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Superior Colliculus and Active Navigation: Role of Visual and Non-Visual Cues in Controlling Cellular Representations of Space

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ABSTRACT: To begin investigation of the contribution of the superior colliculus to unrestrained navigation, the nature of behavioral representation by individual neurons was identified as rats performed a spatial memory task. Similar to what has been observed for hippocampus, many superior collicular cells showed elevated firing as animals traversed particular locations on the maze, and also during directional movement. However, when compared to hippocampal place fields, superior collicular location fields were found to be more broad and did not exhibit mnemonic properties. Organism-centered spatial coding was illustrated by other neurons that discharged preferentially during right or left turns made by the animal on the maze, or after lateralized sensory presentation of somatosensory, visual, or auditory stimuli. Nonspatial movement-related neurons increased or decreased firing when animals engaged in specific behaviors on the maze regardless of location or direction of movement. Manipulations of the visual environment showed that many, but not all, spatial cells were dependent on visual information. The majority of movement-related cells, however, did not require visual information to establish or maintain the correlates. Several superior collicular cells fired in response to multiple maze behaviors; in some of these cases a dissociation of visual sensitivity to one component of the behavioral correlate, but not the other, could be achieved for a single cell. This suggests that multiple modalities influence the activity of single neurons in superior colliculus of behaving rats. Similarly, several sensory-related cells showed dramatic increases in firing rate during the presentation of multisensory stimuli compared to the unimodal stimuli. These data reveal for the first time how previous findings of sensory/motor representation by the superior colliculus of restrained/anesthetized animals might be manifested in freely behaving rats performing a navigational task. Furthermore, the findings of both visually dependent and visually independent spatial coding suggest that superior colliculus may be involved in sending visual information for establishing spatial representations in efferent structures and for directing spatially-guided movements. *Hippocampus 1998;8:340–372.*

KEY WORDS: spatial learning; tectocortical; single unit; multisensory integration

INTRODUCTION

It has been suggested that adaptive navigation is mediated in part via the tecto-limbic visual pathway to hippocampus (Mizumori and Williams, 1993). Individual structures within this circuit may make unique contributions to spatial memory performance. In particular, results of electrophysiological investigations and lesion studies using restrained or anesthetized animals indicate that the superior colliculus importantly contributes to spatial orientation and spatial attention (for review see Stein and Meredith, 1993). Neurons in the intermediate and deep layers of superior colliculus show greater responses to the presentation of multimodal stimuli than to presentation of the unimodal components (Meredith and Stein, 1990, 1996; Stein and Meredith, 1993; Wallace and Stein, 1994). The efficiency of this multisensory integration process is likely facilitated by the fact that visual and somatosensory spatiotopic maps and the auditory (computational) spatial map are aligned with each other; either type of sensory input along the horizontal meridian is located along the rostral-caudal dimension of the colliculus while the vertical meridian follows a medial-lateral organization. It is thought that neurons that comprise the multisensory maps also exert control over specific motor responses via efferent hindbrain and nigral connections (Grantyn and Grantyn, 1982; Huerta and Harting, 1984). The organization of movement 'fields' within the collicular motor efferent system is roughly aligned with those of the sensory maps (McIlwain, 1990; Stein and Clamann, 1981; Sparks, 1986; Jay and Sparks, 1987; Sparks and Nelson, 1987). This relationship between the numerous sensory and motor maps allows not only precise spatial coding of the sensory surround, but also quick and appropriate orientation and/or attentional behavioral responses to stimuli. Consequently, the superior colliculus may ultimately control behaviors important for accurate navigation such as the approach or avoidance of environmental stimuli. Of interest in this regard, stimulation of superior colliculus leads to approach or avoidance responses (Dean et al., 1986, 1988; Sahibzada et al., 1986; Westby et al., 1990), and superior colliculus lesions result in navigation, orientation, and visual attention deficits in rats (Goodale and Murison, 1975; Dean and Key, 1981; Dean and Redgrave, 1984; Lines and Milner, 1985 [but see Foreman and Stevens, 1982]).

In addition to superior colliculus, other structures play a role in accurate navigation. Lesions of the hippocampal formation produce reliable and significant

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learning impairments on a variety of spatial navigation tasks (Olton et al., 1978b; Morris et al., 1982; Sutherland et al., 1983). Moreover, hippocampal pyramidal neurons fire as a function of an animal's location in an environment; accordingly they are referred to as "place cells" (Ranck, 1973; O'Keefe and Dostrovsky, 1971; Olton et al., 1978a; McNaughton et al., 1983a; Muller et al., 1987; O'Keefe and Speakman, 1987). Visual input is critical to establish normal hippocampal place-specific firing. If rats are carried into the testing environment in darkness, place cells do not show location-specific firing. Place cells can maintain their place fields in darkness, however, if the animals are allowed to view the environment before visual input is removed (Leonard and McNaughton, 1990). This indicates that hippocampal place cells are visually dependent and may contribute to a spatial memory system.

"Head-direction cells" (i.e., cells that fire when animals orient their heads in particular directions in space irrespective of location) have been recorded within hippocampal afferents such as the lateral dorsal nucleus of the thalamus, or LDN (Mizumori and Williams, 1993), as well as the anterior nucleus of thalamus (Taube, 1995). The LDN receives projections from superior colliculus and, similar to hippocamus, it appears to be part of a spatial memory system (Thompson and Robertson, 1987b; Mizumori and Williams, 1993). LDN head-direction cells have visual mnemonic properties that appear qualitatively similar to place cells: When lighting is removed, LDN head-direction cells maintain their directional correlate for short periods of time in darkness. Furthermore, temporary inactivation of LDN impairs spatial memory performance and, concomitantly, alters spatial coding of hippocampal place cells (Mizumori et al., 1994). These data suggest that spatial processing within the LDN is critical for accurate navigation and also normal hippocampal function. Therefore, the LDN and hippocampus may be components of a larger neural system that mediates effective visuospatial navigation in rats.

In the rat, a nocturnal animal, the tectocortical visual pathway dominates compared to the geniculostriate pathway. Ninety percent of the retinal ganglion cells in the rat project to superior colliculus (Linden and Perry, 1983). The intermediate layers of superior colliculus in turn project to LDN (Thompson and Robertson, 1987b); LDN efferents synapse within a variety of limbic structures such as the presubiculum, parasubiculum, postsubiculum, as well as retrosplenial and entorhinal cortices (Thompson and Robertson, 1987a; van Groen and Wyss, 1992). While past studies have shown that the LDN and various subregions of the hippocampal formation code location and directional information that animals may use to solve navigation problems, the possible contribution of the superior colliculus to tectolimbic function in freely navigating animals remains unclear. The extensive work that exists regarding the functional properties of superior collicular cells has been carried out almost exclusively in anesthetized or restrained cats and primates. Such studies have shown that overlapping visual, auditory, and somatosensory maps of sensory space are dynamic in that receptive field properties change as a function of behavioral context or experience (Jay and Sparks, 1984). A similar phenomenon has also been demonstrated in freely behaving rats (Weldon and Best, 1992). This type of modulation of superior collicular neuronal discharge is at least in part controlled by corticotectal afferents (e.g., Ogasawara et al., 1984). These complex and dynamic sensory and motor properties are consistent with the hypothesis that the superior colliculus is multifunctional; that is, it may perform both multisensory and sensory-motor integration, in the context of experience-dependent navigation.

Foreman and Stevens (1987) have argued for a somewhat similar view of dynamic interactions between superior colliculus and hippocampus. Based in part on similar behavioral effects following lesions of superior colliculus and hippocampus, namely water maze performance, they postulated that superior colliculus may provide input to hippocampus about novel spatial features relevant for spatial coding. Cortical modulation of orienting behaviors mediated by superior colliculus, on the other hand, was argued to be provided by indirect limbic connections from hippocampus.

As a first step to understanding the contribution of the superior colliculus to unrestrained navigation, the efferent messages of this structure were examined by recording single unit activity in freely behaving animals. Experiment 1 recorded such neural activity as rats performed a spatial navigation task that has been used extensively to study limbic navigational functions. In Experiment 2, animals were tested on the same spatial memory task, but the maze was enclosed in a controlled cue environment, thereby enabling manipulations of the visual surround while behaviorally correlated neurons were recorded from superior colliculus. Portions of these experiments have been presented in abstract form (Miya et al., 1993, Experiment 1; Cooper and Mizumori, 1994, Experiment 2).

GENERAL METHODS

Subjects and Apparatus

Male Fischer-344 retired breeder rats (n = 12) were obtained from Charles River Laboratories (Raleigh, NC) at age 9 months. They were housed individually and given free access to food and water for 1–2 weeks, after which time behavioral training began. During maze training, the rats were maintained at about 80% of their ad libitum body weights. The lights were on in the colony room between 7 a.m. and 7 p.m. Behavioral testing occurred between 8 a.m. and 5 p.m.

The black Plexiglas radial maze was identical to the one described in previous reports (Mizumori and Williams, 1993). Briefly, the maze was comprised of a round central platform with eight alleys (or arms) extending radially. Each maze arm (58.0 cm $\times$ 5.5 cm) was hinged such that the experimenter could provide access to individual arms from the central platform. Food reward (0.2 ml chocolate milk) was located at the distal end of each maze arm. The entire maze was elevated (79.0 cm) and all alleys were open. For the first experiment, the maze was located in

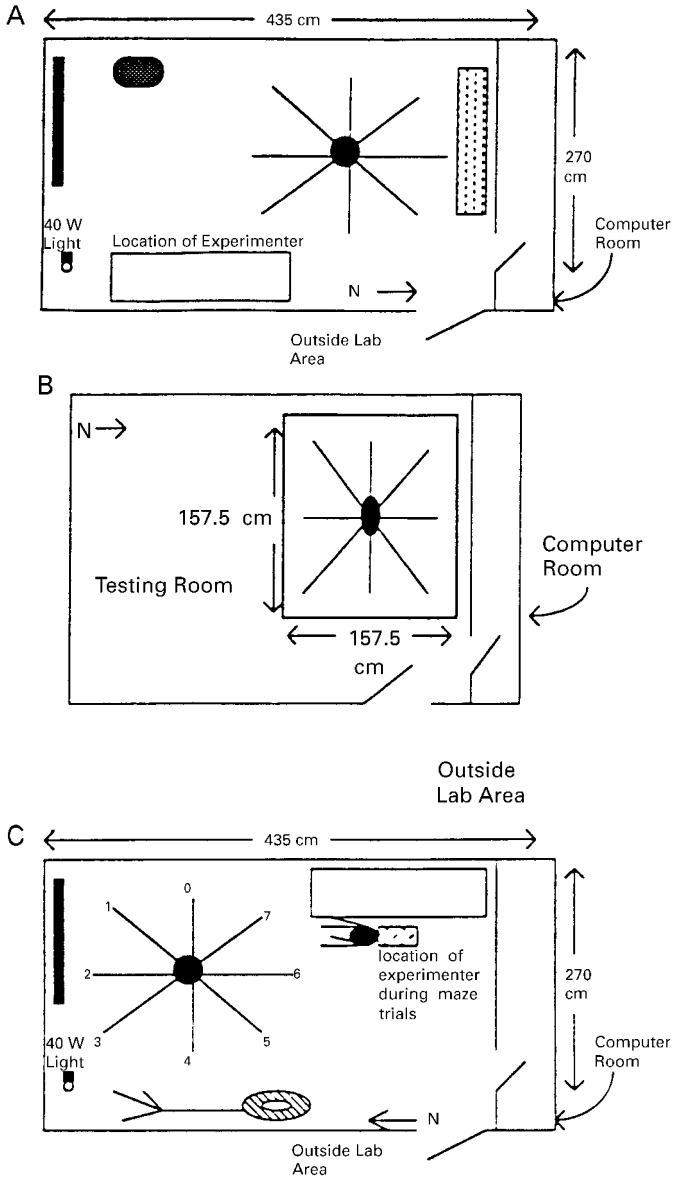


FIGURE 1. Schematic diagram of the visual environments in which superior colliculus neural activity was recorded. A: In Experiment 1, the radial maze was surrounded with various laboratory objects, such as tables, chairs, wall hangings, and the experimenter. The primary auditory cues available to the rat were the motor sounds of the remote controlled maze arms, and the electronic sounds of the recording equipment and computer located in an adjacent room. B: Experiment 2 was conducted with curtains surrounding the maze. Several distal cues were included inside the curtains to serve as polarizing cues. C: The novel environment was very similar to the environment used in Experiment 1. Similar to Experiment 1, the experimenter was present in the maze room during maze trials. Several other distal cues that were present in the environment are represented in the figure.

a 3.0 × 3.7-m room that was illuminated by a single 40-W incandescent light. The testing room contained several items that could serve as distal visual cues to rats performing the maze task (Fig. 1A). In the second experiment, a controlled cue environment was constructed that surrounded the maze (Fig. 1B). This testing room consisted of black curtains forming a square (157.5 cm × 157.5 cm) around the maze, and there were several objects in the maze room that could serve as distal visual cues. A canopy style ceiling was used that started at the camera above the maze and draped down to the top of the curtains. Because of the camera location, the ceiling was slightly off-center above the maze. Animals may have used this as a spatial cue, especially when distal cues were removed. The testing room was illuminated by four 15-W incandescent bulbs (mean illumination = 3 lux) placed in each corner of the curtained environment at the point where the ceiling and walls met. The curtains of the controlled-cue environment cover the floor to ceiling, restricting potential outside light sources from reaching the maze. When the room lights are extinguished the camera is unable to detect any light sources other than the infrared diode (camera is sensitive to 0.5 lux). Auditory and olfactory cues likely came from the computer located in the room just north of the behavioral testing room and a single air vent located at the north end of the maze. A separate recording room was used as a novel environment for testing several animals. This room was virtually identical in size and layout as the room used in Experiment 1, but contained a different constellation of distal cues (Fig. 1C).

Behavioral Training

The partial forced-choice procedure (Mizumori et al., 1990) involves presenting individually and sequentially four randomly selected arms to the rat, followed by the simultaneous presentation of all eight arms. The rat was trained to enter each arm once per trial to obtain the reward. Reentries resulted in no reward and as such constituted errors. After the rat entered all eight maze arms, the trial ended, and a 2-min intertrial interval began. During the intertrial interval, the maze was rebaited with food while the rat remained on the central platform. When each rat performed eight trials within 1 h for 7 consecutive days, free access to food was allowed for 2–3 days. After this time, the recording electrodes were surgically implanted. Postsurgical maze training required rats to perform eight daily spatial memory trials within 1 h for Experiment 1 and 15 trials within 1 h for Experiment 2.

Electrode Construction and Surgical Procedure

Superior collicular single unit activity was recorded according to the stereotrode recording technique (McNaughton et al., 1983b). Two lacquer-coated tungsten wires (25 μm; California FineWire, Grover Beach, CA) were twisted together, dipped in Epoxylite, then baked. The stereotrode was then threaded through a 30-gauge stainless steel tube, and two cannuli were mounted on a moveable microdrive (McNaughton et al., 1989).

For chronic implantation of the recording electrodes, animals were initially injected (ip) with 33 mg/kg Nembutal (50 mg/ml), then supplemented with .05 ml as necessary to maintain surgical anesthesia. Small burr holes were drilled in the skull according to the following stereotaxic coordinates (Paxinos and Watson, 1986): A-P 6.8–7.8 mm posterior to Bregma; L 1.5 mm lateral of the

midsaggital suture; and D–V 1.5 mm ventral of the dural surface. In addition, a burr hole was drilled for placement of the reference electrode (114 μm Teflon-coated stainless steel wire) near corpus callosum. A ground lead (125 μm Teflon-coated stainless steel wire) was attached to a stainless steel jeweler's screw that was fastened to the skull. All recording leads were inserted into a connecting socket that was cemented to the skull with acrylic and nine additional jewelers screws. The animals were given 0.1 ml Bicillin (300,000 units per ml) into each hindleg to guard against infection.

The location of the recording electrodes was verified at the end of each experiment by standard histological methods. The rats were perfused transcardially with 0.9% NaCl followed by phosphate buffered 10% formalin. The brains were removed, then allowed to sink in 30% sucrose formalin. Frozen 40 μm-thick sections were mounted on microslides, stained with cresyl violet, coverslipped, and then observed under a light microscope for verification of the recording site. Electrode tract reconstructions were made and approximate depth of recording sites in superficial and intermediate/deep layers was calculated based on the final depth of the electrode. These were verified by comparing histologically defined depths to depth records maintained as electrodes were lowered in superior colliculus.

Unit Recording and Behavioral Monitoring

The rat was connected to a headstage for all recording sessions. The headstage contained 5 FETs and a light-emitting diode. The rat was placed on the central platform of the maze while the electrode was lowered into the brain. The microdrive allowed the experimenter to advance the electrode in about 20-μm increments.

Single unit activity was recorded simultaneously and independently on each wire of the stereotrode pair. Each signal was amplified (3,000 to 10,000 times), filtered at half amplitude between 600 and 6 KHz, then passed through a window discriminator such that a 1 msec sampling period began when either input surpassed a predetermined threshold. The DataWave "Discovery" data acquisition system recorded each analog trace at a frequency of 32 KHz. The system software allowed the experimenter to isolate individual units from the otherwise multiunit record by comparing spike characteristics recorded simultaneously on two closely spaced electrodes (X and Y). Scatterplots of waveform features recorded on X and Y electrodes were displayed. For separating individual cells from each other and noise, a variety of waveform parameters were used. Particularly useful features included spike amplitude, spike width (time differences between the peak and subsequent trough of an action potential signal), and relative latency to the voltage peak on X and Y. In addition, a template-matching algorithm was utilized to further facilitate spike separation. For each cell, the experimenter stepped through a series of two-dimensional cluster plots, identifying the combination of spike characteristics that were most likely associated with a single-spike generator. Once identified, the specific cluster boundaries that characterized each cell were saved for use in subsequent recording sessions. This provided reasonable certainty that the same cell was being recorded across multiple test days. It should be noted that our intention was not to make direct comparisons to spike measures of other studies since absolute values of spike amplitude, spike width, etc., could vary signficantly depending on filter settings, electrode impedances, etc. Rather, our goal was to use these measures for relative comparisons across unit behavioral correlates, to identify the same cells across recording sessions, and for spike separation, when multiple single units were recorded simultaneously.

