Impairments in Spatial Generalization of Visual Skills After V4 and TEO Lesions in Macaques (*Macaca mulatta*)

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The authors tested the spatial generalization of shape and color discriminations in 2 monkeys, in which 3 visual field quadrants were affected, respectively, by lesions in area V4, TEO, or both areas combined. The fourth quadrant served as a normal control. The monkeys were trained to discriminate stimuli presented in a standard location in each quadrant, followed by tests of discrimination performance in new locations in the same quadrant. In the quadrant affected by the V4 + TEO lesion, the authors found temporary but striking deficits in spatial generalization of shape and color discriminations over small distances, suggesting a contribution of areas V4 and TEO to short-range spatial generalization of visual skills.

Objects can be recognized irrespective of their spatial position in the visual field and of their projection on the retina. The spatial generalization of object recognition, also referred to as *position invariance*, is a fundamental property of high-level vision. A number of studies have investigated the contribution to position invariance of area TE, a visual area at the highest level in the ventral stream for object recognition (Distler, Boussaoud, Desimone, & Ungerleider, 1993; Ungerleider & Desimone, 1986).

Physiological studies have shown that the receptive fields (RFs) of TE neurons are extremely large, spanning both hemifields (Gross, Rocha-Miranda, & Bender, 1972), and that their responses to objects remain relatively constant when translated within these large RFs (Lueschow, Miller, & Desimone, 1994). Lesion studies of the effects of transection of the corpus callosum and anterior commissure in the monkey have shown that the ability to activate TE neurons from the ipsilateral hemifield depends on these crossing fibers, suggesting that spatial generalization across hemifields requires intact commissural connections (Gross, Bender, & Mishkin, 1977; Rocha-Miranda, Bender, Gross, & Mishkin, 1975). This is supported by behavioral experiments in split-brain monkeys (Seacord, Gross, & Mishkin, 1979) and cats (Berlucchi, Buchtel, Marzi, Mascetti, & Simoni, 1978), which demonstrated a lack of spatial generalization of skilled visual discriminations from one hemifield to the other.

The evidence thus suggests that in monkeys, position invariance across hemifields is achieved in area TE, where neurons have RFs that span both hemifields. Gross and Mishkin (1977) further hypothesized that inferior temporal neurons may provide the basis for stimulus equivalence not only across the two hemifields, but also across locations within a hemifield. The possibility remains, however, that neurons in areas at lower levels in the hierarchy of the ventral stream for object recognition (see Desimone & Ungerleider, 1989) contribute to spatial generalization over smaller distances. For neurons whose RFs are centered at an eccentricity of 6°, for example, RF sizes in V2, V4, and TEO are in the order of $2° \times 2°$, $5° \times 5°$, and $10° \times 10°$, respectively, and are restricted to the contralateral hemifield (Boussaoud, Desimone, & Ungerleider, 1991; Gattass, Gross, & Sandell, 1981; Gattass, Sousa, & Gross, 1988). Neurons with these smaller RFs could therefore play a role in the generalization of visual skills over smaller distances within a hemifield.

The present study investigated the spatial generalization of shape and color discrimination after lesions in areas V4 and TEO. Both areas are strongly involved in the processing of shape and color, (Desimone, Schein, Moran, & Ungerleider, 1985; Desimone & Schein, 1987; Gallant, Braun, & Van Essen, 1993; Kobatake & Tanaka, 1994; Schein & Desimone, 1990; Zeki, 1980), and the RFs of V4 and TEO neurons are limited to single visual field quadrants (Boussaoud et al., 1991; Gattass, Sousa, & Gross, 1988). We tested, therefore, whether a lesion in one or both of these two areas would induce a deficit in spatial generalization of shape and color discriminations over small distances within a hemifield.

