believe the role of distractors was crucial. Furthermore, we found similar deficits across a range of different patterned stimuli. A common factor in these tests is that the target can not be located based on local luminance variation, but rather by local shape analysis. Our findings suggest that this ability is impaired in Case 1. Her 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 in monkeys is critical for pattern discrimination [32, 45].

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 [12]. It would be reasonable if these levels of processing were the same levels that the visual system relied upon for judgements of saliency. In many visual domains, stimuli that are physically more prominent elicit more neural activity than those that are less prominent [e.g. 50, 51, 52, 60]. Attending to L stimuli may require a special mechanism to override this more fundamental, perhaps automatic, means of directing attention. The results of this study and that of Schiller’s [49] work with monkeys are consistent with the idea that the visual system may have a built in bottom-up mechanism that favors G stimuli. Perhaps, through learning, a top-down mechanism needed to detect L stimuli is enhanced. Such a mechanism for finding less salient elements in a scene may be localized in areas that are relatively dedicated to processing the relevant visual cues. One set of studies found that monkeys with IT lesions (after relearning the oddball-out task) showed persistent difficulties making form discriminations, but not discriminations of luminance, color, and size [28, 29]. These investigators did not specifically contrast discrimination of greater-than versus lesser-than targets.

Case 1’s pattern discrimination performance improved with practice. Interestingly, similar practice effects were described after V4 lesions in monkeys [49]. 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 [19]. This deficit in learning is sometimes thought to exist with relatively spared discrimination thresholds [3]. We do not believe, however, that such a learning deficit exists in Case 1 without some overall loss of pattern discrimination. On several of the pattern discriminations, Case 1’s initial performance started well below the initial performance of NCS.

Case 1’s performance did not systematically differ across target position. We did not expect to find a strong effect of target position, given that Case 1’s lesions were bilateral, and that the visual cortex in the anterior temporal lobe in monkeys is known to represent left and right portions of the visual field [18, 20].

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 distractors, and/or (b) targets were processed in disturbed retinotopic space, whereas the distractors were processed in intact retinotopic space. In contrast, Case 1 had no local field losses, and her lesions were large. Thus, she displayed a deficit in spite of the fact that the more prominent distractors were also subjected to abnormal processing.

4.2. The role of visual attention

In our experiments, 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 (data not reported here). By that time, however, she had considerable practice with the mixed G and L condition, so we cannot dissociate the effects of practice. Under the mixed conditions, which stress visual attentional resources, finding L targets is especially demanding given their low salience. Braun [6] (using stimuli similar to the ones used here) has provided evidence that the discrimination of L but not G targets by normal human observers is severely disrupted in a dual-task situation that is intended to reduce or eliminate selective attention from the task. We are, however, more reluctant than Braun to interpret the impaired L discrimination after V4 lesions in monkeys to result from a supramodal reduction in visual attention. The differential effect of the V4 lesion may be in part related to the greater difficulty of L discriminations. Another complicating factor is the concomitant perceptual impairments that follow a V4 lesion. Evidence regarding the effects of lesions to other monkey visual areas on G versus L discriminations is lacking. Case 1’s impairments were more selective than the monkeys with V4 lesions, and are hard to explain by a defect in visual attentive capacities alone.

Interestingly, a related debate has occurred over whether the pattern discrimination deficits of monkeys with bilateral temporal-lobe lesions should be explained by perceptual or attentive impairments [3]. Butter [8, 9] suggested that the underlying impairment was attentional, i.e. noting the less salient features of visual stimuli, although his lesioned monkeys were capable of doing so with enough training. Other experiments varied the combinations of cues present in stimuli, as well as the relevance of each cue to the correct response, and monkeys with IT lesions seemed to have trouble focusing attention on the relevant cues [8, 9, 17, 28]. These studies, however, invariably found that attention was not focused on pattern cues when luminance, color, or size information was present. It is more parsimonious to assume that the monkeys have a true loss of pattern perception. They may succeed in pattern discriminations (after prolonged learning) by finding unintended features, such as local size or flux cues [32].

Similarly, the symptoms in Case 1 and monkeys with V4 lesions may best be explained as perceptual impairments. The fact that these impairments dissipate with practice is hard to reconcile with the idea that the anatomical locus of visual attention has simply been
removed. We suggest instead that successful L discrimination relies heavily upon cortical processing in order to make the targets salient enough to detect. The cortical locus of such processing may vary according to the visual cues relevant to the task, and may be differentially affected by cortical lesions. The site of processing is nevertheless likely to be distributed among several visual areas. When one area is removed by a lesion, remaining areas may be recruited to support the improved performance with practice.

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. Thus, L discrimination tasks are particularly sensitive to the effects of visual cortex lesions. A testable hypothesis for future studies is that L discrimination performance will be impaired for a given cue when a visual cortex lesion is made at a site known to be critical for processing that cue (e.g., L motion discrimination affected by lesions to motion sensitive area MT).

Acknowledgements

Support for the MIT Clinical Research Center (CRC) was provided by NIH grant RR00088. J.D.M. was supported by training grants from the National Institute of General Medical Science (T32GM07484) and from the National Institute of Mental Health (T32MH15761). S.C. was supported by NIH grants AGN08117 and AG06605. We wish to thank the staff of the CRC for their assistance with patients, Mark Snow for computer programming, and Joseph J. Locasio for statistical support. Nancy Etcoff generously referred Case 1 for study in our laboratory. Karl Zipser, as well as two anonymous reviewers, provided valuable comments on the manuscript.

References

[31] Iwai E, Mishkin M. Further evidence on the locus of the visual