Lesions in Cat Lateral Suprasylvian Cortex Affect the Perception of Complex Motion

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We examined the effects of bilateral ibotenic acid lesions of cat lateral suprasylvian (LS) cortex on motion perception. Cats were tested on tasks requiring integration of local directional signals, precise judgements of direction and extraction of structure-from-motion. All animals showed permanent deficits in integrating local motion signals. These deficits were most pronounced in the presence of directional noise and at larger spatial displacements. In addition, LS lesions produced a 2-fold loss in the accuracy of direction discrimination and large deficits in the perception of structure-from-motion. All of these losses were most severe during the first few weeks of testing following the lesion. These findings demonstrate that LS cortex plays an important role in the processing of stimuli requiring integration of motion information and limits the spatial scale over which such integration can proceed. Partial improvements in performance with time and/or training may be indicative of post-operative plastic changes in neurons outside of LS cortex.

Physiological recordings from the lateral suprasylvian (LS) cortex of the cat have revealed neuronal properties that implicate this region in the processing of visual motion information (for a review see Spear, 1991). Palmer et al. (1978) identified six subdivisions in LS cortex on the basis of separate topographic maps (AMLS, ALLS, PMLS, PLLS, DLS and VLS). Receptive field characteristics have been studied in only PMLS and PLLS. These two areas exhibit similar receptive field characteristics, including relatively large receptive fields, high proportions of neurons selective for the direction of target motion, general preference for low spatial and high temporal frequencies, and binocularity (Hubel and Wiesel, 1969; Spear and Baumann, 1975; Morrone et al., 1986; von Grunau and Frost, 1983). In preferred directions away from the area centralis (Rauschecker et al., 1987), sensitivity to properties of object movement in three dimensions (Toyama et al., 1985), responses to lens accommodation and the near response (Bando et al., 1984), and visuomotor and purely eye movement-related responses (Yin and Greenwood, 1992). Taken together, these physiological data suggest that PMLS and PLLS may be involved in the processing of both object motion and optic flow fields.

Behavioral evidence from 2-deoxyglucose and lesion studies suggests that PMLS may be involved in the generation of optokinetic nystagmus (Wood et al., 1973; Ventre, 1985; Herdman et al., 1989; Tus et al., 1989) and some aspects of visual orientation, attention and approach behaviors (Hardy and Stein, 1988; but see Spear et al., 1983). Pasternak et al. (1989) showed that while lesions of LS cortex did not affect sensitivity to the direction of motion of simple sinusoidal gratings, they reduced the precision with which cats discriminate differences in the speed of these gratings. The present study examines whether the areas within LS cortex previously implicated in motion processing (PMLS and PLLS) are involved in the discrimination of direction of more complex stimuli, which require integration of local motion information.

Materials and Methods

Subjects

Four adult cats were used. Each was maintained at ~80% of its free-feeding body weight during the course of training and behavioral testing. Free water was provided in the home cage and, in addition to pureed beef baby food received as a reward, intake was supplemented daily with dry cat food. For the duration of the study, animals were cared for according to guidelines as published by the National Institutes of Health.

Stimuli

We used random-dot stimuli identical to those described in Pasternak et al. (1995; see their fig. 12a–c). These stimuli comprise 75 dots (1 dot/deg\(^2\)) in apparent motion against a dark background. The direction of each dot is chosen independently from a specified distribution ranging in width from 0 to 360 deg. When all dots move in the same direction (direction range = 0), the display has the appearance of a coherently moving sheet of dots. When the range of directions in the distribution is >0, the percept of a 'global' direction of motion emerges. With appropriately chosen spatial and temporal parameters, humans, monkeys and cats can reliably discriminate between opposite mean directions of these displays when the range of directions is as broad as 330 deg (e.g. Williams and Sekuler, 1984; Pasternak et al., 1990; Pasternak and Merigan, 1994). The dot stimuli were displayed on a Tektronix 606 oscilloscope with a P31 phosphor. Targets were 7.0 deg in diameter and were viewed through two adjacent, circular apertures from a distance of 35 cm. The dots were 0.08 deg in diameter and their luminance was set at 3.5 log units above the detection threshold for human observers. The mean luminance of the display was 0.1 cd/m\(^2\) and there was no visible streaking of the phosphor when the dots moved across the display.