Method

Subjects and Lesions

The 2 monkeys (*Macaca mulatta*) from De Weerd, Peralta, Desimone, and Ungerleider (1999) were used in the current experiments (M1, ID No. 86042; M2, ID No. RDG2). Both were male and weighed approximately 10 kg. Implant and lesion surgeries, as well as behavioral testing, followed National Institutes of Health guidelines. Implant surgeries involved the placement of a post to immobilize the head and the introduction of an eye-coil in the sclera to monitor eye movements (Robinson, 1963). Details of lesion surgeries have been described elsewhere (De Weerd, Desimone, & Ungerleider, 1996; De Weerd et al., 1999). The lesion in the dorsal part of V4 in the left hemisphere affected the lower, contralateral quadrant of the visual field (Gattass et al., 1988). In the right hemisphere, the lesion in dorsal V4 was extended forward to include all of area TEO, which therefore affected the entire contralateral hemifield in this area (Boussaoud

et al., 1991), in addition to the contralateral lower quadrant affected by the lesion in dorsal V4 (see Figure 1). Lesion reconstruction was based on high-resolution structural coronal slices obtained with MRI (GE 1.5 T, thickness 1 mm, 256 × 160 or 256 × 192 matrix, 4NEX, FOV 10–11 cm). In Monkey M1, all lesions were as intended. In Monkey M2, the V4 lesions were as intended, but the TEO lesion extended anteriorly by about 5mm into area TE (see Figure 1).

Stimuli, Task, and Threshold Measurements

The monkeys sat in a primate chair during daily behavioral testing sessions, and viewed a color monitor from a distance of 57 cm. They were trained to grab a metal lever to turn on a small central red spot, fixate it, and discriminate stimuli presented away from fixation in one of the four visual field quadrants. Trials with eye movements outside a 1.5°-square window centered on fixation were aborted. Standard eccentricity of the stimuli was 5.8°. The standard luminance of the background on which the stimuli were presented was 10.8 cd/m^2 in M1, and 12.0 cd/m^2 in M2. Stimulus and background luminances and colors were re-calibrated frequently with a Minolta spot luminance meter.

Stimuli were presented for 600 ms. During the 1,200 ms after stimulus onset, the monkey was required to release a lever if a standard stimulus was presented, and to hold the lever if the variable comparison stimulus was presented. Correct responses were rewarded with orange juice. Thresholds

were measured by means of an adaptive staircase method, which estimated 84% correct performance (Wetherill & Levitt, 1965). A threshold measurement was based on approximately 100 trials.

A typical testing session consisted of 4 consecutive threshold measurements in each quadrant, with the order between quadrants randomized over sessions. During a single session, one experimental condition was tested in all four quadrants (total of 16 thresholds). Both monkeys executed up to three testing sessions daily, and the experimental condition in each session was picked randomly.

In the shape discrimination task, the monkeys were required to release a lever when a triangle pointed upright, and to hold the lever when the shape deviated clockwise or counterclockwise from the upright position. Threshold performance was expressed as an angle of deviation from the upright position (*shape deviation threshold*). The base of the triangle was 1.5° wide, and the length of the two other sides was 2°. Contrast between the bright triangle and the gray background was 50% (Michelson index, obtained by subtracting the luminance of the background from the luminance of the triangle and expressing the difference as a percentage of the sum).

In the color discrimination task, the monkeys were required to release the lever when a pure blue stimulus was presented (the standard stimulus) and to hold the lever when any mixture of green and blue was presented (the variable stimuli). The variable color stimuli were calibrated so they would fall on a straight line in CIE color space between a pure blue and a
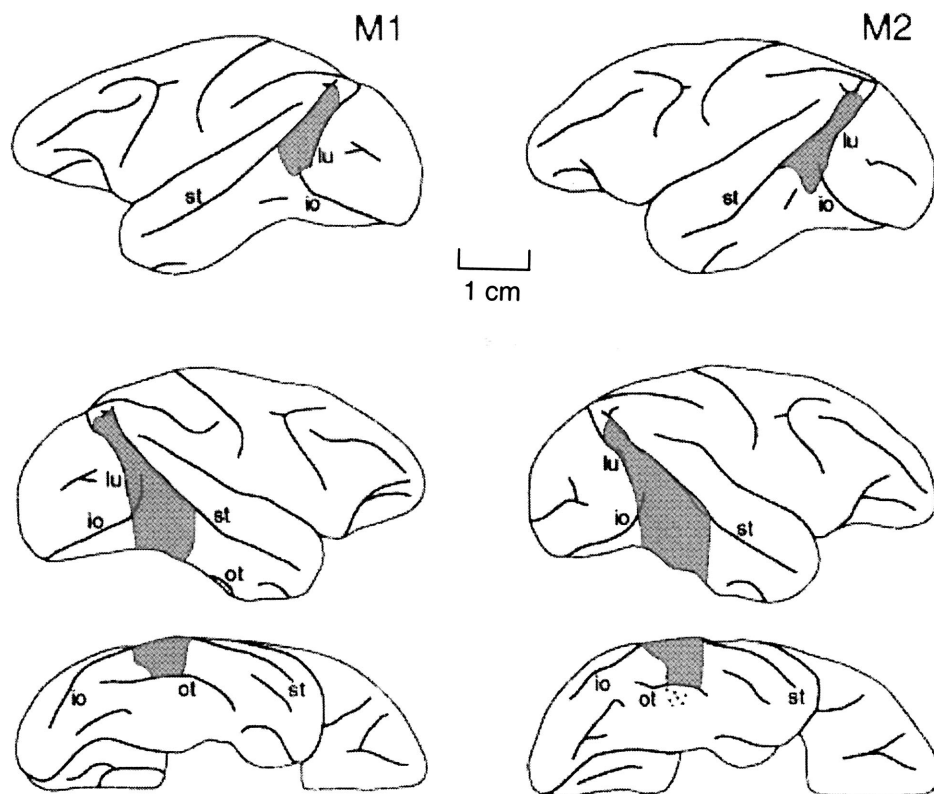