The animal's location and behavior on the maze were monitored simultaneously with the electrophysiological data via an automatic tracking system (Dragon Tracker, Boulder, CO, frequency = 20 Hz) that recorded the X-Y coordinate position of a light emitting diode positioned above the rat's nose.

Data Analysis

To facilitate direct comparison with data previously reported for hippocampal and thalamic neurons (Mizumori et al., 1989; Mizumori and Williams, 1993), the collicular units of this study were evaluated for their spatial correlates and their sensitivity to the movement state of the animal. Spatial correlates of single unit activity were defined as location- and/or direction-specific firing. Location specificity was quantified by calculating the mean firing rate of the cell as the rat moved radially inward or outward on each of the eight maze arms (McNaughton et al., 1983a; Mizumori, et al., 1989, 1992, 1994). For analysis of firing rates on the center platform, the maze center was subdivided into eight equal pie-shaped parts and included as part of the maze arms for analysis of firing rates on maze arms. The highest of the 16 rates on the maze arms was divided by the average of the remaining 15 to arrive at a location specificity score. Cells with location specificity scores of 2.0 or greater were classified as location-sensitive. The location-specific coding was also considered directional if the firing rate in the preferred location and direction was at least twice the rate of the opposite direction. In addition to location-specific directional coding, nonlocation-specific directionality of cells was calculated by taking the average rate in the preferred direction (towards the center of the maze or away from the center of the maze) divided by the average firing rate in the nonpreferred direction. Cells were considered directional if they fired at twice the rate in the preferred direction (inbound or outbound) compared to the nonpreferred direction. Graphic illustrations of the spatially selective discharge were accomplished in the form of 'spot-rate' plots (McNaughton et al., 1989; Mizumori et al., 1989; see Fig. 2 for examples). Briefly, the average firing rate was calculated as the rat remained within a 5-pixel radius of the first position sampled. When the diode moved outside this radius, the new position point served as the integration center for the next position. The graphic output consisted of circles, whose radii are proportional to the local firing rate; and dots, indicating the locations of the maze sampled by the rat. Vectors radiating from the centers of the circles illustrate the direction of diode move-

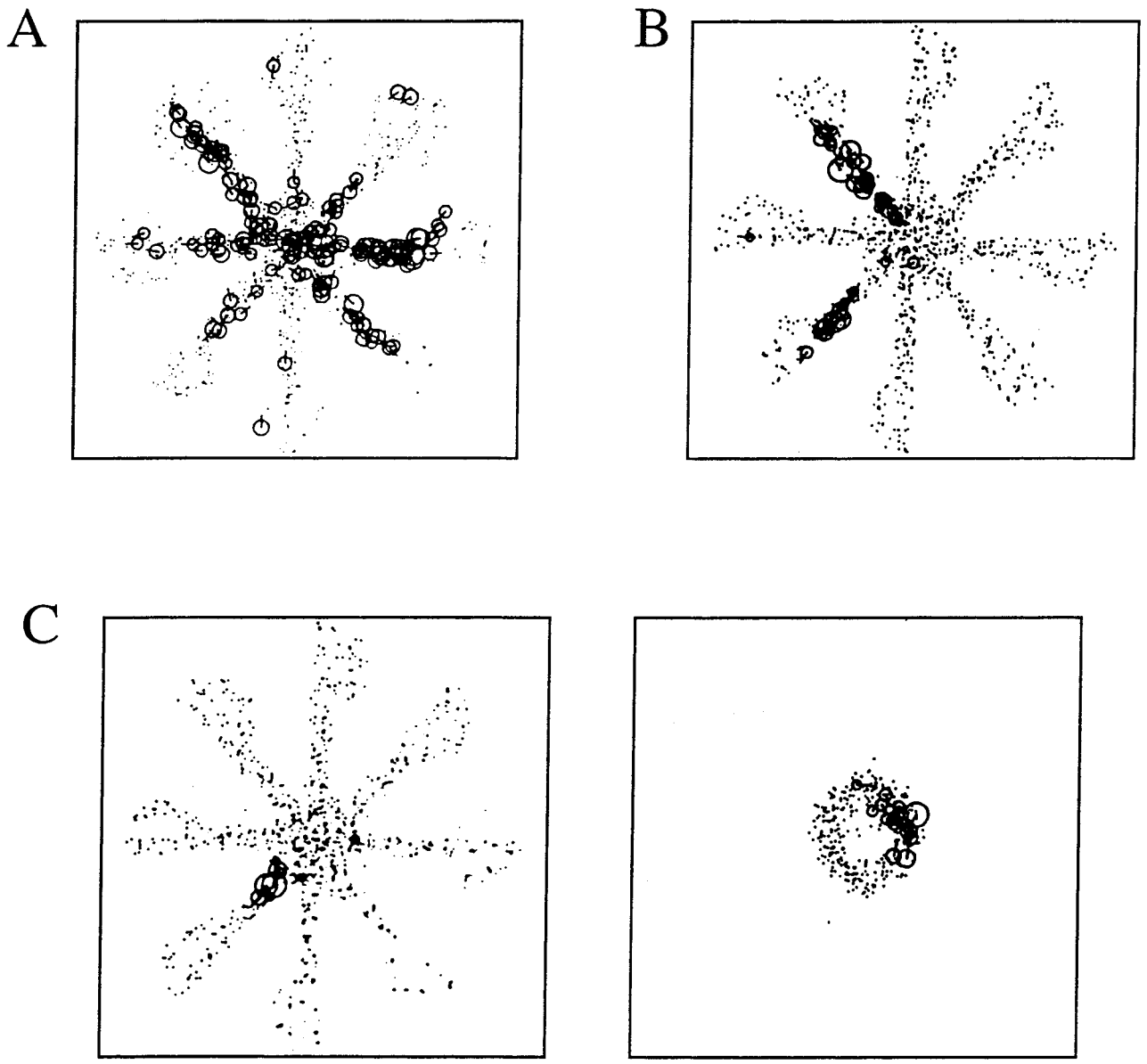


FIGURE 2. Graphic illustrations of location- and direction-specific firing by superior collicular neurons. Dots indicate sampled locations on the maze. Radii of the circles are proportional to the local firing rates of the cell. Vectors indicate the direction of movement by the animal when the cell fired. A: This cell preferentially fired when the rat traversed maze arms in the west and northwest directions. B: Another cell showed elevated firing as the rat moved outward on the northwest and southwest arms of the maze. Similar 'split place fields' have also been observed in previous studies of hippocampal cells (e.g., Mizumori et al., 1989). Unlike that shown for hippocampal cells, however, a third colliculus cell (C) exhibited differential place fields during maze runs and intertrial intervals of a recording session. The left panel illustrates a directional place field located on the proximal portion of the southwest maze arm during maze runs. Note that there is very little activity associated with the central platform. In contrast, during the intertrial interval, this cell increased firing when the rat moved through the northeast quadrant of the central platform. Thus, the behavioral context may significantly influence collicular location codes.

ment when the cell fired. A reliability index reflected the proportion of trials in which the highest mean firing rate of a cell occurred on the arm associated with the identified location/direction field of the cell.

To determine the nonspatial movement sensitivity of neurons, the mean firing rate was calculated for times when the rat moved outward on maze arms, remained relatively still at the arm ends, turned 180° at the arm ends, and finally, moved inward on maze arms. A peri-event time histogram (PETH) was created by first replaying the data on a monitor in the same temporal and spatial sequence as that observed during the recording session, then behavioral event markers were entered into the datafile at points that corresponded to the behaviors of interest. The firing rate of the cell was calculated 2.5 s before and after the occurrence of the

behavioral event marker. Depending on the behavioral correlate, firing rates during the behavior of interest were compared to a control condition.

EXPERIMENT 1: BEHAVIORAL CORRELATES OF SUPERIOR COLLICULUS NEURONS IN FREELY BEHAVING RATS

Numerous experiments have described the sensory and motor correlates of individual superior collicular neurons in anesthetized or restrained animals; however, there are limited data from animals actively engaged in spatial learning and memory tasks. To determine the potential contribution of the superior colliculus to active navigation, single units were recorded during performance of the spatial memory task. Our working hypothesis is that the superior colliculus is part of a broad neural system mediating accurate navigation, and that single units recorded from this structure will reflect sensory and motor correlates useful for directing spatially guided behaviors.

Method

Subjects, apparatus, and procedure

Behavioral, electrophysiological, surgical, and histological techniques were identical to those described in General Methods. Briefly, animals (n = 4) were trained to perform a spatial memory task on an eight-arm radial maze. After animals performed eight trials daily for 7 consecutive days, they were surgically implanted with recording electrodes (two stereotrodes/hemisphere) placed just dorsal to superior colliculus. Following recovery from surgery, animals were retrained on the spatial memory task. Upon isolation of individual collicular units, animals performed the spatial memory task while unit activity was monitored. To maintain asymptote performance on the spatial memory task, animals ran the maze task every third day if single units were not encountered.

Results

In Experiment 1, a total of 125 superior collicular cells were recorded as rats performed the spatial memory task. Individual spike amplitudes were comparable to those of cells recorded in other brain areas using the stereotrode recording technique with awake animals; for example, neocortex (McNaughton et al., 1994), hippocampus (Mizumori et al., 1989), striatum (Lavoie and Mizumori, 1994), and thalamus (Mizumori and Williams, 1993). The mean (±SE) spike amplitude was 144.4 μV ± 5.6 μV, and the average firing rate was 5.43 Hz ± 0.61 Hz. The spike width on the other hand, appeared distinct from what we have typically observed for many other brain areas, even though we used similar electrodes with identical filter settings. The average spike width was 205.2 μsec ± 6.00 μsec, whereas the typical spike width of neocortical, hippocampal, striatal, or thalamic neurons is 250–400μsec. Thus, as the electrode was advanced toward the superior colliculus, it was often possible to correctly ascertain online whether the unit was a collicular neuron.

Cellular correlates

A variety of unit-behavioral correlates were observed as the rats performed the navigation task. A neuron was assigned a correlate if the peak firing rate associated with a particular behavior was at least twice the firing rate shown during the comparison behaviors (see details below). Based on this criterion, the primary correlate of 42.4% (53/125) of the recorded cells was considered to be "spatial." These cells fired preferentially based on either the location of the animal and/or the direction of movement. The second largest category of cellular correlate appeared particularly sensitive to either the general locomotion state of the animal or to somatosensory stimulation (28.0% or 35/125). Less than one-third (29.6%; 37/125) of the cells recorded showed no obvious behavioral correlate in our test situation.

Spatial movement correlates

Different forms of apparent spatial coding were observed. The average location specificity score was 2.98 (±0.61), which contrasts with the average score of 5.0 to 10.0 typically observed for hippocampal CA1 and hilar/CA3 complex-spike (place) neurons. However, location specificity scores of the collicular cells were higher than the average score of 1.0 to 2.0 typically observed for the comparatively nonspatial hippocampal interneuron (e.g., Barnes et al., 1990; Mizumori et al., 1989). To be consistent with past studies (Mizumori et al., 1992), collicular cells with location specificity scores of 2.0 or greater were classified as location-selective neurons (n = 35; 28% of all recorded cells). The mean location specificity score for the spatial location cells (3.85 ± 0.40) was considerably higher than that of the remaining neurons (1.49 ± 0.03). The reliability of the location and nonlocation cells was also substantially different. The averages were 0.28 ± 0.03 and 0.21 ± 0.02, respectively, for location and nonlocation cells. A regression analysis was performed to examine the relationship between the location specificity of a cell and the reliability with which such location specificity was exhibited. An analysis of variance revealed a significant positive relationship between location specificity and reliability, r = .42; F = 9.80 (df = 46), $P < .01$. Thus, the more spatially selective correlates also tend to be the most reliable. Nine of the place-specific collicular cells also exhibited a directional bias within the place field. That is, the firing rate was at least two times greater as the rat moved either in the inward or outward direction through the place field. Figure 2 displays representative spatial correlates that show a location and directional firing bias during performance of the spatial memory task. Note that the cell displayed in Figure 2A may give the initial appearance of a "head direction" cell. However, such a cell is qualitatively different than those that have been previously described in other areas (e.g., LDN). In this case, and for all other directional cells recorded from superior colliculus in this study, the directional vectors were not parallel.

The directional bias to the location preference of superior collicular neurons appeared at least superficially similar to that

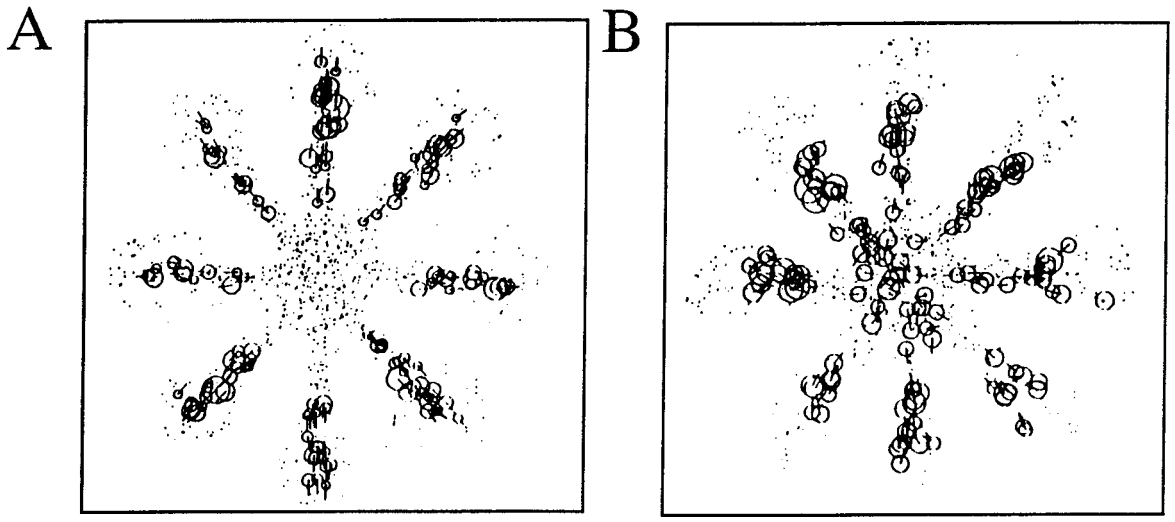


FIGURE 3. The firing of many collicular neurons coincided with forward movement on the maze arms. In particular, cells shown in (A) and (B) increased firing as the rat moved in the outward or inward directions, respectively. There was no apparent location-specific discharge since movement-related firing was observed on all maze arms.

typically observed for hippocampal place cells (McNaughton et al., 1983a; Mizumori et al., 1989), with the exception of one cell that exhibited different place fields depending on the phase of training (see Fig. 2C). This cell preferentially fired as the rat initiated movement outward on the southwest arm of the maze during trial runs. During the intertrial intervals, on the other hand, a different place field was observed for the same cell when the rat moved through the northeast section of the central platform. Importantly, during maze trials, the rat also passed through the same space on the central platform, but the cell did not show elevated discharge.

Many superior collicular neurons also showed particular sensitivity to the direction in which the animal moved about the maze irrespective of the absolute spatial location of the animal. Compared to firing rates as the animal remained relatively motionless at the ends of the maze arms, four cells showed increased firing during active locomotion either in the inward or outward directions on the maze arms (Fig. 3). Other neurons (n = 11) showed elevated discharge just prior to the cessation of outward movement at the arm ends (Fig. 4). Importantly, these cells did not change their firing rates when the rat stopped on the central platform at the end of trials, indicating that they were coding more than just the cessation of movement. Finally, four additional cells selectively increased firing by at least twofold when the rat made right or left turns at the arm ends. Two of these turn-related cells additionally exhibited a clear location bias by preferentially firing during turns on some, but not all, arms of the maze (Fig. 5). Their location specificity scores were 2.67 and 3.62. Also, only one of the four turn cells displayed a directional turn bias when the animal turned on both the ends of the arm and the central platform. The remaining three showed turn correlates at the arm ends but not the maze center. It is worth noting that the number of cells that discriminated direction of turn may have been underestimated, since some of the rats in this study made only left or only right turns at the arm ends. Turn-related cells recorded from these animals were not classified as directionally selective neurons. Similar directional forward-motion and turn cells have been described for posterior parietal and caudate neurons recorded from rats tested in a similar behavioral situation (McNaughton et al., 1994; Mizumori and Cooper, 1995; Mizumori et al., 1996).

Non-spatial movement correlates

In addition to the numerous spatial biases observed, many superior collicular cells were particularly sensitive to the general movement state of the animals. For instance, 23/125 cells (18.4%) more than doubled their firing rate when the animal traversed maze arms relative to times when the rat remained still at the arm ends (See Fig. 6 for an example). This elevation in rate was observed irrespective of the location of the animal and the direction of movement, with the exception of four cells which showed a moderate location bias (location specificity scores: 2.29–2.45). Another forward movement-sensitive cell showed a dramatic reduction in firing (by about two-thirds) during active locomotion. Unlike the movement-related neurons of hippocampus (Mizumori et al., 1989; Ranck, 1973), the autocorrelation functions of these collicular units did not reveal rhythmic modulation of discharge. Rather, these cells closely resembled the movement-related cells of the posterior parietal cortex (McNaughton et al., 1994). A second type of general movement-related cell was that which increased firing during both right and left turns (n = 5).