The structure-from-motion stimulus was similar in design to that used by Siegel and Andersen (1986, 1988) and Treue et al. (1991). Dynamic random dots were used to create an orthographic projection of points on a rotating transparent cylinder which was perceived to rotate around a vertical axis. The stimuli consisted of 128 leftward- and rightward-moving dots which were assigned velocities dependent upon their horizontal position with respect to the center of the cylinder: dots near the middle of the display moved faster than did dots near the edges. This continuous change in velocity across space creates a 3-D percept of a cylinder. Dots survived for a pre-determined time, were plotted anew and eliminated asynchronously. This asynchrony prevented tracking of individual dots as the apparent cylinder rotated. Dot density along the vertical edges of the cylinder was adjusted to prevent accumulation of dots that could serve as a 'non-motion' cue. 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assigned a velocity independent of its position.) This resulted in the display having the appearance of a 2-D field of dynamic noise of the same average velocity as the 'structured' stimulus. The stimuli were 7.2 deg\(^2\) and were displayed on a 16" Apple Monitor.

**Behavioral Procedures**

Cats were trained to perform three basic tasks: (i) discrimination of opposite directions of dot motion; (ii) discrimination of small differences in the direction of dot motion; and (iii) discrimination of 'structured' from 'unstructured' targets (described above) in the structure-from-motion task.

In a two-alternative spatial forced-choice procedure, pairs of stimuli were presented, side-by-side, for a duration of 2 s. The cats were rewarded for pressing with their noses the glass response panel on the side corresponding to the location of the rightward-moving stimulus in the direction discrimination task and the rotating cylinder in the structure-from-motion task. Errors resulted in a 10 s tone and no food reward. To eliminate position bias, a correction procedure was used: three consecutive incorrect responses on the same side resulted in a trial being repeated until the animal responded correctly.

**Direction Discrimination Task**

The cats were first trained to discriminate between opposite directions of motion, with stimuli consisting of all dots moving in parallel (0 deg range, 100% motion signal) and a step size of 0.15 deg. After animals had learned this task to criterion (three successive sessions at 90% correct performance or four successive sessions at 80% correct), the same procedure was used to train them to discriminate between rightward and downward motion in preparation for measuring direction difference thresholds.

**Structure-from-Motion Task**

The cats were trained to discriminate between 100% 'structured' (rotating cylinder) and 'unstructured' (velocity-randomized) targets of the same size. For training, the dot lifetime was set to 2000 ms and the speed of rotation of the cylinder to 187 deg/s. Once animals performed this task at a criterion level, the optimal dot lifetime and speed of rotation were determined for each animal. On that basis, the lifetime and speed of rotation were chosen as follows: cat 148, 500 ms and 180 deg/s; cat 155, 625 ms and 125 deg/s. Under these conditions, human observers were unaware of using extraneous, local cues and their thresholds were ~15% 'structure' (see below).

**Threshold Measurements**

Thresholds were measured with a staircase procedure, in which task difficulty increased after three consecutive correct responses and decreased after a single error. The order of tasks was random within and across cats. Each session consisted of 200 trials and thresholds were determined from the resulting psychometric function as the stimulus value at which performance was 75% correct.

**Direction Range Thresholds**

Direction range thresholds were measured by varying the range of local directions in the dot pattern. When direction range was 0 deg, all dots moved in parallel. When direction range was 180 deg, individual dots moved in a direction chosen from a distribution 180 deg wide.