Figure 1. Extent of V4 and TEO lesions in Monkeys M1 and M2. Lateral view of the left hemisphere showing a lesion (in dark shading) in the dorsal part of V4 for Monkeys M1 and M2, shown on top. Below are lateral and ventral views of the right hemisphere showing a lesion in the dorsal part of V4 and in TEO in M1 and M2. The MRI scans suggest unintended damage medial to the occipital temporal sulcus (ot) in Monkey M2 (stippling). lu = lunate sulcus; st = superior temporal sulcus; io = inferior occipital sulcus. From "Loss of Attentional Stimulus Selection After Extrastriate Cortical Lesions in Macaques," by Peter De Weerd, Modesto R. Peralta III, Robert Desimone, and Leslie G. Ungerleider, 1999, *Nature Neuroscience, 2,* p. 753. Copyright 1999 by Nature Publishing Group. Adapted with permission.

pure green. The threshold was expressed as the distance in CIE space between the standard and the variable stimulus corresponding to 84% correct performance (*color discrimination threshold*). The color stimuli were presented in a 2.2° circular aperture and were equiluminant to the background.

The monkeys were first trained and tested with stimuli presented in the standard location (A) in each quadrant, at 5.8° eccentricity. In the normal quadrant, the coordinate of Location A was (4.1°, 4.1°), and position generalization was subsequently tested at Location B (2.5°, 5.7°), Location C (5.7°, 5.7°), and Location D (5.7°, 2.5°). The coordinates of Location A–D in the three lesion-affected quadrants were symmetrical with the positions in the normal quadrant (see Figure 2A). The distance between Location A and each of the other positions within a quadrant was 2.3°.

Results

Training and testing in both discrimination tasks started postoperatively in Location A (standard location) in the 2 monkeys. Learning in Monkey M1 proceeded at a comparable rate in the normal and lesion-affected quadrants for both the shape (Figure 2B) and the color (Figure 2C) discrimination tasks, as illustrated by the comparable rate of threshold decreases in all quadrants (small capital letters on top of each figure panel in Figures 2B–2D refer to locations indicated in Figure 2A). In Monkey M2, unlike M1, original training in the color discrimination task occurred several months prior to the current experiment. In the intervening interval between original training and the current study, the monkey underwent other behavioral testing. On retesting of the color discrimination, shown in Figure 2D, the monkey required some retraining in the lesion-affected quadrants, but not in the normal quadrant. Like M1, Monkey M2 eventually reached asymptotic performance in all quadrants, after which spatial generalization was tested.

To evaluate whether thresholds were elevated after moving the stimuli from the standard location to one of the test locations, thresholds in test Locations B, C, and D were compared to the 99% upper confidence limit calculated on the second half of measurements obtained in Location A in each quadrant (dashed lines in Figure 2). When the stimuli were moved for the first time to a new location in the normal quadrant (Location B), shape and color thresholds remained unaffected by this change in stimulus position (see Figures 2B-D), indicating that there was immediate spatial generalization for both monkeys in the normal quadrant. In the panel depicting performance in the normal quadrant in Figure 2D, the line indicating the 99% confidence limit is hard to notice because thresholds hovered closely around that limit.