Somatosensory correlates

A past study demonstrated in freely moving rats that superior collicular neurons are sensitive to somatosensory input (Weldon and Best, 1992). Additionally, data from anesthetized or restrained rodents, cats, and primates have shown that the superior colliculus contains a somatotopic map (for reviews, Sparks and

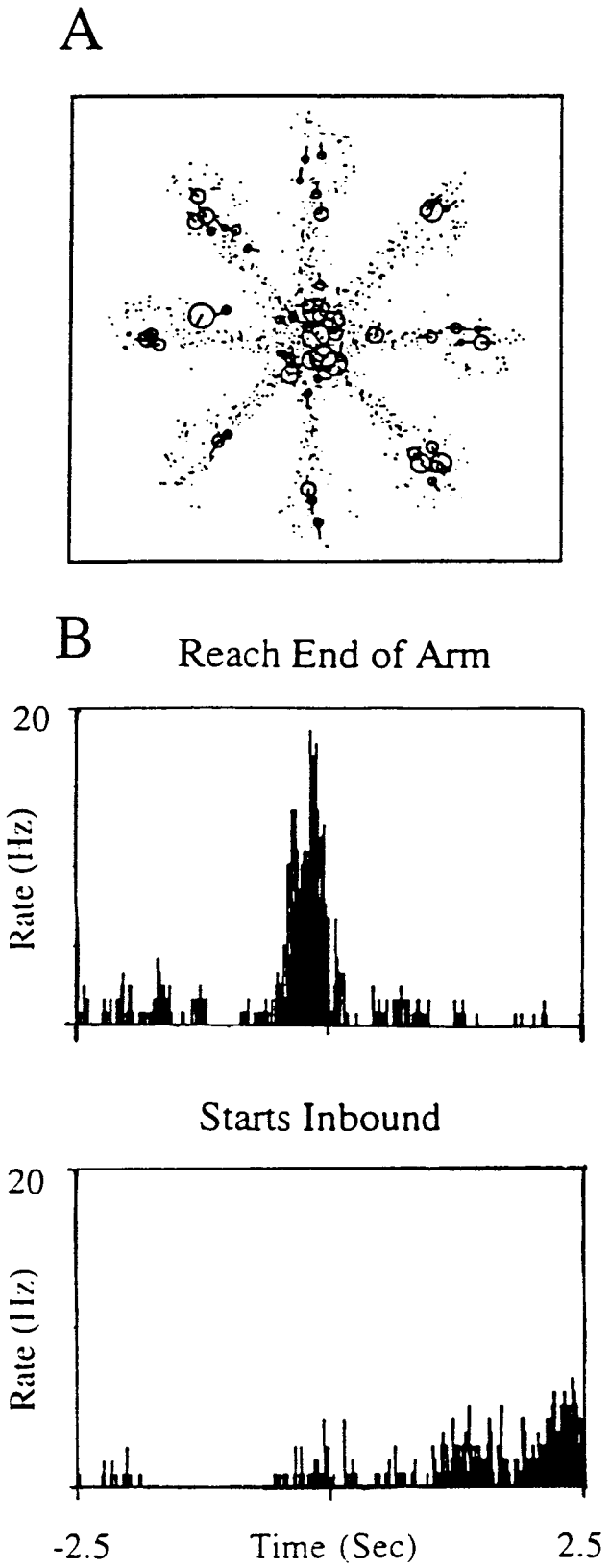


FIGURE 4. Illustration of a subclass of the directional forward movement correlate. A: The spatial plot shows that this cell tended to fire on the distal portion of maze arms. B: In particular, the PETH of 5B shows a sharp increase in firing approximately 500 msec before the animal arrived at the end of the arms. No such increase was observed during inbound forward movement. Bin width is 10 msec.

Nelson, 1987; Stein and Meredith, 1993). Therefore, we also tested cells for their response to strokes of the right and left vibrissae, face, and sides of the body. Six out of 125 cells (4.8%) clearly responded to some form of somatosensory input by at least doubling their discharge rate. While animals were performing the maze task, somatosensory cells fired at the end of maze arms or when the animal was on the center platform in the process of selecting the next maze arm. (See Experiment 2 for further description of the somatosensory correlates observed in superior colliculus).

Discussion

The present study describes for the first time the nature of information represented by superior collicular neurons as rats perform a spatial memory task. The firing rate of a large percentage of these cells was observed to correlate with what is generally considered to be spatial aspects of behavior, such as the location and/or the direction of movement of an animal. Other neurons were sensitive to the general locomotion state of the animal or to specific somatosensory stimulation.

Given the connections of the superior colliculus to motor structures, including the spinal cord (Sahibzada et al., 1987; Yasui et al., 1994), it is not surprising to observe cellular correlates relating to various motor behaviors that commonly occurred during performance of the spatial memory task. Some cells fired during movement on the maze arms, while others fired when the animal was relatively still at the end of the maze arm, consuming chocolate milk. Interestingly, cells that are sensitive to changes in osmolarity have been previously reported in superior colliculus (Malmo, 1976). Although it was viewed as unlikely that superior colliculus has osmoreceptors for mediating thirst, it is possible that input from hypothalamic areas may mediate drinking responses of superior collicular neurons (Malmo, 1976).

Cells that correlated with turning, or angular head movements, were also observed in superior colliculus. Turn-related neurons have also been reported in posterior parietal cortex (McNaughton et al., 1994) and caudate nucleus (Mizumori and Cooper, 1995). Interestingly, firing rates of head direction cells in anterior thalamic nuclei are modulated by angular head movements; these head direction cells fire maximally during turns 40 to 50 ms prior to reaching the preferred head direction (Blair and Sharp, 1995). At the present time, it is not known where head direction cells in anterior thalamic nuclei derive information about angular head movement. The possiblitiy that turn-related neurons such as these may contribute to the neural system-mediating knowledge of changes in directional heading has been suggested by Skaggs, Knierim, Kudrimoti, and McNaughton (1994).

It remains to be determined what sensory information controls the spatial and nonspatial correlates observed in superior colliculus. The initial observation of this experiment suggests some similarities to hippocampal place cells. However, there are numerous possibilities for why a cell may fire when a rat is in a specific location or heading in a certain direction, and different sensory modalities may have differential effects across brain structures. For example, grooming behavior, somatosensory cues, specific motor movements made by the animal, and visual cues may be

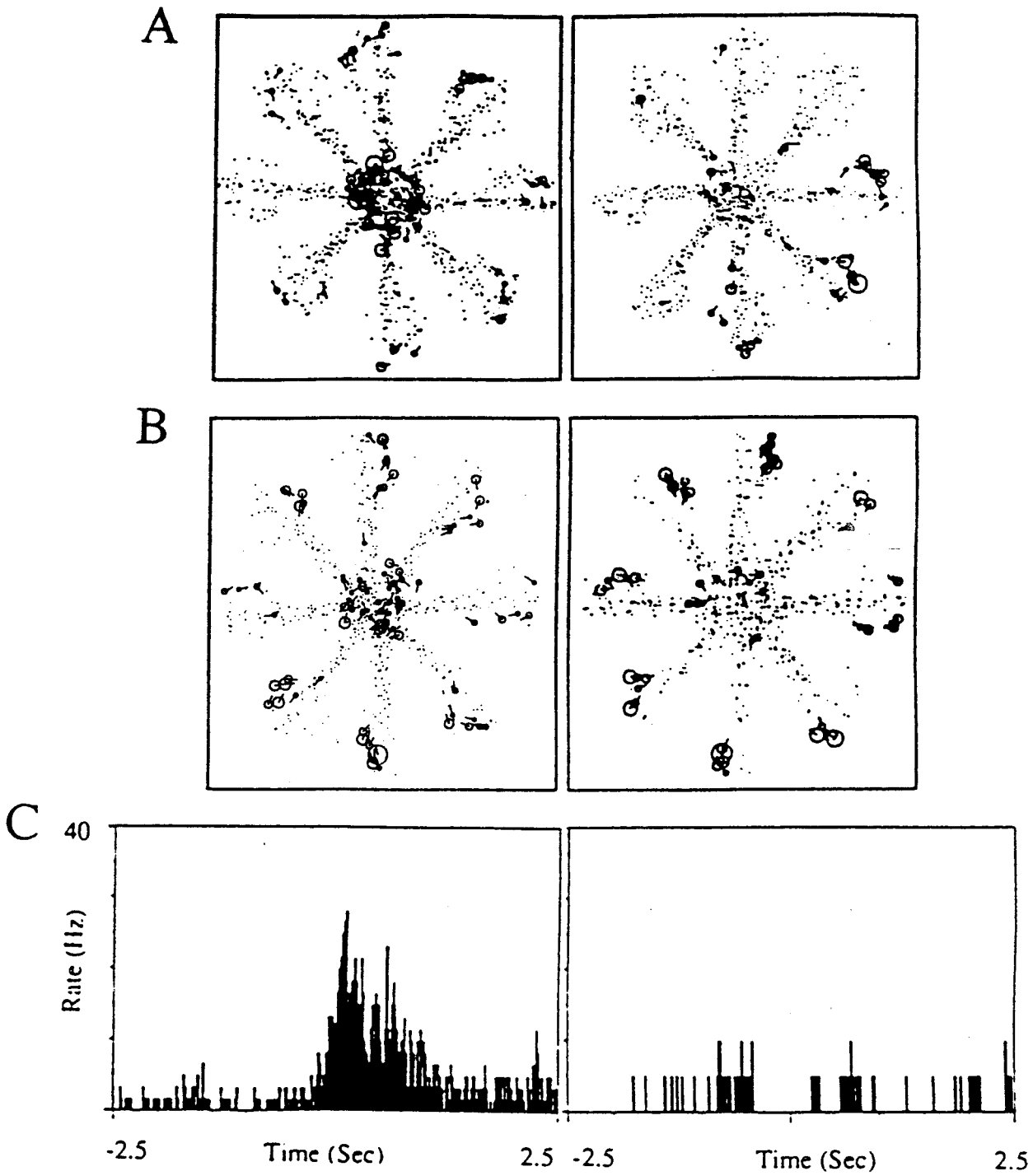


FIGURE 5. Another form of spatial coding was shown by neurons that preferentially fired during turns either to the right or left. A: For two neurons, there appeared to be a location bias to the turn selectivity. The left panel illustrates a stronger preference for left turns on the east arm of the maze, or when the rat made left turns on the center platform. In contrast, the right panel shows the left turn bias on only the south, southeast, and east arms of the maze. In this case, left turns made on the center platform did produce elevated firing. B: Two right turn cells did not show a consistent location bias to their discharge. Notice that the cell shown in the left panel fired during turns on the center platform, while the cell shown in the right panel did not. C: PETHs illustrating the turn selectivity of the cell shown in the left panel of B (above). The center of each histogram reflects the beginning of left (left panel) or right (right panel) turns made at the arm ends. Bin width is 10 msec.

responsible for the observed correlate in superior colliculus. In hippocampus, however, grooming behavior is unlikely to influence, and in fact suppresses complex spike-cell activity. Thus, there is no a priori reason to suspect that similar spatial coding should be similarly influenced by sensory input across structures. Grooming behavior is an unlikely explanation because these

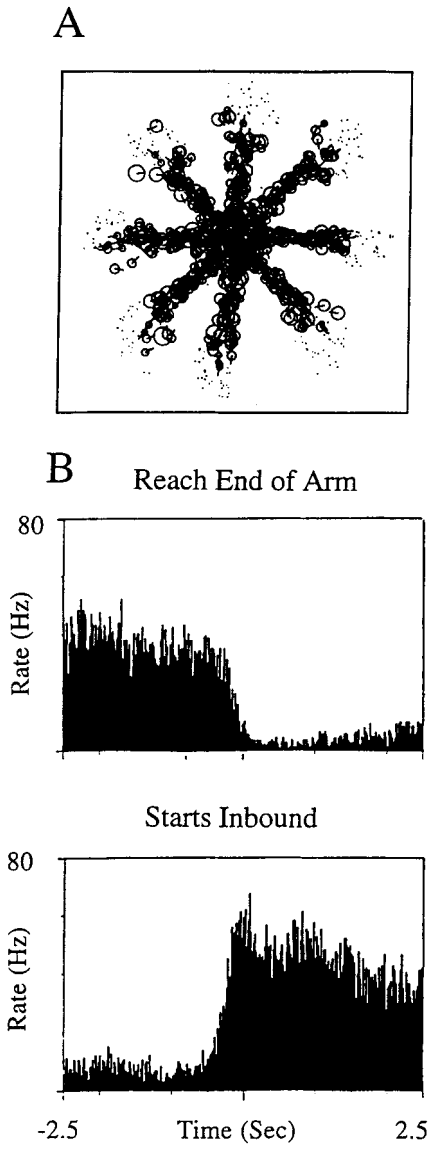


FIGURE 6. The general locomotion sensitivity of some collicular neurons is shown by this cell which (A) exhibited relatively high firing rates during outbound and inbound forward movement, and during traversals of the central platform. The spatial plot includes data collected only during maze runs, and not the intertrial interval. Therefore, firing localized to the central platform corresponded to both forward movement and turning behavior between choices. B: The firing rate of the same cell was greatly diminished while the rat remained relatively motionless at the arms ends, and during turns at the arms ends (left side of lowest PETH).

behaviors almost exclusively occurred during the intertrial interval and not during maze trials. Differential somatosensory input from the maze also appears to be an unlikely explanation for causing spatially localized discharge, because neurons sensitive to somatosensory stimulation did not show elevated firing on particular maze arms. Thus, it is most likely that location- and direction-specific firing of the cells in superior colliculus are due to either location-specific visual information or specific motor behaviors on the maze. The motor interpretation may be less likely than the visual because it seems reasonable to conclude that animals would make the same motor movements across the symmetrical maze arms. Of course, without simultaneous electromyogram recordings, a motor interpretation cannot be conclusively ruled out.

Cells sensitive to forward movement may reflect the motor activation patterns, internally generated self-motion (i.e., idiothetic) cues, or visual information (e.g., optic flow). These possibilties are explored in Experiment 2.

The observation of somatosensory neurons is consistent with data from anesthetized animals showing that superior colliculus contains a precise somatotopic map (Meredith and Stein, 1990). Previous work has shown that a discrete area of the intermediate/deep layers of colliculus serves approach behaviors. Furthermore, neurons in this "approach" area of the superior colliculus are activated by somatosensory and auditory information. Thus, the somatosensory neurons observed in the present study may mediate approach behaviors via projections to the tecto-spinal tract (Westby et al., 1990). Certainly, navigation in the natural environment likely capitalizes on somatosensory information in addition to distal visual and internally generated self-motion cues.

The diversity of spatial movement and nonspatial movement correlates observed in the present study is consistent with the hypothesis that the superior colliculus gives rise to spatial information that can be used by limbic afferent structures. Cells with location or directional correlates were recorded in the intermediate layers of superior colliculus, and this layer projects to LDN (Thompson and Robertson, 1987b). Therefore, LDN head direction cells may derive at least part of their directional code from collicular input. Experiment 2 explores critical environmental stimuli that maintain and establish the different cellular correlates observed in superior colliculus. These data further the argument that superior colliculus is an active part of the tectocortical neural system mediating experience-dependent navigation.

EXPERIMENT 2: THE CONTRIBUTION OF VISUAL INFORMATION TO CELLULAR CORRELATES RECORDED FROM SUPERIOR COLLICULUS OF FREELY BEHAVING RATS

Experiment 1 demonstrated that spatial and nonspatial behaviors are coded by individual superior collicular neurons during active navigation. However, the contribution of environmental cues to establishing and maintaining the cellular correlates were not identified. Previous work has shown that spatial correlates recorded from limbic structures are visually dependent, that is to say that visual information importantly contributes to the observed location and/or directional coding (Leonard and McNaughton, 1990; Mizumori and Williams, 1993). The present study was designed to evaluate the role of global visual information and distal visual cues in maintaining and establishing the spatial correlates observed in superior colliculus. It was hypothesized that

visual information would be critical for maintaining spatial correlates and that nonspatial movement correlates would not require visual information to maintain the cellular correlate.

Method

Subjects, apparatus, and procedure

Nine animals were trained to perform a spatial memory task on an eight-arm radial maze (Olton and Samuelson, 1976) enclosed in a visually controlled cue environment (See Fig. 1B). One animal from Experiment 1 was included in the present study. Spatial memory training was identical to Experiment 1, except that animals were trained to perform 15 trials daily in less than 1 h. All of the surgical, electrophysiological, and histological techniques were identical to those described in General Methods, with the exception that following identification of a cell with a behavioral correlate, we attempted to perform a series of environmental manipulations in a pseudorandom order.

Environmental manipulations

Manipulation control trials. To determine the stability of behaviorally correlated neurons recorded from superior colliculus, animals performed 15 consecutive trials without explicit environmental manipulations.

Light–Dark–Light. To evaluate the contribution of visual input for maintaining a behavioral correlate, animals performed five trials under normal testing conditions, and during the intertrial interval between the fifth and sixth trials, lights in the testing room were turned off. Animals were then tested for five trials in darkness. Prior to starting the eleventh trial, all lights in the room were turned back on, and animals were tested for five more trials under standard lighting conditions.

Dark–Light. This test evaluated the requirement for visual input to establish a behavioral correlate. To reduce vestibular information available about the path from the animal colony room to the maze room, animals were carried into the testing environment via a circuitous route in darkness. During transportation along a circuitous route, animals were covered with a laboratory coat and the experimenter carried the animal in darkness to a variety of random locations in the outside laboratory room before finally entering the maze testing room. After animals were brought into the testing room and connected to the recording equipment (in darkness), rats performed five spatial memory trials still in darkness. Immediately prior to the sixth trial, the lights were turned on and animals were then tested for five trials under standard lighting conditions.

Cues–No Cues–Cues. This test was designed to evaluate the contribution of distal visual cues to maintain the behavioral correlate. Animals were tested for five trials under normal conditions, and during the intertrial interval between the fifth and sixth trials, all of the distal cues were either covered with a black curtain or removed from the environment while the animal remained on the center platform of the maze. Animals then performed five trials in the absence of distal cues. During the intertrial interval between the tenth and eleventh trial, the cues were restored, once again in front of the animal. Animals were then tested for five trials in the presence of the distal cues. Originally, cue rotations, and not cue removal, were going to be performed on cells recorded from superior colliculus; however, pilot data demonstrated that simply carrying animals out of the testing room (which was necessary to rotate the cues) disrupted the average firing rate and the correlate of many spatial cells. Thus, all manipulations were conducted without removing the animal from the maze room following the onset of behavioral testing. The control procedure for cue rotation required the animal to run five trials, then the animal was removed from the testing room, and waited outside of the testing room laboratory area for 5 min (See Fig. 1B for maze room relative to outside laboratory area). Then the animal was carried back into the testing room, hooked up to the recording equipment, and run for five more trials. These data are discussed briefly in the Results section.