**Varying Directional Noise**

Direction range thresholds were also measured in the presence of a variable proportion of dots moving in random directions ('noise'), created by assigning each dot an independent direction chosen from a range of 360 deg. Thresholds were measured by setting the direction range of 'signal dots' to 0 deg and varying the proportion of randomly moving ('noise') dots in the display. For example, a motion signal threshold of 10% means that the observer requires 10% of the dots to be moving in parallel while the remaining 90% move at random.

**Motion Signal Thresholds**

Motion signal thresholds were measured by varying the proportion of dots moving in random directions ('noise') in the display. For example, a motion signal threshold of 10% means that the observer requires 10% of the dots to be moving in parallel while the remaining 90% move at random.

**Varying Spatial Displacement**

Range thresholds were also measured at various spatial displacements (i.e. step size, ∆x). The spatial limit (d\(_{max}\)) of direction discrimination was determined by varying the size of the spatial displacement of the dots. The temporal interval (Δt) between new frames was varied to maintain a constant speed (15 deg/s, unless noted otherwise).

**Direction Difference Thresholds**

Direction difference thresholds were measured by varying the angular difference between the directions of motion of the two comparison stimuli, one of which moved rightward (correct choice). We measured direction difference thresholds as a function of the range of dot directions. When measuring direction difference thresholds, the proportion of motion signal was held constant at 100%. The side on which the rightward moving target appeared was random from trial to trial.

**Structure Thresholds**

Structure thresholds were measured by varying the proportion of dots in the 'structured' stimulus which moved with a velocity appropriate for their spatial location in the stimulus. 'Percent structure thresholds' are the lowest percent structure required for reliable discrimination of this partially structured stimulus from the unstructured stimulus.

Post-operative testing began 2-10 days after the lesions and continued over a period of approximately 6 months. Although the study was not designed to evaluate the early effects of the LS lesion, we were able to collect such data from two of the animals (cats 155 and 148) by measuring several thresholds a day during the first postoperative week. After that time, and throughout postoperative testing, performance on each task was studied in more detail by concentrating on a particular task and stimulus manipulation for many consecutive sessions before switching to another task. All thresholds were re-measured at numerous dates throughout the course of the study. Animals were tested 5 days per week, except during the first 2 months post-lesion, when they were tested 6-7 days per week.

**Lesions**

The lesions were made by injecting the glutamate agonist, ibotenic acid (10 μg/μl; pH normal phosphate-buffered saline vehicle), at multiple sites in the medial and lateral banks of the lateral suprasylvian sulcus in both hemispheres, covering a range from ~P-2.0 to A8.0 in Horsley-Clark stereotaxic coordinates. In three of the cats, 24-28 μl injections were made at 2-3 depths at multiple sites separated by 2 mm. In cat 140, eight injections of 1-1.2 μl were made into PMLS (medial bank) in each hemisphere. These injections were made at two depths at each of four sites separated by 4 mm. Surgeries were performed under sterile, aseptic conditions and animals were maintained in a surgical plane of anesthesia with isoflurane gas.

**Histology**

At the conclusion of behavioral testing, each animal was killed with an overdose of sodium pentobarbital and perfused with a phosphate buffer rinse followed by 4% paraformaldehyde in 0.1 M phosphate buffer (pH 7.4). The brain was removed, blocked and sectioned at a thickness of 40 μm. At intervals of 160 μm, sections were stained for cytochrome oxidase (Wong-Riley, 1979) and Nissl substance.

**Results**

**Lesion Reconstruction**

In sections stained for cytochrome oxidase, the lesions appeared as well-defined regions of little or no reactivity (for an example photomicrograph of a CO-stained coronal section through LS cortex see fig. 1 in Pasternak et al. (1989)). In cresyl violet-stained sections these regions were characterized by an unusually high density of glia and few, if any, normal neurons. The borders of the lesion defined by the two techniques corresponded very closely.
The areas of damage were reconstructed using both the cytochrome oxidase and cresyl violet-stained sections (Fig. 1).