By contrast, when the stimuli were moved for the first time to a new location (Location B) in the V4 + TEO lesion-affected quadrant, thresholds increased strongly, both for the shape discrimination task (Figure 2B), and for the color discrimination task (Figures 2C and 2D). On the order of 10 threshold measurements in M1 (Figure 2B, C) and on the order of 30 measurements in M2 (Figure 2D) were required to bring thresholds back within the range of thresholds obtained in the standard location. By the second or third time the stimuli were moved to a new location (Locations C and D, respectively), the change in location was no longer followed by a threshold increase.

The effect of positional translation was small or absent in quadrants affected by a single lesion. The only exception was the V4-affected quadrant of Monkey M1, where the shape discrimi-

nation thresholds increased significantly after the first change in location, but not after the second. As documented in a previous study with the same 2 monkeys (De Weerd et al., 1999), both monkeys retained excellent acuity and contrast sensitivity in all lesion-affected quadrants.

Discussion

We trained 2 monkeys in easy color and shape discriminations in a fixed, standard location of quadrants affected by a lesion in V4 and/or TEO and found only minimal impairment, in agreement with previous reports on the effects of V4 lesions (Desimone, Wessinger, Thomas, & Schneider, 1990; Heywood & Cowey, 1987; Merigan, 1996; Schiller, 1993; Schiller & Lee, 1991; Walsh, Carden, Butler, & Kulikowski, 1993; Walsh, Kulikowski, Butler, & Carden, 1992; Wild, Butler, Carden, & Kulikowski, 1985), TEO lesions (Iversen, 1973; Iwai & Mishkin, 1969), lesions of V4 and TEO combined (Cowey & Gross, 1970), and lesions of TEO including TE (Britten, Newsome, & Saunders, 1992; Dean, 1976, 1978; Gaffan, Harrison, & Gaffan, 1986; Huxlin, Saunders, Marchionini, Pham, & Merigan 2000; Iwai, 1985). However, we found that the presentation of the discriminanda in a new location (2.3° from the standard location) systematically impaired performance in the V4 + TEO-affected quadrant. In 1 monkey, we also observed a spatial generalization deficit in a quadrant affected by a V4 lesion alone. No such deficit was observed in the normal quadrant in either monkey. Thus, whereas Gross and Mishkin (1977) proposed that area TE was the substrate for spatial generalization not only across hemifields, but also within hemifields, the present study indicates that areas V4 and TEO also contribute to the ability to generalize perceptual skills, and these areas may be particularly important for generalization over small distances within a hemifield.

Within lesion-affected quadrants, the ability to generalize the skill recovered with repeated repositioning of the stimuli. This recovery was unlikely to be related to the particular locations we chose. The second generalization test (in Location C) was performed at a greater eccentricity than the first generalization test (in Location B), and therefore, a decline in performance might have been predicted, rather than the recovery that we observed. What then is the mechanism for this recovery? One possibility is that the recovery is mediated by V2 neurons, which often show stimulus selectivity for shape and color (DeYoe & Van Essen, 1985; Kruger & Gouras, 1980; Zeki, 1973, 1978) and have RFs of approximately 2° at our standard location of 5.8° eccentricity (Gattass et al., 1981). Alternatively, TE neurons, which can be driven visually even after a combined lesion in V4 and TEO (Buffalo, Bertini, Ungerleider, & Desimone, 2000), could be instrumental in the recovery.