Visual, auditory, and somatosensory correlates. In addition to recording behavioral correlates during maze performance, all collicular cells were tested for visual or somatosensory sensitivity while animals were relatively inactive on the center platform of the maze. Visual correlates of cellular activity were assessed by the experimenter waving his hand (rostral to caudal, caudal to rostral, etc.) parallel to the rats' heads, approximately 6 to 12″ away from one or the other eye. This allowed for reasonable lateralization of visual stimulus presentation. Somatosensory correlates were assessed by gently stroking the vibrissae (rostral to caudal) of the animal with a pen, by touching the front legs, or by touching the hind legs of the animal. All cells that showed a visual or somatosensory correlate were checked for auditory sensitivity. Cellular activation by auditory stimuli was typically assessed by either jingling keys on one side of the animal or by snapping fingers under normal luminance conditions. Similar to the visual stimuli, auditory stimuli were presented parallel to the rats' heads, about 6 to 12″ away from the rat. In some cases auditory sensitivity was tested in darkness. In all cases, both sides of the animal were tested to determine if the cell showed a lateralized response. PETHs were created based on the simultaneous entry of an event flag (via a keystroke) at the onset of stimulus presentation. Because the event flag entry and sensory stimulus were performed by an experimenter, rather than automated, there likely were errors in marking the precise onset of the stimulus presentation (on the order of 200 to 400 ms). Data were quantified by taking the average firing rate of the cell for 1.5 s following stimulus presentation, compared to 1.5 s before the onset of the stimulus.

Multisensory integration was tested in several cells by jingling keys and waving simultaneously (visual and auditory stimulus). Visual stimuli were presented by waving a hand 6–12″ away from one side of the animal. Auditory responses were presented by jingling the keys on one side of the animal while the animal was in darkness, and presumably not able to see the visual stimulus. The multisensory and visual alone stimulus conditions differed slightly.

In the multisensory condition a cupped hand was waved (thereby blocking the view of the keys being shaken), whereas in the visual only condition the hand was waved open-faced. Not all cells with unimodal responses were tested for multisensory integration; data were only quantified for those cells that the experimenter observed enhanced responses online to waving and jingling keys simultaneously compared to waving alone.

It is important to note that only those cells which showed clear correlates to these sensory stimuli (i.e., experimenter could identify the correlate online) were recorded. Thus, the total number of cells with visual, somatosensory, or auditory correlates may be underestimated. Additionally, these tests were conducted while the animal was resting on the center platform of the maze. Thus, while the movement of the animal was only slightly restricted (i.e., it could only circle), specific body movements were not controlled for during these sensory tests. However, during the course of these sensory tests animals usually moved little, if at all, and typically were fixated on the experimenter.

Unique manipulations

In several cases, animals were tested in a novel environment (See Fig. 1C). The behavioral procedures in the novel environment were identical to those previously described. Animals were tested daily in both the familiar testing room for five to eight trials, and in the novel environment for five to eight trials (a total of 10 to 16 trials per day). The novel environment contained multiple distal cues (e.g., table, chair, box, large lamp) in a large rectangular testing room (270 cm $\times$ 435 cm) which was illuminated by a single 40-W incandescent light (mean illumination = 7.5 lux) placed in one corner of the room. The novel environment provided a much "richer" visual environment with a higher ceiling, textured walls, more distal cues, larger size, and a more spatially extended three-dimensional structure that was not present in the controlled cue environment. Other unique manipulations, including passive movement tests and changes in the normal testing procedure, were performed on a smaller number of cells. Detailed descriptions of these manipulations are explained in the Results section.

Behavioral data analysis

The mean number of errors made by each animal across each phase of the manipulation (two to three blocks of five trials) was calculated. A repeated measures one-way analysis of variance (ANOVA) was used to determine if the number of errors changed significantly ($\alpha = .05$) across the phases of testing.

Single unit analysis

Effects of manipulations were determined by comparing the average premanipulation firing rate to those obtained during the manipulation and postmanipulation trials. The cellular correlate was considered to have been altered if following baseline trials, the mean firing rate increased by twofold or decreased by one-half during the manipulation condition, and then returned to baseline during the postmanipulation condition. The cells recorded from the superior colliculus in this study showed about an equal number of enhanced and depressed responses to the various manipulations. Thus, to facilitate comparisons among groups of cells, it was necessary to calculate a change in firing rate that would be sensitive to both excitation and inhibition of the cell. A change in firing rate index (CFI) was calculated for the manipulation conditions by subtracting the lowest firing rate from the highest rate, then dividing by the highest firing rate, regardless of whether the lowest firing rate occurred during the baseline or manipulation condition. If the average firing rate of a cell during maze trials increased by twofold or decreased by one-half during the manipulation, the CFI equaled .50.

TABLE 1.

Percentages of Cellular Correlates Recorded From Superior Colliculus in Experiments 1 and 2

	Spatial movement	Non-spatial movement	Somatosensory	Multiple-correlate	No obvious correlate
Experiment 1	53/125 (42.4%)	29/125 (23.2%)	6/125 (4.8%)	N/A[a]	37/125 (29.6%)
Experiment 2	41/127 (32.3%)	23/127 (18.1%)	9/127 (7.1%)	13/127 (10.2%)	41/127 (32.3%)

[a]This category was only included in Experiment 2 because of the more extensive sensory tests performed as part of that experiment.

Results

Spatial memory performance

During the Light–Dark–Light manipulation, the average number of errors made by the animal increased significantly ($F = [2,14] = 7.25$; $P = .007$). For the Light–Dark–Light manipulation, mean number of errors across each block of five trials was 0.07 ($\pm$ 0.03), 0.74 ($\pm$ 0.23), 0.27 ($\pm$ 0.11), respectively. A Newman–Keuls post hoc analysis ($\alpha = .05$) confirmed that compared to the intial light testing, the mean number of errors was significantly greater in the dark and final light phases ($P < .05$). During all other manipulations, the mean numbers of errors made across each phase of testing was not significantly different from each other.

Cellular correlates

A total of 127 cells were recorded from nine animals. One animal included from Experiment 1 contributed seven cells to the present experiment. The percentages of the different cellular correlates observed in Experiment 2 were virtually identical to those of Experiment 1 (see Table 1 for percentages of cells in each category in Experiments 1 and 2).

Similar to Experiment 1, the spatial movement category consisted of the three subcategories: *direction-specific* (n = 8), *location-specific* (n = 16), and *location- and direction-specific* (n =

17). The nonspatial movement category was comprised of *reach-end-of-arm* (n = 3), *movement-sensitive* (n = 12), *forward-movement* (n = 4), and *turn* (n = 4) cells. Because almost all of the animals made left or right turns exclusively, it was difficult to assess whether turn cells showed directional specificity. Somatosensory cells (n = 9) fired at twice their baseline rate during the presentation of vibrissal sensory stimuli presented by the experimenter. Although visual and auditory stimuli were also presented by the experimenter, these cells only showed unimodal somatosensory sensitivity.

Thirteen cells displayed *multiple correlates*. This category is included in the present experiment and not in Experiment 1 because of more extensive sensory testing performed as part of this experiment. There were three subcategories of multiple correlate cells. The first consisted of cells that responded at twice their baseline firing rate during the presentation of visual, auditory, and/or somatosensory stimuli (n = 3). Multisensory integration was demonstrated in four multiple correlate cells (see Fig. 15). These cells showed at least twofold increases in firing rate during the simultaneous presentation of visual and auditory stimuli, compared to the presentation of either stimulus alone (visual or auditory). In addition to these sensory cells, neurons that fired in response to combinations of maze-related behaviors or stimuli were included in the *multiple correlate* category. There were three types of cells that correlated with multiple maze-related behaviors. The first type fired when the animal was engaged in turning behaviors only when the animal was on particular arms of the maze (*turn and location*, n = 2). The second type was active only when the animal was turning and moving toward the center platform (*turn and inbound*, n = 1). The last type of *multiple correlate* cell was active when the animal remained relatively motionless at the end of the maze arms and was turning (*still and turns*, n = 3).

Only 41 out of the 127 cells recorded in this study did not show an obvious relationship to maze-related behaviors. These cells were classified as having *no obvious correlate*.

The mean firing rates of the single units in superior colliculus varied across the behavioral correlates. The average firing rates differed significantly between groups, F (3,78) = 24.48, $P < .0001$. The overall mean rate (±SE) for *spatial movement* cells was 1.29 (±0.26) Hz; the *nonspatial movement* cells showed a higher firing rate than all other categories of correlates. The average firing rate for this category was 11.38 (±1.61) Hz. *Sensory* cells fired at an average rate of 4.96 (±1.55) Hz during maze trials, and *multiple correlate* cells fired with an average rate of 1.40 (±0.55) Hz.

TABLE 2.

Location Specificity, Reliability, and Average Firing Rate, Across 15 Trials*

	Trials 1–5	Trials 6–10	Trials 11–15
Location specificity	3.24 (±0.42)	4.09 (±0.50)	4.06 (±0.95)
Reliability	.25 (±.04)	.30 (±.04)	.30 (±.05)
Average rate	0.92 (±0.38)	0.80 (±0.36)	0.67 (±0.31)

*The mean scores are presented ± the SE.

TABLE 3.

CFI Across 15 Trials of Testing Without Explicit Environmental Manipulations (at the Left Side of Each Column)*

	1–5	vs.	6–10	1–5	vs.	11–15
Spatial (n = 15)	.27		6+ 6− 3+−	.30		8+ 7+−
Movement (n = 10)	.16		5+ 4− 1+−	.25		4− 4+ 2+−
Somato (n = 2)	.27		2−	.26		2−
Multiple (n = 1)	.25		1−	0		1+−
NOC (n = 2)	.19		2−	.32		2−

*The "+" sign indicates excited, "−" indicates inhibition, and "+−" indicates no change relative to baseline for each of the cells contributing to the mean on the right side of each column. Numbers indicate the number of cells which showed excitation, inhibition, or no change from baseline. Abbreviations: Spatial, *spatial movement;* Movement, *nonspatial movement;* Somato, *Somatosensory;* Multiple, *Multiple correlate;* NOC, *No obvious correlate.*

Environmental Manipulations

Manipulation control trials: Are cellular correlates stable?

To determine the validity of the a priori criterion chosen to determine the effect of the manipulations, the fifteen trials were broken down into three sets of five trials. The first five trials served as a baseline for determining changes in firing rates across trials during the remaining two blocks of five trials.

Spatial movement cells. One-way repeated measures ANOVAs were calculated on the mean firing rate, location specificity, and reliability and for the 12 *location* and *location and direction* cells. These analyses demonstrated that the measures of spatial coding did not change significantly across trials: F (2,22) = 2.15, 0.61, and 0.41, respectively; $P > .05$. For the *location* and *location and direction* cells, the average location specificity across 15 trials was 3.76 (±0.38) and reliability was .28 (±0.02). This closely approximates the average location specificity and reliability scores observed in Experiment 1: 3.85 (±.40) and .28 (±.03), respectively. This indicates that spatial coding is stable across repeated maze trials. Table 2 displays the location specificity, reliability, and average rate across 15 trials for these 12 cells. Table 3 summarizes

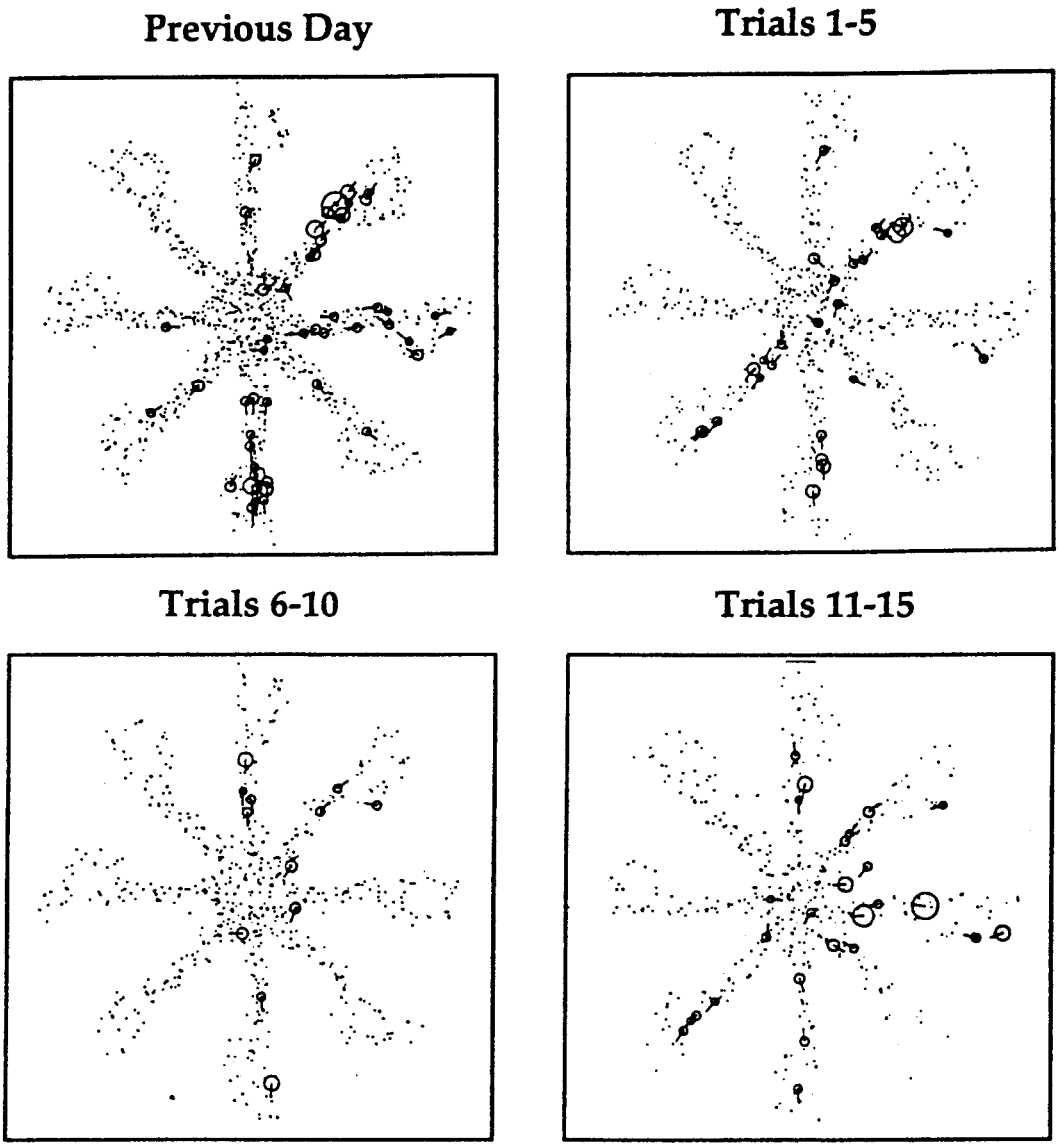


FIGURE 7. To determine the reliability of spatial coding, 15 trials were broken down in three blocks of five trials: 1–5, 6–10, and 11–15, respectively. An example of spatial cell that showed a distributed firing field inbound on the northern maze arm, and outbound on the northeastern and southern maze arms, is shown in this figure. For reference, the spatial firing from the previous day is displayed in the top left corner. Given the broad distribution, it is unlikely that a single cue is controlling the activity of this cell. As is demonstrated with this cell, the firing field was consistent across days; however, the location of the preferred field varied across trials.

the average CFI changes during trials 6–10, and 11–15 compared to the initial five trials for all categories of cellular correlates. Two of the 15 *spatial movement* cells tested for 15 continuous trials without intervening manipulations showed above criterion changes in firing rate (e.g., CFI $>$ .50). Both of these cells showed a progressive decline in firing rate across trials. One of the two cells was tested on the next day, and the firing rate had returned to baseline levels. The remaining 13 spatial cells did not show above criterion changes in CFI.

Although location specificity scores did not change across the five trial blocks, the exact location of the preferred firing field changed across blocks of trials. This change was restricted in that the field generally maintained a bias to one of three arms over the course of 15 trials. Figure 7 displays an example of a *location and direction* correlate that maintained its spatial bias to the northern, southern, and northeastern arms across 15 trials of testing. The previous test day revealed the same pattern of activity. This indicates that the broad field of the cell remained stable across days. In a different case, a *location and direction* cell maintained the same location bias across trials, but the preferred direction changed across trials. In four other cases, *location* and *location and direction* cells were recorded for the subsequent test day; for three out of four cells the preferred firing field was maintained on two out of the three arms across days. Only one cell showed a spatial bias unique from the previous day. Thus, the majority of spatial cells appear to maintain the same preferred firing field across days. When the location correlates are viewed within short periods of time (i.e., five trials or 20 min), the preferred field is localized to a

small area of the maze. But when viewed across longer periods of time (i.e., 15 trials or 60 min), the fields are distributed across a larger area of the maze. Most of the cells recorded for multiple days show that the broad fields are maintained to the same location across days, and this suggests that these cells contribute to spatial mapping of environmental features. The slight variations in preferred fields within the testing session may allow for superior collicular spatial cells to encode both stable features of the environment, and also dynamic information important for navigation. During the 15 continuous trials, the three directional cells (two outbound and one inbound) maintained their behavioral correlates throughout the trials (i.e., fired at twice the rate in the preferred direction across all three blocks of five trials).

Nonspatial movement cells. All 10 of the *nonspatial movement* cells maintained near baseline firing rates during 15 continuous trials. An example of the activity of a *forward movement* selective cell across three blocks of five trials each is shown in Figure 8. In this case there was a slight increase in firing rate during the last 10 trials compared to the first five; however, this subtle variation in firing rate is well within the normal range for cells recorded in this study. A one-way ANOVA confirmed that average firing rates did not change: $F(2,18) = .92$, $P > .05$, across the three blocks of trials. (See Table 3 for CFIs for all *nonspatial movement* cells.) Four *nonspatial movement* cells were recorded across days without intervening manipulations. In all of the cases, the observed behavioral correlates were the same across test days (2–3 days).

Somatosensory and multiple correlate cells. Both of the *somatosensory* cells were stable across 15 trials of testing (CFIs are displayed in Table 3). One *somatosensory* cell was tested for 2 days without intervening manipulations, and in this case the correlate remained the same across days. One *multisensory* cell was tested for 15 continuous trials, and the firing rate did not exceed criterion level changes (see Table 3). This cell also showed a spatial bias. The preferred field for this particular cell remained stable to a single arm over the course of the maze trials. The spatial coding combined with multisensory responses in this cell illustrates that although the categories of cellular correlates are not necessarily mutually exclusive, they do however provide a useful heuristic for evaluating the types of cellular coding that occur within a structure. Three *multiple correlate* cells were tested across days without manipulations and in all cases the correlate remained the same for 2–3 days of repeated testing.