In interpreting the extent of the lesions and their effects, it is important to keep in mind two factors. First, areas within LS cortex contain retinotopic maps which can vary greatly between animals. Since our lesion reconstructions were based on published retinotopic maps (Palmer et al., 1978) and there are no obvious cytoarchitectonic borders between areas within LS cortex, our assignment of damage to specific subdivisions and specific visual field representations should be treated only as an approximation. Second, the eye movements of the animals were not controlled during psychophysical testing, and thus the cats were likely to use any spared representation even if it was limited to a single hemisphere. Therefore, it is mainly bilateral damage to an area, including most of the representation of the central visual field in both hemispheres, that will have the most pronounced effects on behavior.

**Cat 140**

PMLS was damaged bilaterally, with probable involvement of the representation of the area centralis, but with some sparing of the near peripheral visual field representation. In PLLS and DLS of both hemispheres there was only minor involvement affecting the more central representation. Area 7 was damaged substantially in the left hemisphere but to a lesser extent in the right hemisphere. There was also a unilateral involvement of areas 21a, 18 and 19.

**Cat 151**

All of the subdivisions of LS cortex except VLS were affected by the lesion. The damage was confined largely to the superficial layers (layers I-III), with the exception of PLLS in the left hemisphere, which was damaged throughout much of its extent through all six layers. It is possible that there was sparing of the central representation in PLLS and PMLS in the left hemisphere.
Cat 148
PMLS, PLLS and DLS were completely lesioned in both hemispheres. There was also some damage to AMLS and ALLS, possibly including some of the representation of the central visual field in these areas, a small amount of damage to the more peripheral representation in area 19 (beyond 10 deg) and a very small amount of disruption in area 7.

Cat 155
This lesion included most of PMLS and PLLS in both hemispheres, sparing only the most anterior portions, which do not contain representation of the area centralis. In addition, area DLS sustained extensive bilateral damage and there was partial damage to area VLS. There was unilateral, partial damage to area 18, which affected only a portion of the posterior representation. There was also substantial bilateral damage to area 19, but the central representation was likely spared. Damage to area 7 was primarily to the more posterior portions and substantial in only one hemisphere. Finally, there was some bilateral damage to area 21a and unilateral damage to 21b.

In summary, all cats received bilateral damage of areas PMLS, PLLS and DLS. In addition, there was partial damage bilaterally to AMLS and ALLS in cats 151 and 148, and to VLS, 19 and 21a in cat 155. This damage, however, was largely peripheral and was unlikely to include all of the central representation in any of these other areas.

Inspection of the lateral geniculate nucleus and medial interlaminar nuclei of the thalamus of each cat revealed no visible cell loss or abnormalities.

Global Motion Thresholds
The effects of LS cortex lesions on integration of local directional signals are shown in Figure 2. Range thresholds are plotted as a function of the proportion of dots with biased direction distributions (% motion signal). In the absence of randomly moving dots (100% signal), pre-operative range thresholds for discriminating opposite directions of motion were >300 deg. As the percentage of motion signal decreased, the cats were able to perform the task only with stimuli containing narrower ranges of direction. The limit of this performance (i.e. the motion signal threshold) was measured with stimuli containing variable proportions of coherently (0 deg range) and randomly (360 deg range) moving dots. Preoperatively, this limit was determined in three of the cats and ranged from 4.5 to 9%. In cat 140 the motion signal threshold was not measured directly prior to the lesion.

The lesion resulted in elevations of range thresholds in all cats. Deficits were greatest at lower levels of motion signal and were most evident in postoperative elevations of motion signal thresholds (2-fold for cats 140, 151 and 155; -6-fold for cat 148).

The data shown in Figure 24 represent thresholds measured during the last few months of the study. We were able to measure performance at relatively early times after the lesion in two animals. In cat 155 we measured range thresholds during the first week following the lesion and in cat 148 during the second post-operative week. These data (Figure 2B) show that during the first 2 weeks after the lesion range thresholds were strongly affected even in the absence of directional noise. Range thresholds improved with time to the level represented by the final measurements (Figure 2A). Note that the deficit in cat 148 first measured during the second week after the lesion was modest compared with that measured in cat 155 during the first week after the lesion. This difference may be an indication that partial recovery of motion integration takes place during the first post-lesion week.