A deficit in generalization over space has also been observed by Li and Desimone (1991) in a monkey in which one visual field quadrant was affected by a V4 lesion and the remaining quadrants were intact. Shape discrimination was tested in each quadrant by presenting stimuli away from fixation (about 5° eccentricity), using a match-to-sample paradigm. Slightly lower performance was found in the V4-affected quadrant (82% correct) compared with the normal quadrants (95% correct). However, when the choice stimuli (match or nonmatch) were presented in a different location than the sample in the V4-affected quadrant, performance
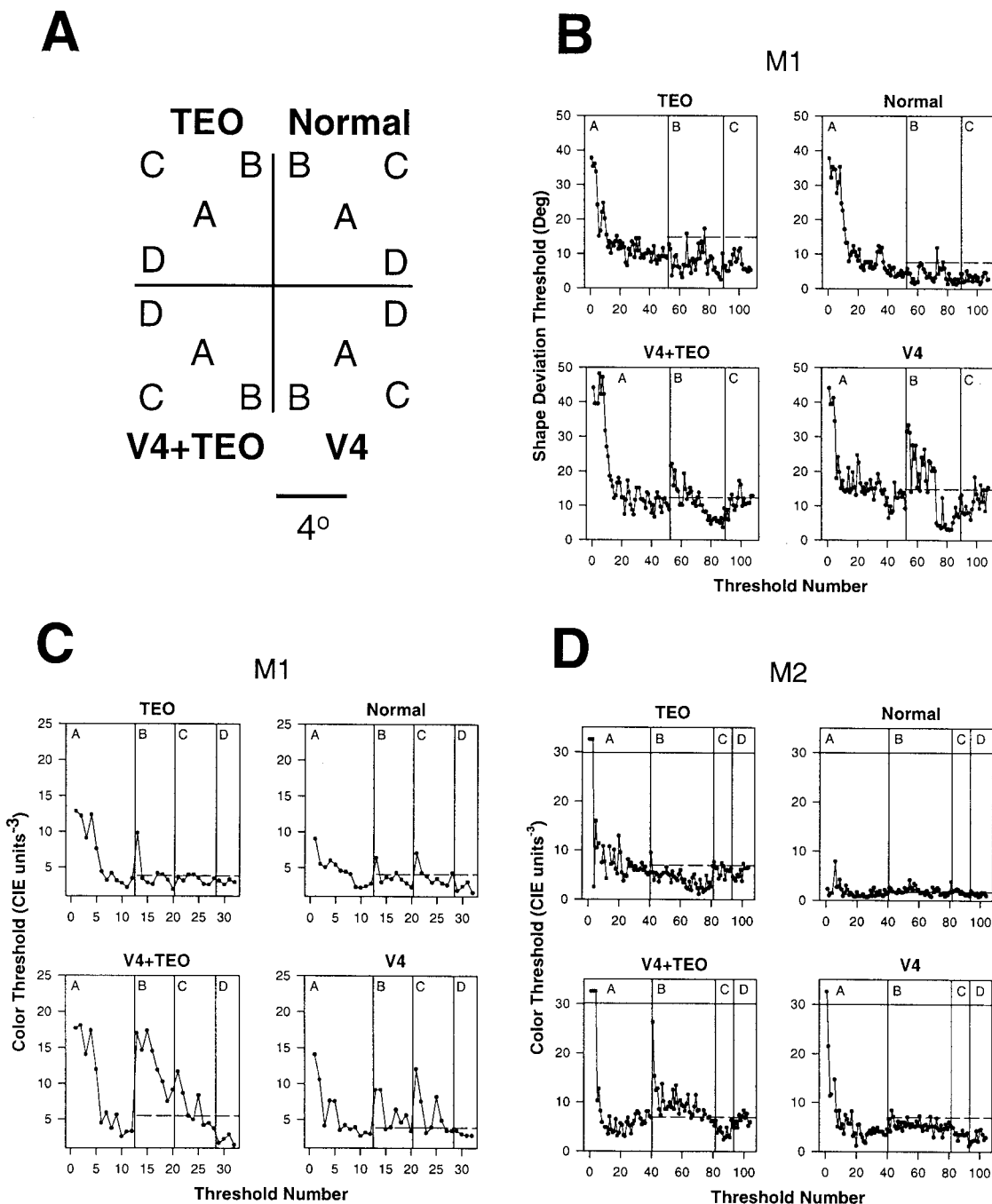
Figure 2. Generalization of visual skills across space within quadrants. A: Schematic representation of the
standard location (A) and test locations (B, C, and D) in the normal quadrant, and quadrants affected by a lesion
in V4, TEO, or V4 and TEO. For exact coordinates of the stimulus positions, see the Method section. B:
Generalization of shape discrimination in the normal and three lesion-affected quadrants (V4, TEO, V4 + TEO)
from a standard location (A) to two other locations (B and C) in Monkey M1. C: Generalization of color
discrimination in the normal and three lesion-affected quadrants (V4, TEO, V4 + TEO) from a standard location
(A) to three other locations (B, C, and D) in Monkey M1. D: Generalization of a color discrimination in the
normal and three lesion-affected quadrants (V4, TEO, V4 + TEO) from a standard location (A) to three other
locations (B, C, and D) in Monkey M2. Each data point represents 84% correct thresholds from approximately
100 trials, and the dashed line represents the upper limit of a 99% confidence interval for normal performance
(see the Method section for details).

fell to chance (48% correct), indicating a deficit in the ability to compare stimuli presented sequentially in different locations. No such impairment was found in the normal quadrants (92% correct). Although the task in this study differed from the one used in the present study, these findings provide further support for the notion that spatial generalization is impaired after extrastriate lesions upstream from area TE.