No obvious correlate cells. The average firing rate of two *no obvious correlate* cells tested for 15 trials was stable (see Table 3 for CFIs). Two *no obvious correlate* cells were tested across days, and an obvious correlation with behavior on the maze was not observed across days.

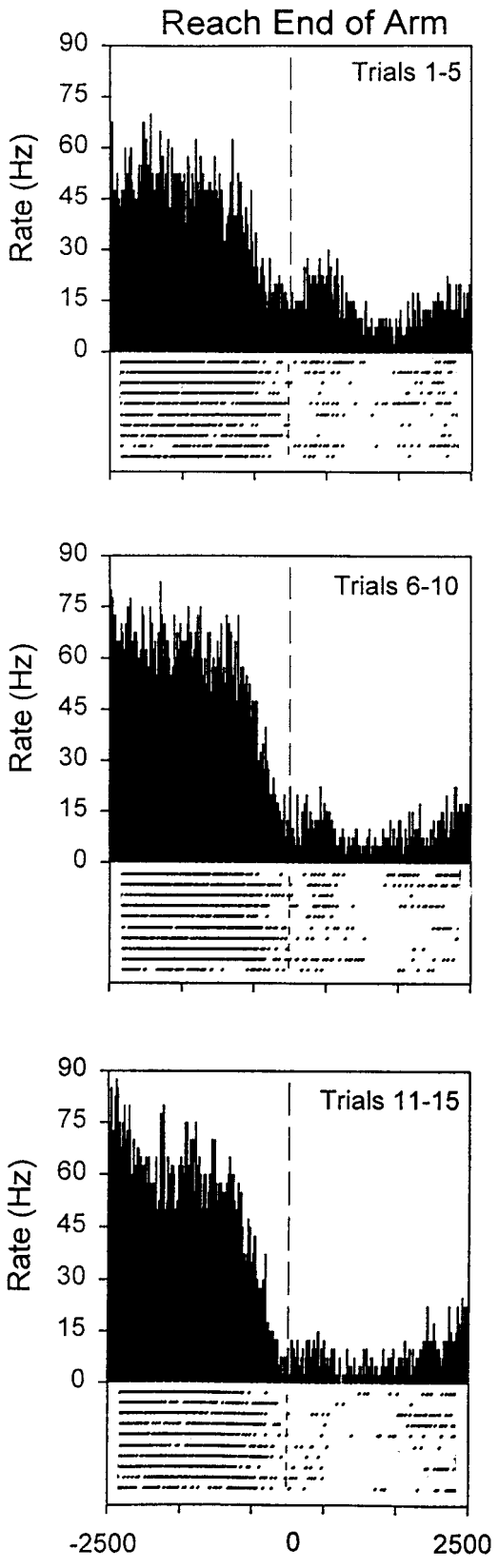


FIGURE 8. The activity of a movement cell across three blocks of five trials is shown in this figure. The top panel corresponds to the first five trials, middle panel to the second block of five trials, and the bottom panel to the final five trials. The PETHs display the activity of the cell as the animal moved toward the end of the arm, with T_0 (indicated by dashed line in PETH) marking the cessation of forward movement. The correlate and firing rate remained stable across maze trials. The rasters below the PETHs display a representative set of 10 (out of 40) events. Bin width is 10 msec.

Summary. In this experiment, almost all *spatial movement* cells maintained a consistent firing rate across 15 trials, but the preferred fields were not exclusively restricted to individual maze arms across trials. Instead, it appeared as if *spatial movement* cells maintain broad, distributed firing fields when animals are tested for up to 1 h in a restricted, controlled cue environment, and that when tested across days the preferred fields remain stable. *Directional*, *movement*, *somatosensory*, and *multisensory* cells maintain consistent firing rates and behavioral correlates across trials. In the absence of experimenter-controlled environmental manipulations, there are minor nonsignificant fluctuations in the firing rates across trials and behavioral correlates, but these variations never reached a CFI of .50.

Light–Dark–Light: Is visual input required to maintain the behavioral correlate?

Spatial movement cells. Six of the 12 spatial cells tested in the Light–Dark–Light condition showed dramatic changes in firing rate during the dark condition. One *location-sensitive*, three *location- and direction-sensitive*, and two *directional* cells had a CFI score of greater than .50 during dark trials. Of these six cells, two of the cells were inhibited and four were excited during darkness. Interestingly, one *location and direction* cell increased its firing rate dramatically in darkness (CFI $>$ .50) and lost its original location and direction correlate. In this case, both the reliability and location specificity decreased in darkness, and did not return in the following light trials until the fifth light recovery trial (see Fig. 9A). The remaining three *location* and *location and direction* cells showed a similar pattern of effects. In darkness, reliability of the correlate was significantly decreased and did not completely return to baseline levels in final light trials ($F[2,6] = 9.92$, $P = .01$). Newman–Keuls post-hoc analysis showed that reliability during both the dark ($P < .05$) and final light trials ($P < .05$) were significantly different than the baseline condition. The average reliability (mean ± SE) for the light, dark, and light conditions were .55 (±.09), .25 (±.01), and .20 (±.03). Mean firing rate and location specificity did not change significantly across the three phases of testing ($F[2,6] = 0.01$ and 0.05, respectively; $P > .05$). Individual cell data (presented in Fig. 10A) revealed CFIs $>$ .50. The lack of statistical significance in average firing rate across phases of testing is not a discrepancy because one *location and direction* cell showed pronounced excitation, while the remaining three cells were inhibited.

The two *directional* cells (one outbound and one inbound) had a CFI greater than .50. The directional preference was maintained in the inbound cell and lost in the outbound cell during darkness. The outbound correlate did not return in the final light trials, despite the fact that the cell was active during these trials. Unfortunately it was not possible to record the cell the next day to determine if the correlate returned at a later time.

Two *directional*, three *location-*, and one *location- and direction-sensitive* cells did not reach the CFI criterion of .50 or greater during dark testing. Figure 10B shows that the location and location and direction cells that did not reach the criterion change in firing rate during darkness also did not show significant changes in mean firing rate, location specificity and reliability across the phases of the manipulation, $F[2,6] = 4.05$, 0.61, and 0.22, respectively; $P > .05$. The *directional* (outbound) cells that did not show dark-induced changes in firing rate also maintained their directional firing preference across the three phases of testing.

Nonspatial movement cells. Two out of 15 movement cells had a CFI of .50 or greater during the dark phase of the manipulation; one was excited and one was inhibited in darkness. The *reach-end-of-arm* cell showed a general increase in firing rate in darkness during all maze-related behaviors, and thus the behavioral correlate was lost. During the final light trials, the firing rate returned to near baseline levels, as did the behavioral correlate.

The *turn* cell decreased its firing rate during dark trials (CFI = .82) and returned to baseline levels in the final light trials. The cellular correlate also changed during dark trials; the cell showed a location and direction correlate (location specificity = 10.23, reliability = .60) in darkness. When lights were restored, the location and direction correlate was not maintained and, although the cell fired on some turns, the turn correlate did not completely return (see Fig. 9B). Because of these unusual changes, the Light–Dark–Light manipulation was repeated the subsequent day, and the firing rate changes were replicated (CFI = .80). The behavioral correlate, however, was absent in this cell for the initial light and dark trials, but in the final light trials the cell showed a clear location and direction bias (location specificity = 5.99, reliability = .60). It is important to note that the cluster boundaries of this cell did not change across days and the firing rate showed a similar pattern in response to the manipulation across days. Thus, it is likely that the same cell was being recorded across days and that this seemingly motor-related cell was modulated by visual information and maze testing conditions.

The majority of movement-sensitive cells (13/15) did not reach criterion level of change in firing rate during dark trials. Additionally, the behavioral correlates remained stable regardless of changes in room luminance. A *nonspatial movement* turn-related neuron that was not influenced by changes in room luminance is shown in Figure 9C.

Somatosensory cells. A CFI $>$ .50 was not observed in the six *somatosensory* cells tested with the Light–Dark–Light manipulation. During the course of dark testing the firing rate was maintained during maze trials.

Multiple correlate cells. Five out of seven multiple correlate cells had a CFI of .50 or greater during dark trials. These included a *turn and location* cell, *still and turn* cell, a cell sensitive to visual, auditory, and somatosensory stimuli, and two *multisensory* cells. All of these cells were inhibited in dark conditions. In the case of the *turn and location* cell, the cell was inhibited in darkness, and then the firing rate returned to baseline levels when room lights were restored. Different components of the *turn and location* cell were differentially affected by changes in room lighting; during dark testing the turn correlate remained but the location bias was lost. When room lights were restored, the cell continued to fire during turns and the location bias returned to the preferred area of the maze on the final light trial (see Fig. 11). A similar time-course of restoration was observed for a *location and direction* cell described above.

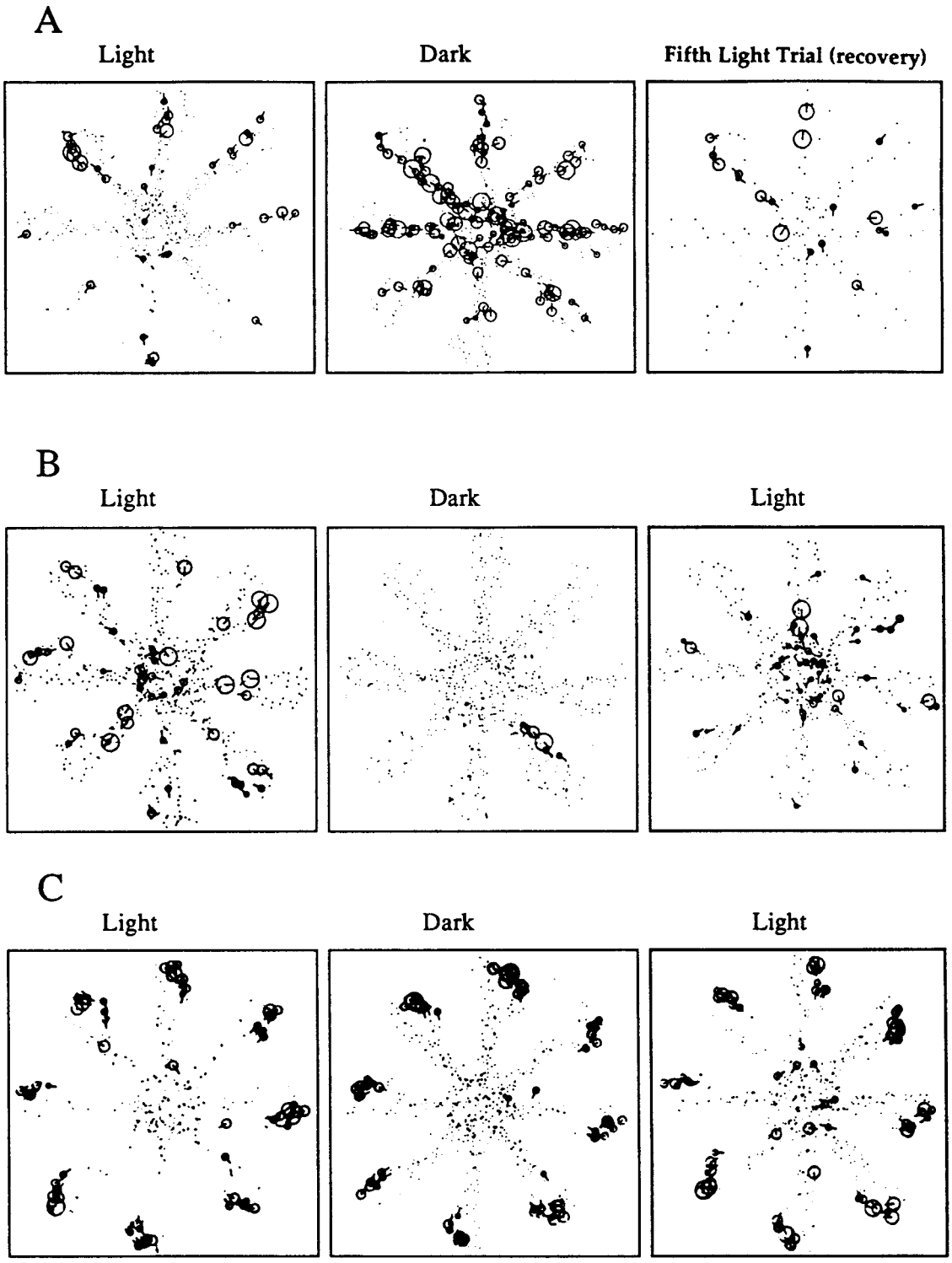


FIGURE 9. The Light–Dark–Light manipulation disrupted half of the spatial cells and the minority of movement cells. A: The top panel displays a location and direction cell that increased its overall firing rate during darkness and required five trials for the location and direction firing field to be reestablished. B: In the middle panel a turn-related neuron that was inhibited in darkness is displayed in this figure. Interestingly, the behavioral correlate was altered with illumination changes; the cell showed a location and direction firing field in darkness. When room lights were turned on, the turn correlate only partially returned. C: Not all turn cells were influenced by changes in the visual environment, and this turn-related neuron was not influenced by changes in room illumination (bottom panel).

The *still and turn* cell also showed a reduction by over one-half in firing rate during dark trials (CFI = .77). This cell was active when the animal was relatively motionless at the end of the maze arms (still component) and during turns either at the end of the maze arms or on the center platform (turn component). The decrease in mean firing rate was due to the fact that turn

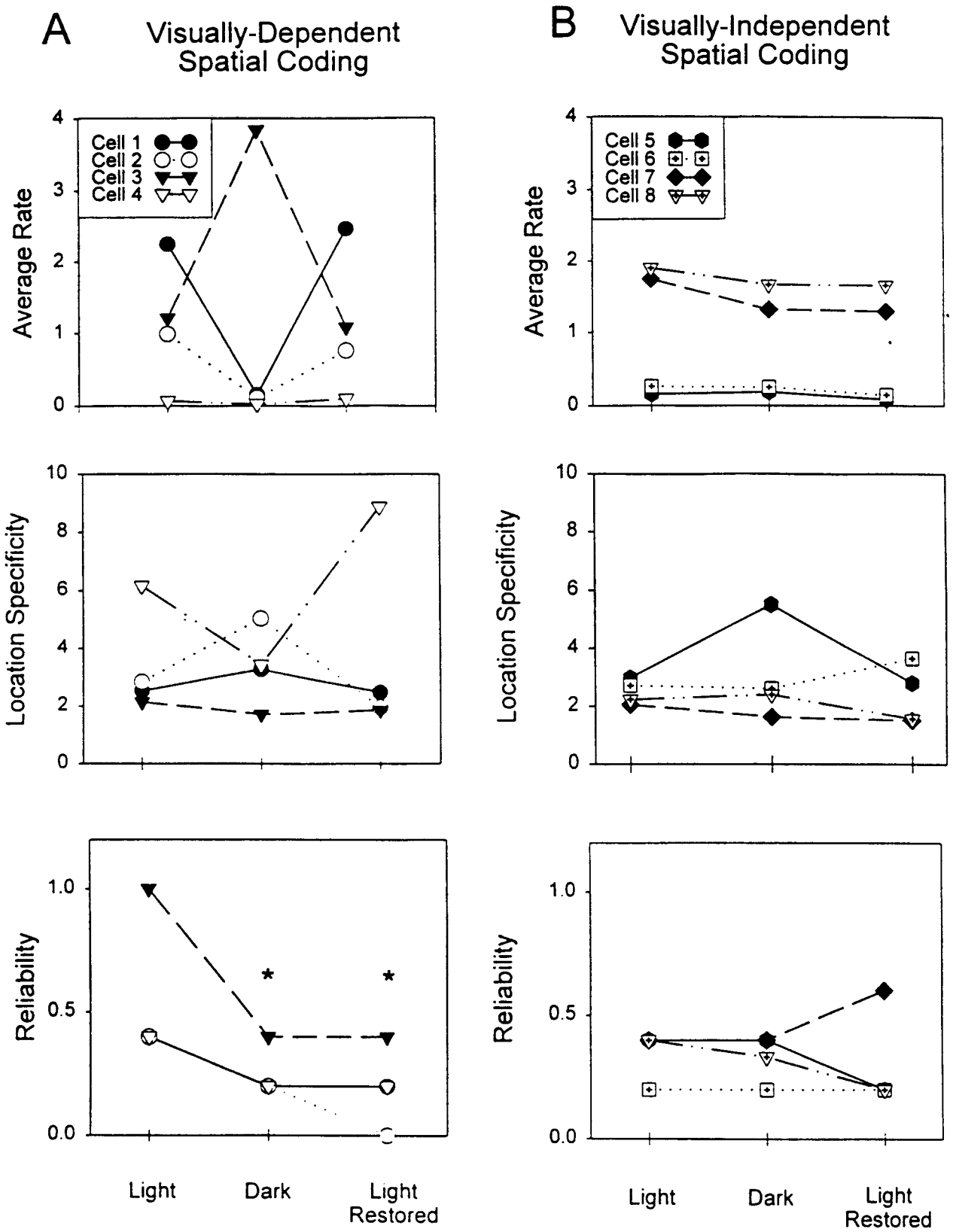
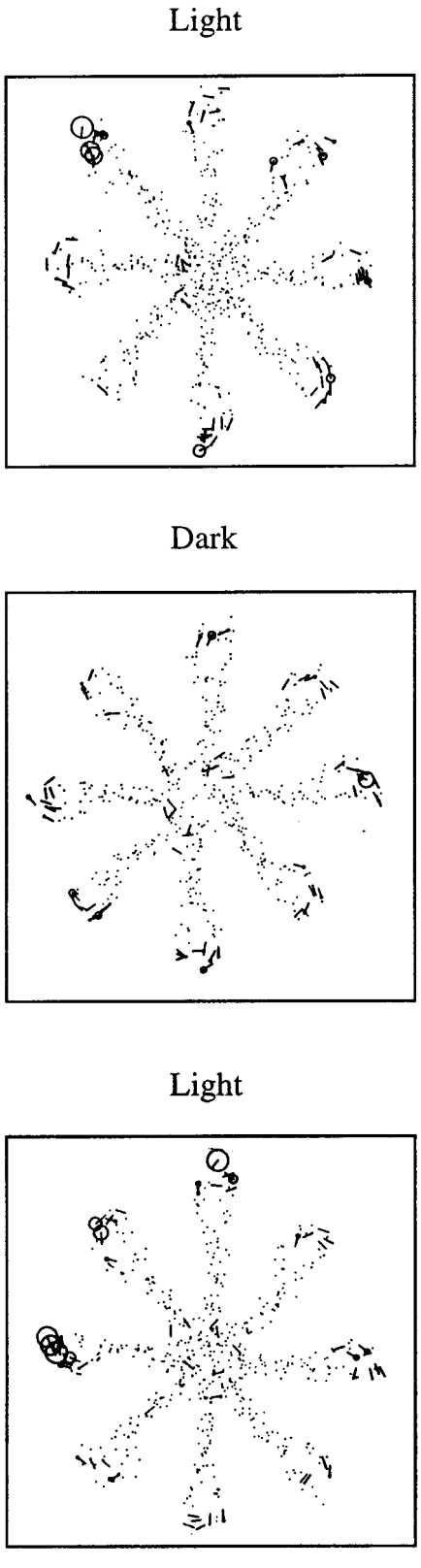


FIGURE 10. The Light–Dark–Light manipulation revealed that some spatial cells in superior colliculus are dependent on visual information, whereas others are not. A: Four location or location and direction cells showed above criterion changes in firing rate (mean rate in Hz, errors bars represent SE). Location specificity did not change predictably across lighting conditions; however, reliability of the spatial correlate decreased significantly during darkness and did not completely return (* indicates $P < .05$). In the absence of visual information, the accuracy of spatial coding is diminished in some superior collicular cells. B: The mean firing rate of four other *location* or *location and direction* cells was not changed during manipulation of the visual environment. Reliability did not decrease during darkness in these cells. In these cases, visual information was not necessary to control the spatial coding.

component was lost in darkness. Importantly, the still component of the correlate was maintained in darkness. The original firing rate and the turn component were restored on the first trial when room lighting was restored.