The effect of LS lesions on the spatial limit of motion integration is shown in Figure 3. Pre-operative range thresholds decreased with increasing step size. The limit of performance (dmax), which was measured by varying the step size of dots moving in parallel (direction range set to 0 deg), ranged between 1.2 and 1.6 deg.

At small step sizes (0.15 deg) the effect of the lesion was rather limited. However, at larger spatial displacements, the
deficits were more pronounced and the maximal spatial displacement ($d_{max}$) was decreased. Early effects of the lesion were measured only in cat 155. These data show that the severe deficit in range thresholds observed in the first post-operative week was even more pronounced for large spatial displacements.

![Figure 3](image1.png)

**Figure 3.** Range thresholds for opposite direction discrimination as a function of dot step size ($\Delta x$). All dots in the display had a pre-determined, non-random distribution of directions (100% signal). $d_{max}$ was measured directly for cats 151, 155 and 148 only, by keeping the direction range constant at 0 deg while varying $\Delta x$. Postoperatively, cat 140 was unable to perform the task at a step size of 0.75 deg (indicated by an arrow). $\Delta t$ was co-varied to keep speed constant at 15 deg/s for all cats except cat 140, for whom $\Delta t$ was co-varied to keep speed constant at 5 deg/s. Error bars are SEM.

The effect of LS lesions on the ability to discriminate small differences in direction is shown in Figure 4. Before the lesion, direction difference thresholds for stimuli consisting of dots moving in parallel (0 deg range) ranged between 6 and 20 deg for the four cats. As the direction range increased beyond 90 deg, accuracy decreased substantially.

![Figure 4](image2.png)

**Figure 4.** Direction difference thresholds as a function of direction range. On each trial, cats discriminated between two stimuli differing in direction by 90 deg or less. One of the targets always moved rightward and the other, in a direction between downward and rightward. Motion signal: 100%. Error bars are SEM. For cat 140, $\Delta x = 0.15$ deg, $\Delta t = 30$ ms (5 deg/s). For cats 148 and 151, $\Delta x = 0.225$ deg, $\Delta t = 15$ ms (15 deg/s). For cat 155, $\Delta x = 0.15$ deg, $\Delta t = 10$ ms (15 deg/s). Error bars are SEM.

The lesions produced an ~2-fold loss in accuracy and this effect was largely independent of direction range. An exception was cat 155's final threshold for 270 deg range. Four weeks after the surgery, this animal showed threshold elevations under all conditions, and was unable to discriminate directions when dots moved in a 270 deg range of directions. However, at the time of final testing (~6 months post-op), intact and lesioned performance in this condition were the same.

**Structure-from-Motion**

The data in Figure 5A show that preoperatively, the cats learned to perform the structure-from-motion discrimination in <20 sessions.

Immediately after the lesion, the cats were unable to perform the task. With extensive training, cat 148 relearned the task and we were able to measure the percentage structure threshold under conditions identical to those used in pre-operative training. This threshold remained substantially elevated even 6 months after the lesion (Figure 5B). Cat 155 never again performed even the simplest version of the task at better than chance level. In an attempt to find stimulus conditions which would support some residual performance, we tried longer dot lifetimes (1600–3000 ms), higher speeds of rotation (134–257 deg/s) and doubling the size of the stimulus. However, none of these changes facilitated relearning, even after 60 training sessions, some of which took place soon after the lesion and others up to 8 months post-lesion.

**Discussion**

Lesions of LS cortex resulted in deficits in the integration of local motion information which were most pronounced in the presence of directional noise and at larger spatial displacements. The lesions also produced a loss in the accuracy of direction discrimination and a severe deficit in the perception of structure-from-motion. The magnitude of the behavioral deficits was related to the extent of the lesion. Large, bilateral lesions of areas PMLS, PLLS and DLS produced larger deficits in tasks requiring 2- and 3-D motion integration than did sub-total lesions of these areas. The accuracy of direction discrimination, on the other hand, was significantly affected in all animals.