Despite the significant degree of spatial generalization found within the normal quadrant for the monkeys in this study, and across hemifields in normal monkeys (Gross et al., 1977; Seacord et al., 1979) and cats (Berlucchi et al., 1978) in prior behavioral studies, other studies have demonstrated that when a visual discrimination is trained in a given location, the skill that is achieved with practice can be highly specific to that location (Crist, Kapadia, Westheimer, & Gilbert, 1997; Fahle, 1997; Karni & Sagi, 1991, 1993; Schoups, Vogels, & Orban, 1995). For example, Karni and Sagi (1991) trained human subjects to detect a target defined by three line segments on a background of differently oriented line segments. Target detection performance in a trained location was compared with performance in a symmetric location in another quadrant, and no evidence for generalization was found. Even more impressive, Schoups et al. (1995) found a virtually complete lack of generalization in orientation discrimination when a small grating (with a diameter of 2.5°) was shifted by only 2.5°.

These data on orientation discrimination appear to be at odds with the greater generalization we found with shape and color discrimination in the normal quadrant of the visual field in our monkeys. Because of the similar design and methods used in our study and the one from Schoups et al. (1995), technical differences are insufficient to explain the greater generalization in our study. However, a possible explanation is that the different degrees to which performance in particular discrimination tasks generalizes over space reflects properties of the neural substrates that contribute to the discrimination. In particular, it has been suggested that the lowest level at which sensory analysis during skill learning takes place is an important site for the formation of procedural memories for that skill (Karni & Sagi, 1991, 1993). Direct support for this idea has come from both neurophysiological studies in monkeys (Crist, Li, & Gilbert, 2001; Schoups, Vogels, Qian & Orban, 2001) and imaging studies in human subjects (Schwartz, Maque & Frith, 2002; Vaina, Belliveau, des Roziers, & Zeffiro, 1998). Thus, the high level of position specificity after training on a simple line orientation discrimination task might reflect mechanisms at the earliest level of visual analysis, possibly as early as V1 (for review, Karni & Bertini, 1997), where RFs are small. By contrast, the greater degree of spatial generalization for more complex shape and color discriminations might reflect the recruitment of higher level extrastriate areas, such as V4 and TEO (Desimone et al., 1985; Desimone & Schein, 1987; Gallant et al., 1993; Kobatake & Tanaka, 1994; Schein & Desimone, 1990; Zeki, 1980), where the RFs are larger. According to this reasoning, neurons with smaller RFs may be involved in the formation of procedural memories that support skilled orientation discriminations, whereas neurons with larger RFs may be involved in the formation of procedural memories that support skilled shape and color discriminations. If the RFs of neurons involved in the formation of procedural memories set a limit on spatial generalization, then a larger degree of spatial generalization would be expected during skilled color and shape discriminations than during skilled orientation discriminations.

Selective attention to a visual target stimulus is usually a condition for the acquisition of skilled discriminations of that stimulus (Ahissar & Hochstein, 1993; Ahissar et al., 1992; Karni & Sagi, 1991; Shiu & Pashler, 1992). Previous physiological (Chelazzi, Miller, Duncan, & Desimone, 1993; Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999) and brain imaging (Kastner, De Weerd, Desimone, & Ungerleider, 1998; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999) studies have shown that the spatial extent over which competitive attentional interactions take place is determined by RF size. Further, De Weerd et al. (1999) showed that the spatial extent over which distracters interfered with target discriminations in quadrants affected by a lesion in V4 or TEO could be predicted from the size of RFs of neurons removed by the lesions. In combination with these findings, the current study suggests that RF size may set an upper limit to both the spatial extent of attentional competition and the extent of spatial generalization to which an area can contribute. Hence, in normal vision, the competitive attentional mechanisms recruited during the acquisition of a visual skill may set limits on subsequent spatial generalization of performance.

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