One multiple sensory correlate and two *multisensory* cells had a CFI of .50 when animals performed the maze task in darkness. These cells were inhibited in darkness and returned to baseline when the animal was tested in the final light trials.

The *multiple correlate* cells that did not show twofold changes in firing rate (e.g., CFI $<$ .50) due to visual changes were a *turn and inbound* cell and a *multisensory* cell. The firing rate and behavioral correlates did not change across testing conditions. These data, combined with the data from the *still and turn* and *turn and location* cell, demonstrate that turn correlates recorded from superior colliculus can be either visually dependent or independent of visual information.



No obvious correlate cells. Three out of nine cells tested that did not have an obvious correlate had a CFI of .50 or greater during the dark phase of the Light–Dark–Light manipulation; all three were inhibited in darkness. In one case, a cell that maintained a broad-preferred firing field across several days (location specificity = 1.76) showed a slight increase in the location-specific firing in the light trials following dark testing (location specificity $>$ 2.0). This cell may have been coding a general area of the maze but not with the same location specificity required by our a priori criterion.

Summary. Taken together, these data suggest that not all spatial cells are dependent on visual information; about half of those recorded show visual sensitivity, the remaining did not. The utility of examining firing rate changes is exemplified by the spatial cells with a location bias that showed changes in firing rate corresponding with a decreased reliability of spatial coding. This suggests that *location* cells whose firing rates were influenced by visual information were coding visuospatial features of the environment and in darkness the accuracy of the correlate was disrupted. In contrast to the common argument that turn-related cells reflect angular head movement, at least a subpopulation of superior collicular turn cells were shown to be visually dependent. Most of the *multiple correlate* and *multisensory* cells were inhibited when visual input was eliminated. Movement sensitive and somatosensory cells generally were not affected by changes in the visual environment. The different correlates of *multiple correlate* cells were differentially sensitive to visual information: A dissociation of dark effects (within cell) suggests that individual neurons integrate both visual and nonvisual information.

Dark–Light: Is visual input required to establish the correlate?

Spatial movement cells. In the one case in which a directionally selective cell was tested with this manipulation, visual input was not required to establish the normal firing rate or the preferred directional firing. When tested in light, this cell fired preferentially

FIGURE 11. A cell that fired during turns also showed a spatial bias as indicated by elevated activity on a small subset of the maze arms. When the animal was tested in darkness, the spatial bias of the turn correlate was lost and did not return until the final recovery light trial. Importantly, the cell continued to fire during turns in darkness, illustrating that the multiple correlate can be dissociated by manipulation of the visual surroundings. The location bias required visual information, but the turning correlate did not.

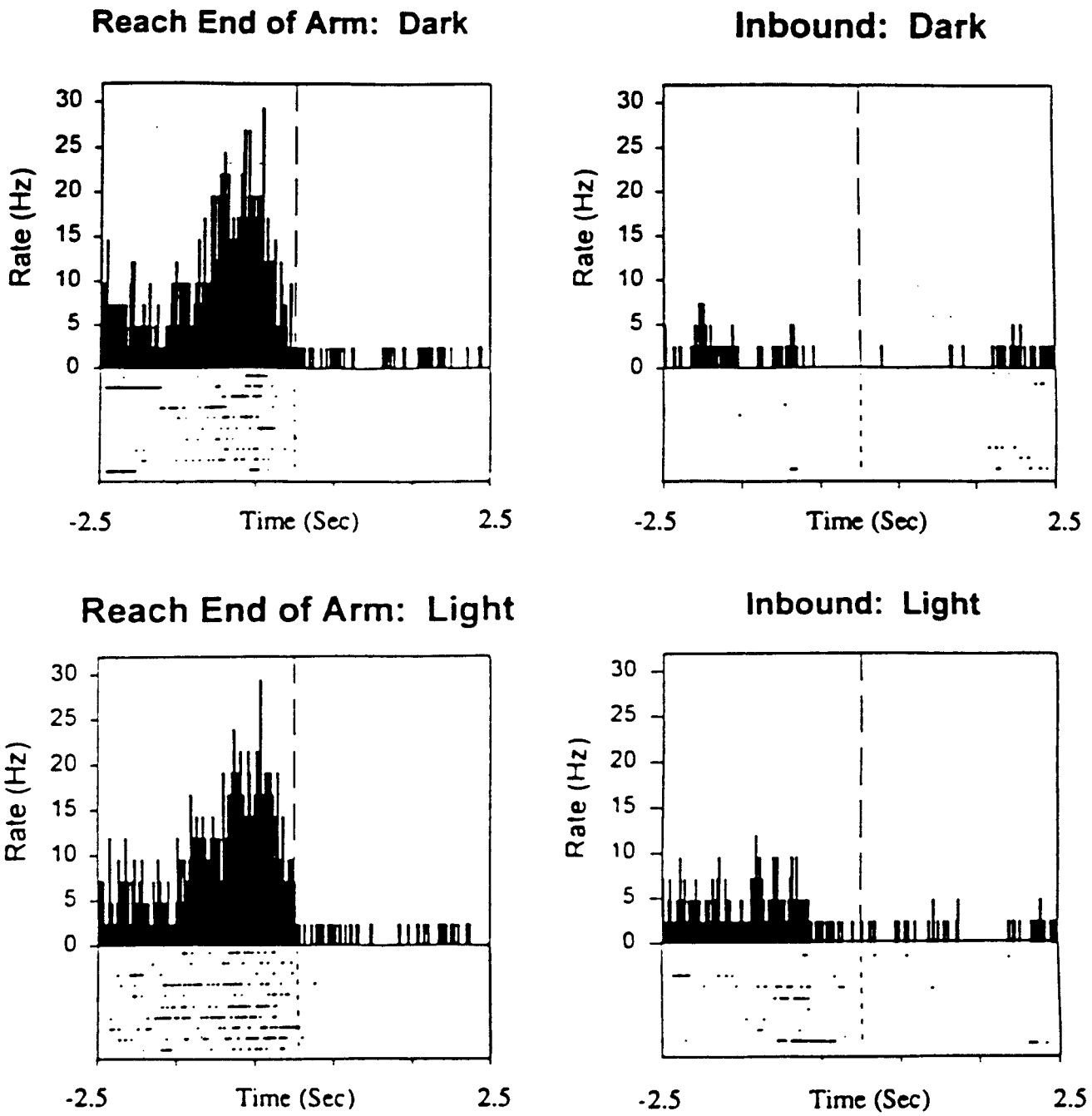


FIGURE 12. Directional coding of space was observed to be independent of visual input in this superior collicular neuron. When the animal was brought into the testing environment in darkness, the cell showed preferential activity when the animal was heading toward the end of the maze arm (outbound). T_0 (indicated by the dashed line in the PETH) marks the cessation of forward movement in the panels on the left half of the figure. In the right half of the figure, T_0 marks the onset of forward movement toward the center platform. When the animal was moving toward the center of the maze (inbound), the cell was not active. The behavioral correlate was the same regardless of lighting conditions. The rasters below the PETHs show a representative 10 out of 40 events. Bin width is 10 msec.

when the animal was headed away from the center platform (outbound). Figure 12 shows that this correlate was observed irrespective of maze room lighting conditions. Importantly, the Light–Dark–Light manipulation performed the previous day demonstrated that visual input was not required to maintain the correlate of this cell. Thus, coding of directional heading can be independent of visual information in superior collicular neurons.

Nonspatial movement cells. One of the seven movement sensitive cells tested (*forward movement*) with the Dark–Light manipulation had a CFI of .90 during light trials compared to the dark trials. The firing rate was increased during dark trials compared to light trials. The other movement-sensitive cells did not show changes in firing rate when animals began maze trials in darkness.

Multiple correlate cells. The one multiple correlate cell tested with this manipulation was a *still and turn* cell. Testing in darkness caused a dramatic reduction in firing rate, CFI = .77, and differentially affected the multiple correlates of the cell. The still component was unaffected by starting maze trials in darkness, but the turn correlate was abolished when visual information was not available. When lighting was restored, the turn correlate returned (see Fig. 13). Further dark testing revealed the same pattern of results: when the animal was subsequently tested in darkness, the still correlate remained, but the turn correlate was abolished until lighting was restored to the maze room (data not shown).

No obvious correlate cells. The one *no obvious correlate* cell tested did not show firing rate changes during this manipulation.

Summary. In the one *directional* cell tested, visual information was not required to establish or maintain the directionally selective firing. Starting the animals in darkness affects a minority of the movement-sensitive cells, but the majority of movement cells are not affected by this manipulation. As with the Light–Dark–Light manipulation, a dissociation between components of multiple correlates can be demonstrated with these changes in the lighting conditions. This dissocation of visual sensitivity within-cell furthers the hypothesis that multiple sensory modalities control the activity of the *multiple correlate* cells.

Cues–No Cues–Cues: Are distal cues critical to maintain cellular correlates?

Spatial movement cells. None of the four spatial cells tested with the cue removal manipulation showed the above criterion changes in firing rate. Interestingly, the location specificity continually increased across the phases of testing in one of the four spatial cells tested (2.74 in the initial trials to 5.62 when the cues were returned). The reliability of the cellular correlate also increased across the three phases of testing (0 to 40). When animals were removed from the testing room and then returned, all five of the *spatial* cells tested showed pronounced inhibition of activity (CFI $>$ .50) despite the fact that the rats were returned to the same visual environment. A *spatial movement* cell (*inbound*) was influenced by this control procedure and also the Light–Dark–Light manipulation.

Nonspatial movement and somatosensory cells. None of the seven *nonspatial movement* cells were affected by cue removal. Seven other *nonspatial movement* cells were also tested with the removal from the testing room, and none of these were influenced by this control procedure. The two *somatosensory* cells tested with cue removal were not influenced by this manipulation.

Multiple correlate cells. Cue removal did not influence the one *multiple correlate* cell tested with this manipulation. Two *multiple correlate* cells underwent the procedure of removing the animal from the testing room and returning to the maze room. The firing rate of one *multiple correlate* cell (the cell fired when the animal was relatively still at the end of the arm and during turns on arm ends) was inhibited when the animal was returned to the maze room and testing continued. Furthermore, as with the inbound cell described above, this cell was similarly affected by the Light–Dark–Light and Dark–Light manipulations (see Fig 13 for effects of Dark–Light manipulation). Illumination changes and dark adaptation processes represent a possible interpretation for these data. Under normal testing conditions the animals are brought into the dark maze room from the brighter outer room, attached to the recording equipment, and generally remained in the darker environment for several minutes before maze testing began, thereby inadvertently allowing the animal time to adapt to the dimly lit environment. The procedure of removing the animal from the testing room, then returning the animal to the maze room and beginning maze trials may not have allowed the animals visual system to completely adapt to the darker maze room. To control for this possibility, the *multiple correlate* cell was recorded the subsequent day, with maze trials commencing as quickly as possible following introduction into the darker maze room. This procedure did not influence the normal correlate of the cell, and reduces the likelihood that visual adaptation processes can completely explain these data.

No obvious correlate cells. The two *no obvious correlate* cells tested did not show above criterion changes in firing rate during the course of the Cues–No Cues–Cues manipulation. Two other *no obvious correlate* cells were also tested following removal from the testing room. One cell was inhibited and the firing rate of the other was not affected by this procedure.

Summary. The distal cues used in this study do not appear to be critical for cellular activity in superior colliculus. Although it may initially appear somewhat surprising that only one spatial cell changed during cue removal, this pattern of data suggests that more global environmental features (e.g., geometry, illumination conditions of the room, etc.) are critical determinants for establishing and maintaining spatial correlates in the superior colliculus. Removing the animal from the testing room inhibited the firing rate of a variety of cellular correlates: One potential factor common across two of the cells was dependency on visual information. The control procedure for the illumination changes indicates that dark adaptation processes alone are insufficient to completely explain the observed effects; therefore, contextual or attentional factors may be responsible for the inhibition of cellular activity.

Sensory Responses and Multisensory Integration

Somatosensory cells. All of the *somatosensory* cells identified showed clear responsivity to contralateral brushes of the vibrissae with a pencil. Figure 14 shows an example of a somatosensory neuron that shows a lateralized response to contralateral vibrissae stimulation. Some neurons that were activated by vibrissal stimulation also showed responses to light touches on the body by the experimenter's finger. The responses to body touches, however, did not always appear to clearly discriminate between sides of the body.

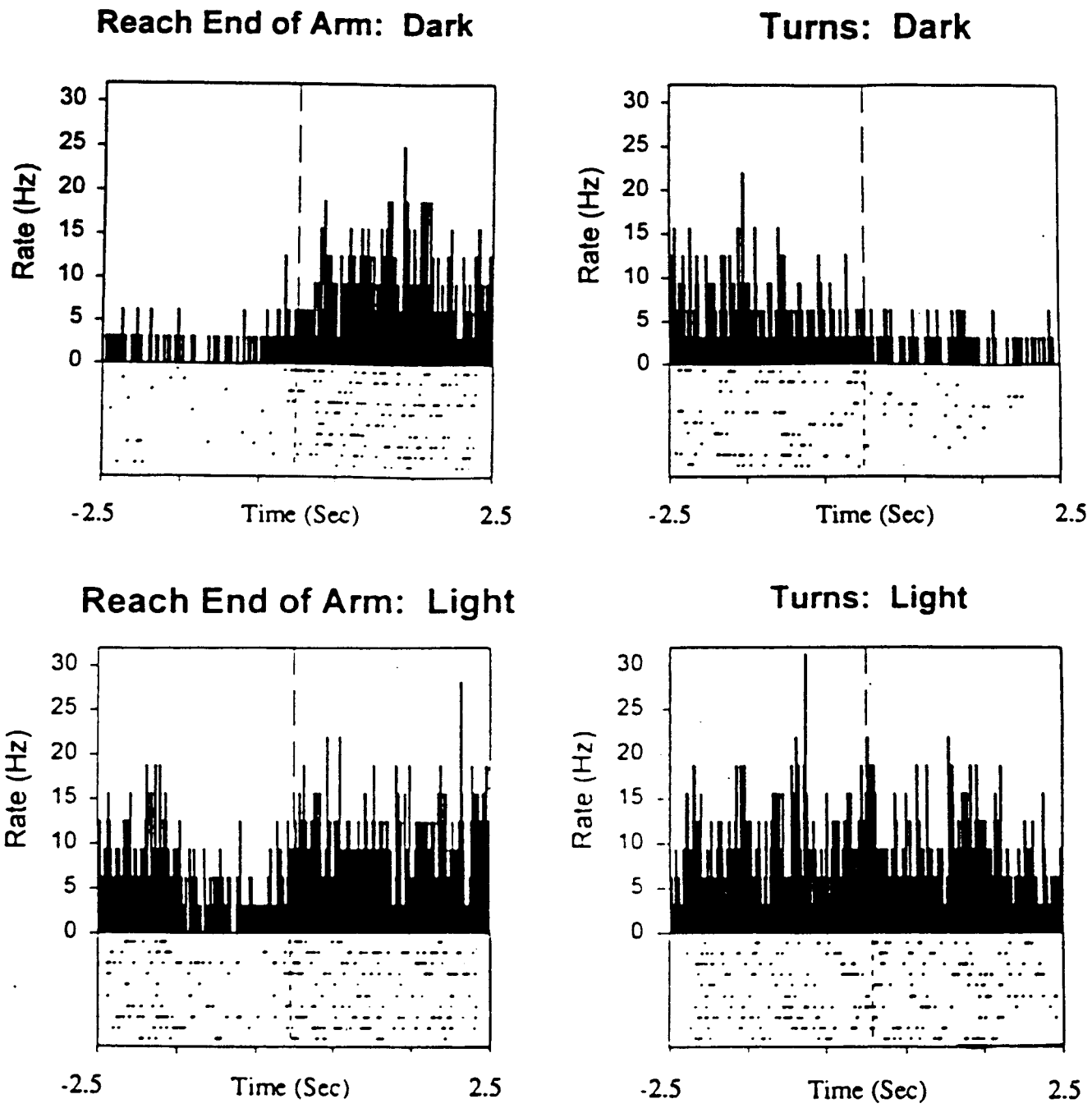


FIGURE 13. The Dark–Light manipulation confirmed that multiple correlates could be dissociated. When the animal was carried into the testing room in darkness, this particular cell was active only when the animal was relatively motionless at the end of the maze arms, and not during turning behaviors (top of figure). T_0 for the "Reach End of Arm" PETH marks the cessation of forward movement on the maze arms. T_0 for the turn correlate designates the onset of turning behaviors. When room lighting was reinstated, the cell then showed activity during both still behaviors and turning and the end of the maze arms (bottom of figure). Turning on the center platform, in addition to the end of the maze arms, caused this cell to fire only when room lighting was available. This activity, occurring prior to the animal heading down toward the end of the maze arm, is apparent during the −2.5 s to −1.5 s range on the "Reach End of Arm" PETH in light. Bin width is 10 msec.