**Correlation of Behavioral Deficits with Lesion Extent**

**Opposite Direction Discrimination**

The magnitude of the deficits on this task generally scaled with the degree of anatomical damage to LS cortical areas. Cat 148, whose psychophysical results show the greatest effect of the lesion, had complete damage to PMLS, PLLS and DLS, and some damage to the representation of the central visual field in areas AMLS and ALLS as well. By comparison, cat 155's deficit was a bit less pronounced and the lesion in this animal spared some tissue in anterior PMLS and PLLS as well as in the central representation.
of DLS. The lesions were even less extensive in cats 140 and 151, with some sparing of the near peripheral representation in PMLS, PLLS and DLS. These animals showed deficits only at lower levels of motion signal and at larger spatial displacements. The deficits in cat 151 were somewhat greater than those in cat 140, which might be related to significant involvement of AMLS and ALLS in that animal's lesion.

Small Direction Difference Discrimination

The effects of the lesion on this task also scaled fairly well with lesion size. At first glance, it appears that the data for cat 155 are an exception to this rule, since that animal's loss was less dramatic than that of cats with less extensive lesions. However, the pre-operative performance of this animal was not nearly as good as that of cats 140 and 151, so that the smaller effect of the lesion may be related to insufficient pre-operative training, resulting in relatively high pre-lesion thresholds. Note that post-operative thresholds of this animal fall between those of cats 140 and 151 (less damage) and the post-operative thresholds of cat 148 (more damage).

Structure-from-Motion

Since this task was studied only in the two animals with the largest lesions, it is difficult to relate the magnitude of the behavioral deficit to the extent of the lesion. While the effect of the lesion was significant in cat 148, it was even more severe in cat 155, the animal with the less extensive lesion. One possible explanation for the more profound deficit in cat 155 may be partial damage to areas 19 and/or 21a, which have been hypothesized to play roles in form perception (for a review see Spear, 1991). Further studies are needed to clarify which cortical area(s) involved in the lesion in cat 155 played a critical role in the performance of this task.

Motion Integration

While permanent deficits in motion integration were greatest in the presence of directional noise, during the first 2 weeks following the lesion there were also severe deficits even in the absence of noise (see Fig. 2B). The severity of the early deficits may indicate that LS cortex plays an important role in the integration of local directional signals. It is possible that the limited extent of the permanent deficits in the absence of noise is due to cortical reorganization after the lesion. Whether the improvement in performance is due to extensive behavioral training or to the passage of time is not clear.

The effect of LS lesions on motion integration was similar to that observed in monkeys with large bilateral lesions of areas of MT and MST (Pasternak and Merigan, 1994). As in the present study, severe loss in the noise-free condition was seen only shortly after the lesion. Moreover, monkey MT/MST lesions did
not affect contrast sensitivity for the direction of motion of simple gratings, like the result previously reported for LS lesions in the cat (Pasternak et al., 1989). The similarity between the effects of LS and MT/MST lesions on motion integration supports the notion that the two areas may make similar contributions to the processing of complex motion in the two species (Spear, 1991).

This proposal, however, was questioned by Gizzi et al. (1990), who recorded physiological properties in PMLS and failed to find neurons with selectivity for pattern motion, a property found in many neurons in monkey MT (Movshon et al., 1985). Since responses to pattern motion are an indication of the capacity of neurons to integrate local directional information, the absence of this property in PMLS could indicate that this area lacks the machinery necessary for the analysis of complex motion. On the other hand, our results suggest that neurons in LS cortex do make an important contribution to the integration of local motion information contained in random-dot patterns. One possibility is that, because they contain a larger number of directional components, dot stimuli are more effective in stimulating 'pattern direction' selective neurons in PMLS than the gratings stimuli used by Gizzi et al. (1990) to create their plaid pattern motion. Alternatively, it may be the case that neurons in PMLS are not themselves pattern direction selective but provide the necessary input to pattern direction selective neurons elsewhere in cortex. Indeed, neurons responding selectively to pattern motion have recently been identified in area EVA (Scannell et al., 1994), which receives inputs from LS cortex (Symonds and Rosenquist, 1984).

Accuracy of Direction Discrimination
The lesion resulted in a loss of accuracy in direction discrimination which appears to be unrelated to the deficit in motion integration, since increasing direction range did not substantially increase the deficit. Similar deficits have been observed in cats with widespread reduction in the number of directionally selective cells (Pasternak et al., 1990; Rudolph et al., 1994) and in monkeys with MT/MST lesions (Pasternak and Merigan, 1994). This similarity suggests that the decrease in accuracy may be related to the loss of a large number of DS neurons. A line-element model of direction discrimination (Watamaniuk et al., 1989; Rudolph et al., 1994) predicts loss in precision with decreased number of directionally tuned mechanisms, since the sensitivity of these mechanisms, the sharpness of their direction tuning and the fidelity of the process with which these signals are pooled are the major factors in direction judgement accuracy. Since LS lesions do not result in decreased sensitivity to the direction of motion of drifting gratings (Pasternak et al., 1989), reduced sensitivity of simple directional mechanisms is unlikely to be a factor in the reduced accuracy observed here. The most likely explanation for this deficit is variability in the pooling process, resulting from the loss of 'higher level' directional neurons in LS cortex.

Extracting Motion Information from Noise
There is evidence for a role of neurons in monkey MT and in the superior temporal region of human cortex in the extraction of motion information from noise (Newsome et al., 1989; Baker et al., 1991; Pasternak and Merigan, 1994). The similar effects of LS lesions on this ability support the possibility that this area performs functions analogous to those performed by cortex in the superior temporal sulcus of primates (Spear, 1991).

Dramatically increased susceptibility to directional noise has also been observed in cats with severely reduced incidence of directionally selective neurons in striate and extrastriate visual areas, including LS cortex (Pasternak et al., 1985; Spear et al., 1985). While in the absence of directional noise these cats had only slightly depressed range thresholds, the addition of noise produced large deficits in performance (Pasternak et al., 1990). Thus, there are striking parallels between the effects of a widespread loss of directional selectivity and the more localized loss of directionally selective neurons produced by lesions in areas where these neurons are concentrated (e.g., this study; Newsome and Paré, 1988; Baker et al., 1991; Pasternak and Merigan, 1994). One implication of this similarity is that it is the reduction in number of directional neurons produced by lesions of areas rich in directional selectivity that may be responsible for the deficit in extraction of motion signals from noisy backgrounds.

Spatial Scale of Motion Mechanisms in LS Cortex
Psychophysical measurements of the maximal spatial displacement ($d_{\text{max}}$) supporting correct direction discrimination have been shown to correlate with the spatial properties of directionally selective neurons (Baker and Braddick, 1985; Mikami et al., 1986). Indeed, $d_{\text{max}}$ for performance of motion tasks with random-dot stimuli has often been used to infer the spatial scale of underlying motion mechanisms (Braddick, 1974; Cleary and Braddick, 1990; Rudolph et al., 1994; Pasternak et al., 1995).

The deficit in range thresholds at larger spatial displacements after LS lesions (Figure 3) provides further evidence for the involvement of LS neurons in motion integration, since it shows that these neurons determine the spatial scale that limits performance of this task. Such a role for neurons in this region might be predicted since they have large receptive fields and lower spatial resolution than neurons at preceding stages of the system (Movshon et al., 1978; Morrone et al., 1986). In the absence of LS cortex, the spatial scale over which direction discrimination is supported may be limited by neurons with smaller receptive fields.