Multisensory integration. Four cells showed enhanced (CFI > .50) responses to the simultaneous presentation of an auditory and visual stimulus compared to the presentation of auditory or visual stimuli presented alone (see Fig. 15 for an example). In the case of the cell presented in Figure 15, the mean rate for 1.5 s following visual or auditory stimulus presentations was 4.0 Hz and 6.0 Hz, respectively. The multisensory response was not simply an additive response of the individual sensory modalities;

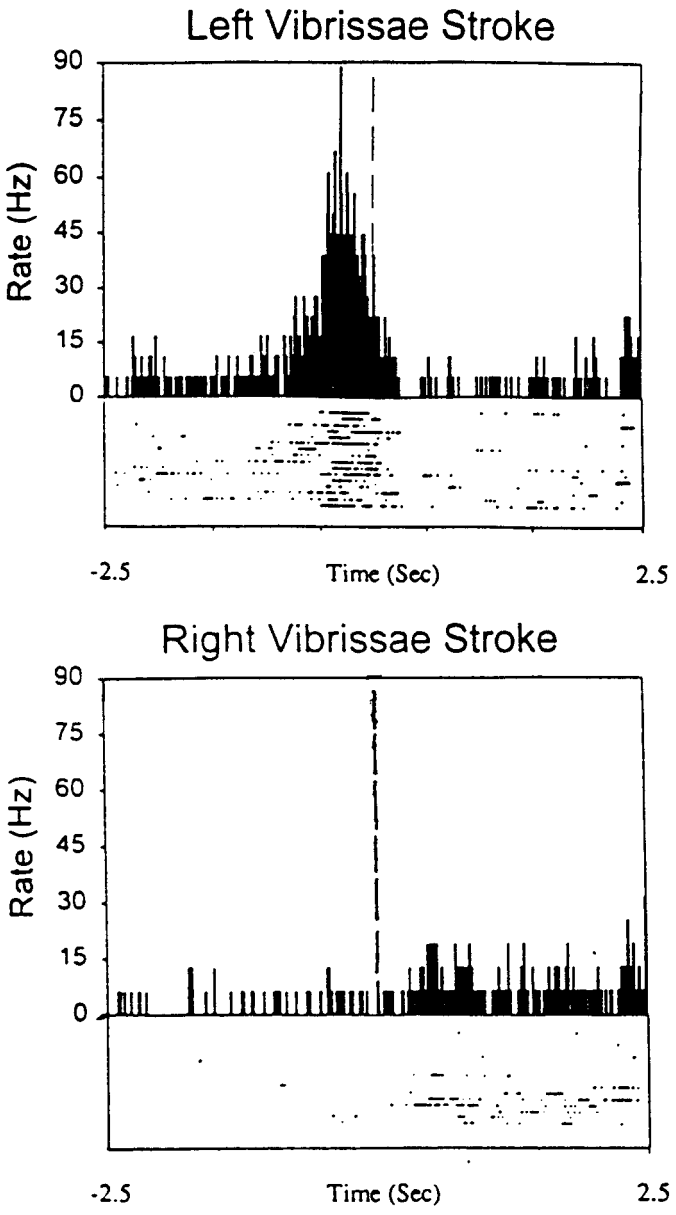


FIGURE 14. Lateralized somatosensory responses were observed by several superior collicular neurons. This cell responded preferentially to left vibrissae stimulation. The activity prior to onset of stimulus presentation may reflect motor activation of the vibrissae prior to the sensory input, or may be due to slight errors in marking the onset of stimulus presentation. The rasters display the 16 stimulus presentations on the left vibrissae and the 12 presentations on the right. Bin width is 10 msec.

rather, when visual and auditory stimuli were presented together, this cell fired at an average rate of 15.9 Hz for the 1.5 s following the stimulus presentation. The multisensory cell presented in Figure 15 also responded to vibrissal stimulation (data not shown); regrettably it was not possible to reliably stroke the animal's vibrissae in darkness, and therefore we were not able to assess the potential for trimodal sensory integration. A similar pattern of data was observed for the other three multisensory cells. The response to the multisensory stimulus was well above twice the rate following unimodal input.

Summary. Similar to previous data, superior collicular cells were activated by sensory stimuli. Furthermore, it has been well documented that multisensory stimulation caused enhanced responses in individual cells recorded from anesthetized and restrained cats. To the best of our knowledge, this represents the first demonstration of mulitsensory integration occurring in superior colliculus of freely behaving rats.

Unique manipulations

Novel environment: Spatial movement cells. Two *spatial movement* cells were differentially affected by testing the animals in a novel environment (see Fig. 1C for description of novel environment). One location cell did not fire for the first two days of testing in the novel environment, while continuing to show a spatial bias in the familiar testing environment. On the third day of testing, this cell began to fire in the novel environment but the preferred firing field and location specificity were not isolated to a single location. In the familiar environment, the preferred location of the firing field could be controlled by placing novel cues (e.g., visual, auditory, somatosensory, gustatory, or olfactory) on the maze or at the end of maze arms. When an experimenter jingled keys outside of the curtains (auditory), quietly stood at the end of one arm (visual), placed novel food (gustatory and olfactory), or textured paper on a maze arm (somatosensory), the preferred field was always located on the arm with the currently novel stimulus. All of these tests were conducted in a single day in the familiar environment with three trials given for each stimulus.

One other *location* cell, recorded from a different animal than the previously described cell, was tested in both the novel and familiar environment. This cell showed both different and similar results compared to the previously described cell. Unlike the previous cell, this cell showed a relatively high location specificity score and reliability (location specificity = 3.97, reliability =.50) on the first day in novel environment. The preferred firing field remained in the same location for the first 4 test days in the novel environment (outbound on arm 7), but the specificity and reliability of the field changed across days (range; spatial specificity = 1.72 to 5.75 and reliability = .50 to 0). After the fourth day of testing in the novel environment, the location of the firing field began to shift unsystematically. After the first 4 days of testing in the novel environment, the changes in the location of the firing field were similar to the observation that the location bias also varied across test days in the familiar environment (see Fig. 16 for familiar environment changes across days).

In the initial novel environment testing, the location and direction bias was outbound on arm seven. This happened to be the arm facing directly towards the location of the experimenter during behavioral testing (see Fig. 1C). To assess whether the presence of the experimenter was influencing the cellular correlate, the animal ran five trials with the experimenter in the normal position, five trials with the experimenter rotated 180°, and five trials with the experimenter returned to the original position. The

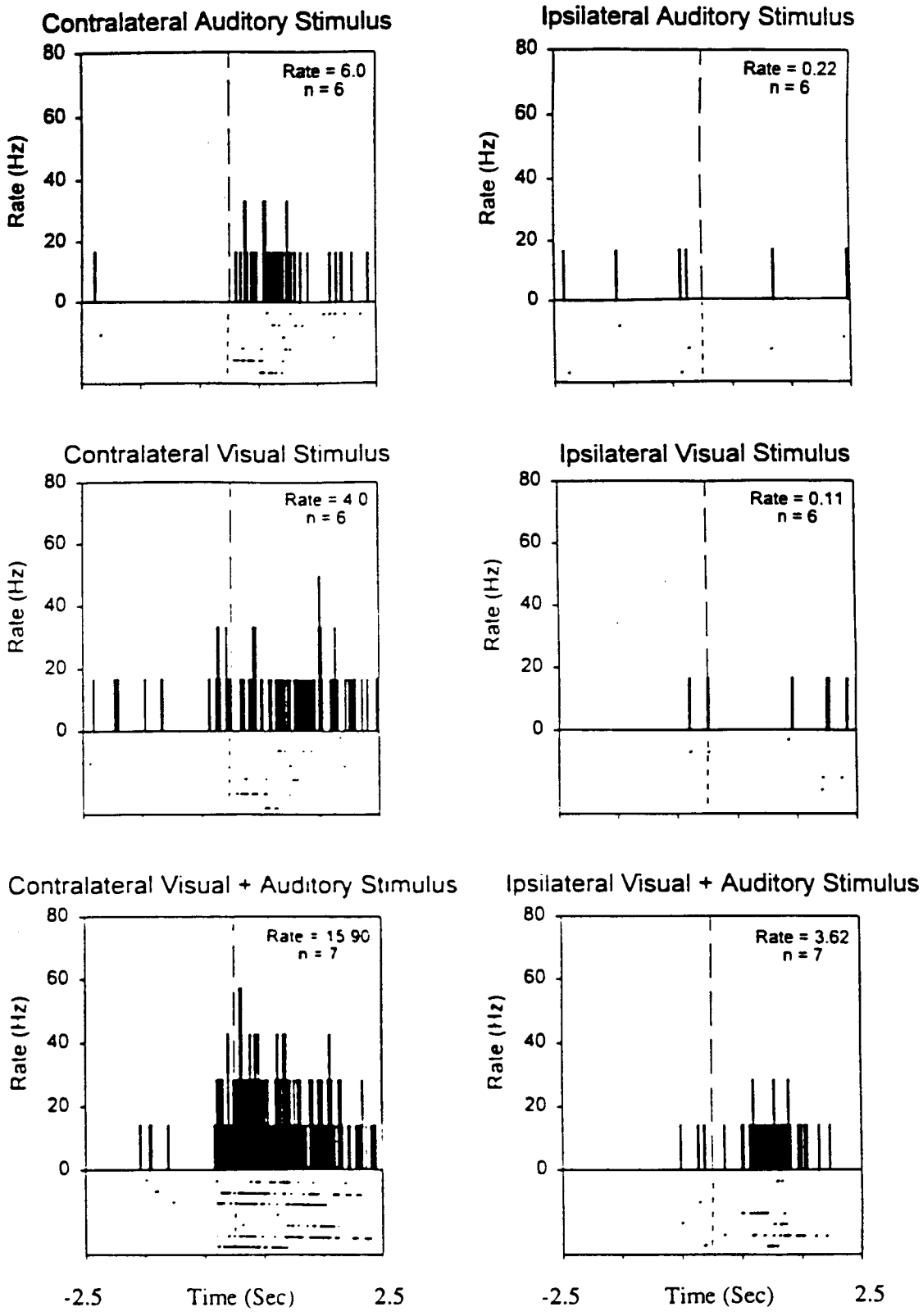


FIGURE 15. **Multisensory integration was demonstrated in four cells. In all cases the response to the multimodal stimuli was not a simple additive response of the unimodal components. T_0 (indicated by the dashed line) marks the approximate onset of the stimulus for a representative cell that showed multisensory integration. The rate displayed in the top right corner of the figure is the average rate of the cell for 1.5 s following stimulus onset. The rasters display the individual responses of the cell to the six auditory and visual stimulus presentations and the seven multisensory presentations. Bin width is 10 msec.**

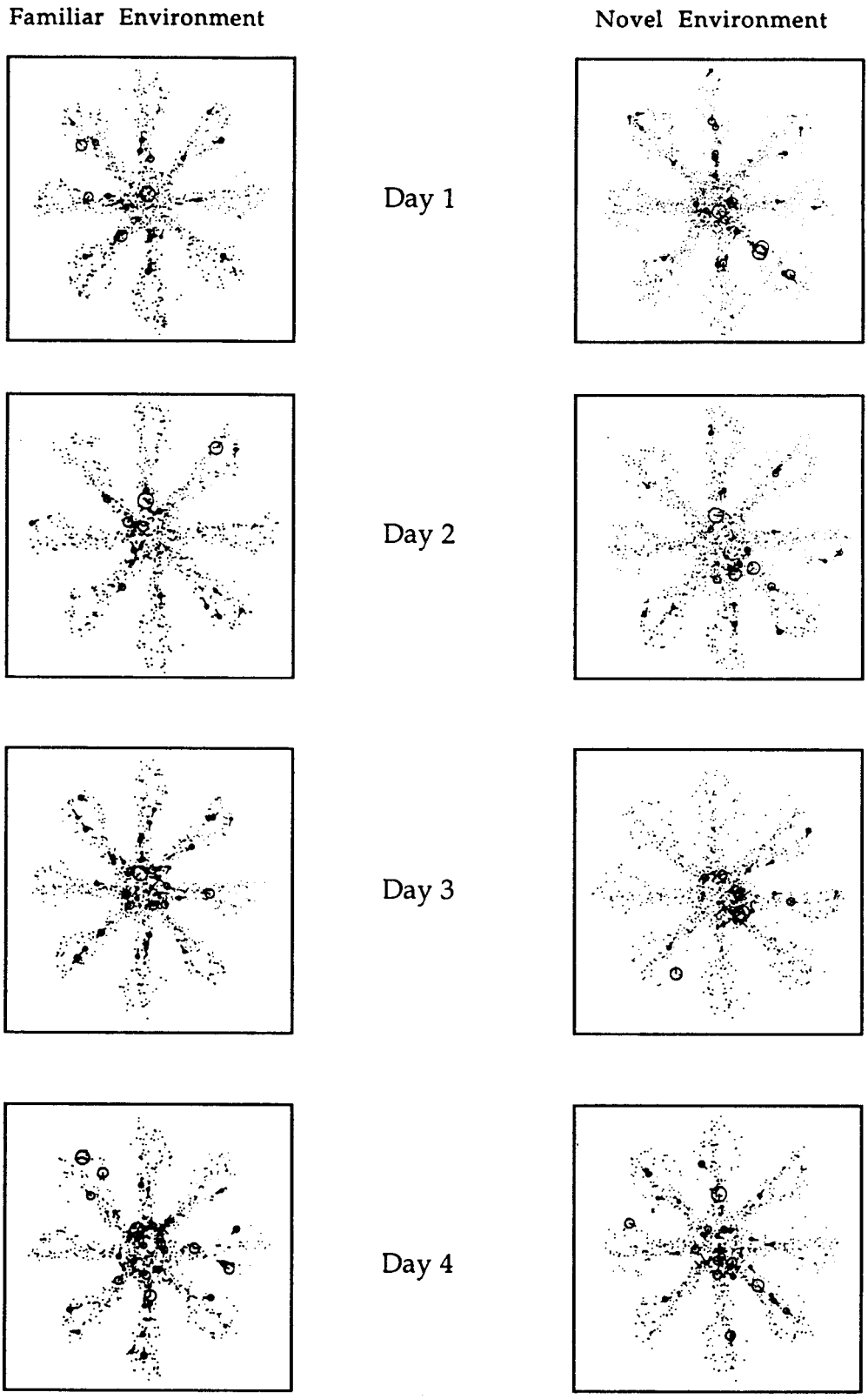


FIGURE 16. A spatial cell maintained a preferred firing field localized toward the location of the experimenter in the novel environment for the first 4 days of testing. The experimenter was positioned in the southeast corner of the room (see Fig. 1C) during maze trials, and the preferred firing field fired on the center platform and maze arm directed toward the experimenter. In the familiar environment, this cell did not show a predictable pattern of change in preferred firing location across days. However, it generally fired more when approaching the center platform in the southern direction. Changing the location of the experimenter during maze trials in the novel environment demonstrated that the location of the preferred firing field was largely influenced by the spatial location of the experimenter (data not displayed).

preferred direction of the field, but not the location, rotated with the experimenter but did not return until the subsequent test day (i.e., the cell fired when the rat moved toward the center platform (inbound) on arm seven).

Two other tests were performed on this cell to evaluate the contribution of room geometry and salient distal cues to the observed spatial correlate. The effects of room geometry were tested by enlarging the original controlled cue environment and adding unique distal cues to the "new" room. Additionally, the curtains were removed, leaving a room similar to the original novel environment. When the animal was tested in the enlarged room with novel distal cues the location specificity decreased slightly but reliability increased. Removal of the curtains, which left a room virtually identical to the original novel environment (see Fig. 1C), caused location specificity to increase and did not affect reliability. To evaluate the contribution of a salient distal cue in the environment, a novel experimenter (different from the one in the original novel environment) sat in a chair by arm 7 during the first four trials of testing. The cell showed high location specificity (4.55) and reliability (.75) as the animal moved out toward the experimenter. Rotation of the experimenter by 90° caused an equal rotation of the field (location specificity = 9.62, reliability = .5), but when the experimenter was returned to the original location the field did not return. These results are similiar to what was observed in the first novel environment: when the experimenter was moved, the field shifted accordingly, but did not return with the reinstatement of the original test situation. Regrettably, the cell could not be isolated on the subsequent day to determine if the correlate would return.

Novel environment: Nonspatial movement cells. One *movement* and one *turn* cell were tested in the novel environment. Both of these cells were not affected by testing in the novel environment.

Novel environment summary. These results make several important points. First of all, increasing the size of the testing room and providing more geometric features within an environment enhanced both reliability and location specificity of spatial coding in superior colliculus. Secondly, regardless of which environment the cells were tested in, location specificity could be controlled for by the introducing a salient stimulus (i.e., novel cues or an experimenter) into the room. Lastly, even though the cells did not maintain a consistent spatial bias restricted to a single arm in the familiar environment, the location bias remained stable in the novel environment for the first 4 test days. Thus, spatial coding in superior colliculus can represent both stable features of environments and novel stimuli that occur within them. In contrast to the spatial cells, the movement related cells are completely unaffected by testing in the novel environment.

Passive movement. In order to assess the contribution of voluntary movement to the activity of *nonspatial movement* (n = 3) and *spatial movement* (n = 1) cells, passive movement tests were conducted by carrying the animal by hand about 15 cm above each maze arm, with a 2-min ITI, for five trials. During passive movement, three movement-sensitive cells fired at a very high rate, and one *spatial movement* cell fired at a low rate relative to baseline light trials. Furthermore, the firing of all cells tested did not discriminate between forward movement, stopping or turning behaviors. In three of the four cells (two *nonspatial movement*, one *spatial movement*), the passive movement tests were followed by five maze trials, and the normal firing rate and behavioral correlate returned during these maze trials. This suggests that if stress during passive movement was responsible for the observed changes in firing rate, it did not have a long-term effect on the observed correlate. These data indicate that active movement is required for normal spatial and movement coding by superior collicular neurons.