Pasternak and Merigan (1994) reported that MT/MST lesions produced no detectable deficit in direction discrimination at the largest step sizes and a somewhat increased $d_{\text{max}}$ threshold, a result contrary to that found with LS lesions. Assuming that the spatial scale increases at subsequent levels of cortical motion analysis, and that $d_{\text{max}}$ is an indicator of the spatial scale of the mechanism, a decrease in spatial scale after LS lesions would indicate that the neural basis underlying the residual performance may have shifted toward earlier stages of cortical processing. The possibility of such a shift is further supported by the recent finding of an increase in the spatial scale of the motion mechanism after lesions of striate cortex in the cat (Pasternak et al., 1995), indicating a shift in the locus of the residual mechanism in the opposite direction, toward the later stages of motion processing. Similarly, normalization of performance at large step sizes observed after MT/MST lesions in monkeys may also be indicative of the reliance of residual performance on later stages of cortical analysis.

Structure from Motion
Perception of 3-D structure-from-motion was dramatically affected by LS lesions, suggesting that LS cortex plays a critical role in either the motion processing which is necessary for perception of the 3-D structure of a moving object or in the recognition of structure-from-motion itself. Since the cue
necessary for perception of the apparent 3-D structure was based on local velocity signals, the inability to perform the discrimination could be explained simply by the deficit in speed discrimination produced by LS lesions (Pasternak et al., 1989). However, Vaina et al. (1990) report that brain damaged patients with deficits in speed discriminations can still recover structure-from-motion.

Another potential explanation for the major effect of LS lesions on structure-from-motion perception relates to the proposed role of LS neurons in extracting motion signal from noise. The 'unstructured' dots in the stimuli are a form of noise in that their velocities as a function of position in space are randomized so as to be inconsistent with the formation of the rotating cylinder percept. Given the role of LS neurons in speed discrimination (Pasternak et al., 1989) and the previous finding that speed discriminations depend upon the integrity of the directionally selective neurons (Pasternak, 1987), it is likely that the directionally selective neurons in LS contribute to the extraction of motion signal from velocity noise (as well as directional noise) and to the integration of these signals across space. It may be that LS lesioned cats are unable to properly segment the signal ('structure') dots from the noise and therefore discount the velocity noise in a manner that enables normal observers to perceive the structure in the presence of higher proportions of noise.

Comparisons between cat LS cortex and area MT in monkeys have been drawn in the literature (Gizzi et al., 1990; Spear, 1991). In this regard, it is noteworthy that a focal lesion of macaque area MT has been reported to have a similarly devastating effect on performance of the cylinder structure-from-motion task (Siegel and Andersen, 1986; Andersen and Siegel, 1990).

Residual Function and Recovery

It is possible that LS neurons are normally responsible for a greater degree of the motion processing required by our tasks than is revealed by the permanent lesion effects. The severity of the early deficits suggests this to be the case. On the other hand, while our results provide evidence for crucial involvement of areas within LS cortex in the perception of global motion, there was substantial residual performance following even the largest lesion, which included nearly all of LS cortex. It is possible that the residual function is due to compensation via significant plastic changes in neurons outside of LS cortex (note that thresholds improve over time even in cat 148, whose lesion was complete). Recovery over time could also include 'tuning-up', or modest adaptation, of the characteristics of neurons outside of LS that are already involved in motion processing. The time-course of this compensation is not known, although even as early as the first few days after the lesion, the animals showed some ability to integrate local motion information. It is also not known whether the recovery is due to either the passage of time or extensive training, or both.

Summary and Conclusions

Following lesions of LS cortex, permanent deficits were observed in the ability to process complex motion information. Early effects were of greater magnitude and included a major deficit in the ability to integrate directional information, even in the absence of noise. These results provide strong support for a role of areas within LS cortex in motion processing in the behaving cat. However, the degree of residual performance that survives even complete ablation of these areas suggests that neurons in other areas are either already involved in the motion processing required by these tasks or are capable of plastic changes in their properties such that they can assume some of the functioning necessary to process global motion in the absence of LS.

Notes

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