To further investigate the role of vestibular input, a *turn* cell was recorded while the animal was subjected to passive body bends of either the front- or hind-half of the body while the other half of the body was kept still (see McNaughton et al., 1994). This cell did not discriminate between either front- or back-half body bends in either the left or right direction. Additionally, the cell did not fire during left or right turns on the center platform. Thus, it appears that specific motor activity occurring only at the end of the arm is required for this turn correlate to be observed.

Histological results

Based upon electrode reconstructions, the locations of cells from each of the different categories of behavioral correlates were determined. Most electrode passes were through the medial portions of superior colliculus, A–P coordinates were generally placed about 6.3 mm to 7.3 mm posterior to bregma. Two passes were farther anterior or posterior to these general locations (5.8 – 7.8 mm). Figure 17 displays the relative distribution of the recording sites for the observed behavioral correlates. *Spatial movement* cells were found in the superficial, intermediate, and deep layers of superior colliculus and a discrete topographical organization did not appear to be present. The other correlates showed more of a topographical organization within superior colliculus. *Nonspatial movement* cells were predominantly found in the intermediate and deep layers. Only one movement-related neuron was found in the superficial layers; and, not surprisingly, this cell was sensitive to changes in the visual environment. *Sensory* cells were also distributed across lamina. One *somatosensory* cell was found in the superficial layers, the remaining in the intermediate/deep layers. The observation of a *somatosensory* cell in the superficial layer may be explained by the cell responding to visual input from the lower visual field. However, visual sensory tests did not elicit obvious neural responses. *Multiple correlate* cells were found in the intermediate and deep layers of colliculus. Consistent with previous studies in cats, *multisensory* cells were also limited to the intermediate and deep layers.

Discussion

The present experiment evaluated the contribution of visual and nonvisual cues that may influence cellular correlates recorded from neurons in the superior colliculus during spatial memory performance. Manipulations of the visual environment (e.g.,

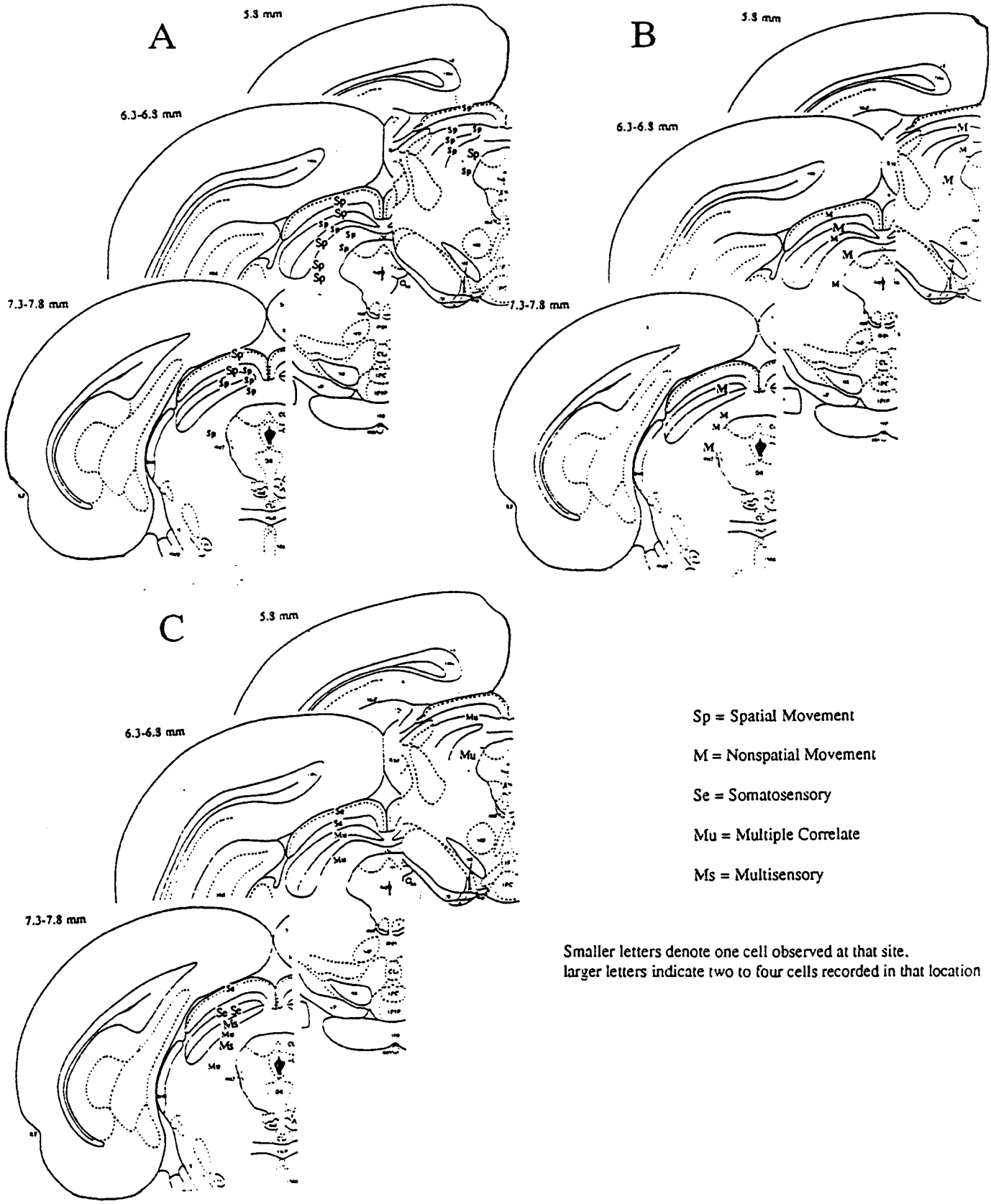


FIGURE 17. The location of the behaviorally correlated neurons within the superior colliculus, based on electrode tract reconstructions varied across the superificial and intermediate/deep layers of superior colliculus. A: Spatial movement cells were observed throughout the superficial, intermediate, and deep layers of superior colliculus. B: Nonspatial movement cells were primarily observed in the intermediate and deep layers of superior colliculus. C: Somatosensory, multiple correlate, and multisensory cells were primarily observed in intermediate and deeper layers of superior colliculus. One somatosensory cell was observed in superificial layers. It is possible that this cell responded to visual stimulation only in the lower visual field.

Light–Dark–Light, novel environment) demonstrated that many, but not all, spatial cells are strongly dependent on general features of the visual environment. Individual distal cues do not appear to importantly contribute to the spatially selective discharge of superior collicular neurons; rather, overall geometry and relative luminance conditions may play a more important role in modulating spatial coding in this structure. The movement- and somatosensory-related correlates remained reliable regardless of changes in the visual environment. Passive movement tests suggest that movement-related correlates likely require motor activity, rather than vestibular input, to control the cellular correlate. This does not mean that vestibular information is not a contributing factor, but that it is not sufficient to drive the representations during maze behavior. Multimodal and multisensory integration was demonstrated for the first time in freely behaving rats. One multisensory cell also had a spatial correlate, which suggests that spatial correlates may utilize multisensory information in superior collicular neurons. These results strongly support the hypothesis that the superior colliculus is multifunctional and can play an active role in experience dependent navigation.

The results from the environmental manipulations suggest that there may be two kinds of spatial coding in superior colliculus: visually dependent and visually independent. Although individual distal cues alone are unlikely determinants of spatial coding in the familiar environment, the Light–Dark–Light and novel environment data suggest that the size of the visual environment and complexity of the visual surroundings may have a strong impact on spatial coding in many superior collicular cells. However, coding of both general directional heading (relative to the maze configuration; i.e., inbound or outbound) and location was also found to be independent of visual information in other spatial cells. Hence, visual information may control spatial coding in some neurons and movement may mediate spatial coding by others. This is in keeping with the multiple output pathways of superior colliculus (Redgrave et al., 1993), in particular, the differential sensory responsiveness of cells in the well-identified approach and avoidance pathways (Westby et al., 1990). Discrete regions of superior colliculus project to areas mediating approach behaviors, and other regions project to areas mediating avoidance responses. Neurons within the "approach" area of superior colliculus were responsive to auditory and somatosensory stimuli, and neurons in the "avoidance" area were responsive to visual and auditory stimuli (Westby et al., 1990). The differential visual sensitivity of spatial coding suggests an input/output scheme similar to what has been identified for orientation behaviors. Thalamic projections from superior colliculus may be strongly influenced by visual information (i.e., visually dependent), whereas projections to motor output structures from superior colliculus may be independent of visual information. Thus, visuospatial information may be sent to thalamus from superior collicular neurons, and spatially guided movements may be mediated via spatial neurons in areas of superior colliculus with motor projections to approach and avoidance pathways (cf. Westby et al., 1990).

Extensive work in primates has revealed a motor map of saccades elicited by stimulation of the intermediate layers of superior colliculus: Large amplitude saccades are evoked by stimulation in the caudal superior colliculus, and small amplitude saccades in the rostral superior collicular stimulation (Robinson, 1972). Furthermore, buildup and burst cells have been identified perhaps relating to preparation for and execution of saccades, respectively (Sparks, 1978; Munoz and Wurtz, 1995). In the rat, stimulation of the superior colliculus also evokes contraversive conjugate eye movements with a similar topography as has been reported in primates (McHaffie and Stein, 1982). Activation of superior colliculus in the rat also evoked movement of the pinnae and vibrissae. Therefore, it is possible that head movements would have been elicited if the animal had not been restrained. Chemical and electrical stimulation in freely moving rodents shows that superior colliculus activation causes discrete behavioral responses resembling approach and avoidance movements, depending on the area of superior colliculus that is stimulated (Dean et al., 1986, 1988; Sahibzada et al., 1986; Westby et al., 1990). The combination of the primate and rat data are consistent with the hypothesis that directing movements toward spatially relevant locations is an important function of superior colliculus. In rats, because they have a very large visual field and do not have a discrete foveal representation, general body movements may be preferentially mediated by superior colliculus; whereas in primates, saccades toward discrete locations in space are critically controlled by collicular activity. In both species, the behavioral function may be conserved despite the difference in specific movements controlled by superior colliculus.

The relationship between turning behaviors and orienting movements may suggest similarities between the current work and that of approach or avoidance studies in freely moving rats. It is possible that the turn-related neurons are part of the orientation system mediated by superior colliculus. In some cases, it may be that turn correlates were dependent on visual information (e.g., *still and turn* cell) and in others they were not (e.g., *turn and location* cell). This suggests that updating movement changes during orienting responses might be coded by neurons in superior colliculus, and these neural codes reflect the current visual input, motor output, or visual-motor integration. Interestingly, vestibular information alone does not appear to be able to drive turn-related neural activity. In the one cell subjected to passive body bends, vestibular turn activation did not occur. Furthermore, this cell only fired when the animal was turning at the end of the arm and not on the center platform of the maze. Thus, specific motor sequences are required to activate some turn-related collicular neurons. In addition to turn-related neurons, individual units were correlated with the general movement state of the animal. These data support the argument that in freely behaving rats the superior colliculus mediates approach and avoidance behaviors, potentially toward spatially important locations.

In a previous study involving freely moving rats, somatosensory, visual, and auditory responses were observed. Forty-eight percent (27/56) of the collicular neurons showed pronounced sensory responses (Weldon and Best, 1992). In the present study, only 12.5% (16/127) of the cells responded to sensory stimulation. This difference in percentage of sensory correlates between the studies may be explained by the finding that a reduction in

receptive field size was observed by placing the animal on a circular platform (Weldon and Best, 1992). Because all sensory tests were conducted while the animal was on the center platform of the maze, the receptive field sizes of the cells may have been reduced, making them harder to detect. Additionally, because of the primary interest in spatially selective discharge, only data from those cells that showed clear sensory responses online were quantified. This may have reduced the total number of cells observed in the present study. Weldon and Best (1992) also reported the presence of bimodal and trimodal sensory neurons (19.6%; 11/56). In the present study we observed multimodal and multisensory responses in 10.2% (13/127) of the neurons recorded. Again, the difference in total number of cells may reflect differences in testing conditions.

Multisensory integration has been extensively studied in anesthetized and restrained animals (see Stein and Meredith, 1993, for review). In the cat, the location of the recording site is a critical predictor for the number of multisensory neurons that are likely to be observed. For example, 84% of the neurons that were activated antidromically by tectoreticulospinal stimulation have been shown to be multisensory (Meredith et al., 1992). Consequently, the neurons projecting to motor structures important for orienting behaviors are predominantly multisensory neurons, and these in turn likely guide orienting behaviors (cf. Wilkinson et al., 1996). In the present study, both multisensory and multimodal integration were demonstrated in freely behaving rats, although at a much lower percentage (10.2%) than reported in cats. The smaller percentage in the current study may reflect species differences, different testing procedures, or a combination of both factors. Despite the difference in the absolute number of multimodal cells observed, the multisensory integrative responses in this study are similar to those that have been reported for cats. In addition to multisensory integration, cells that correlated with multiple maze behaviors showed multimodal integration. That is, one component of the multiple behavioral correlate could be visually dependent while the other was visually independent. For example, when a *turn and location* cell was tested in darkness, the turn correlate remained, but the location bias was lost. In sum, these data suggest that multisensory integration is conserved across species.

An important caveat to note is that precise mapping of receptive field properties of the sensory cells was not a goal of the present study. Therefore, we cannot provide more details about the psychophysical properties of the multisensory integration. Clearly such a study would be of critical importance in the future. Because sensory tests were not the primary goal of the present study, two potential confounds are present in the multisensory tests. The multisensory integration tests were not performed with simultaneous recordings of muscle activity, so the influence of movement cannot be completely accounted for. Furthermore, subtle methodological issues may represent a potential confound in the multisensory tests. Despite these issues, motor activation and differences in testing procedures do not seem likely to have produced the multisensory integration effect. First of all, if waving and jingling the keys caused the animal to move, thereby resulting in increased cellular activity, then jingling the keys in darkness should have caused the animal to make similar movements. The response to the auditory cue in darkness was virtually equal to the visual response, and was clearly less than the multisensory response; thus movement differences are unlikely to explain the current data. Lastly, the shape of the visual stimulus in the multisensory condition was not identical to that of the visual alone condition. It is possible that the enhanced response in the multisensory condition is due to this methodological difference. This explanation does not seem likely because the difference was simply in the shape of the hand (cupped in the multisensory condition and open in the visual alone). Given that the cupped hand covered a smaller visual area than the open hand, it is likely that this condition would elicit less of a visual response. Instead, a dramatic enhancement was observed when waving was combined with the jingling of keys. Thus, although future studies will be required to fully understand the nature of multisensory integration in freely behaving rats, the present study strongly suggests that multisensory integration is an integral part of cellular processing in superior colliculus.

Weldon and Best (1992) first reported that alterations in the testing environment could change the size of receptive fields in collicular neurons. The present study provides further support for the effects of changing testing conditions on the normal activity of the cellular correlates in superior colliculus. Simply removing animals from the testing arena and allowing them to wait in an outer laboratory room before continuing maze trials disrupted the normal activity of many collicular cells. This procedure, which does not affect place cells in hippocampus (Cooper and Mizumori, unpublished observations), profoundly inhibited several superior collicular neurons. Those cells that showed inhibition during the dark phase of the Light–Dark–Light manipulation were also inhibited by this procedure. The control for visual adaptation demonstrated that bringing the animal into the testing room from the brighter outside laboratory room and beginning maze trials immediately failed to change the spatial correlate. Therefore, adaptation alone cannot completely explain the observed effect.

One possibility is that attention and context are playing an important role in controlling cellular representations of space in superior colliculus. On virtually every test day, when the animal was removed from the maze room, the animal was returned to the animal colony room and not tested until the subsequent day. The control procedure, however, presented a novel testing situation in that it required the animal to perform more maze trials when it was not expecting to. It is possible that the animal "expected" to return home, hence superior colliculus activity was inhibited when the animal was removed from the testing room. This argument would suggest that when the animal was not expecting to encounter potentially novel stimuli (i.e., behaviors that the superior colliculus is involved in), then superior collicular activity may be suppressed, perhaps by top-down cortical influences. The duration of suppression, about 15–20 min, was identical to the amount of time required for the cellular correlates to return following the dark phase of the manipulation. This delayed responsiveness following visual and contextual changes may suggest cortical modulation of superior colliculus activity in freely

behaving animals. An additional role of cortical input may also help to define the stimulus encoding properties of spatial cells in superior colliculus of rats.

Introducing animals to a novel environment provided interesting differences in the spatial coding properties of superior collicular cells. The first cell was not active until the third day of testing in the novel environment. A similar, albeit quantitatively different, time-dependent process was required to reinstate two correlates tested with the Light–Dark–Light manipulation. This finding may be taken as evidence that feedback from cortical areas is involved in establishing spatial representations in colliculus. The second spatial cell tested in the novel environment was responsive to, and could be controlled by, salient stimuli introduced in the environment. Therefore, in addition to receiving information from cortical areas, these cells may serve the purpose of updating stable representations in thalamus and hippocampus. Movement cells, on the other hand, do not appear to be influenced by these contextual changes.

The present data suggest that the superior colliculus can contribute to a variety of spatial behaviors. A diversity of cellular correlates was observed in this structure relating to visual environmental features, motor activity, somatosensory, and multisensory stimuli. Similarities between the primate, cat, and rodent superior colliculus literatures suggests that the spatial coding observed in superior colliculus may have comparable functional implications across species. In primates, superior colliculus is thought to mediate saccades toward discrete locations (Sparks, 1978; Munoz and Wurtz, 1995). Superior colliculus in cats, on the other hand, may control gaze (eye and head movements) direction (Munoz et al., 1991). Our data also suggest that an important function of superior colliculus is to direct movements to important locations in space. Additionally, multisensory responses in cats are cortically modulated and important for orienting behaviors (Wallace and Stein, 1994; Wilkinson, et al., 1996). The multimodal and multisensory responses observed in the present study may also be cortically modulated given their delayed response to environmental changes. Thus, as in primates and cats, the rodent superior colliculus may facilitate knowledge of multimodal stimuli present in the environment via feedforward and feedback interactions with cortical areas. The alignment of visual, auditory, and somatosensory maps would facilitate such a process and allow for accurate movements toward spatially relevant locations. Visual, auditory, and somatosensory input may contribute to spatial firing in combination with attentional and contextual modulation. In other words, depending on attentive and contextual factors relevant for spatial behaviors, coding of spatial information may be modified during active navigation. This dynamic and interactive process may function optimally when, in a familiar sensory environment, locations are encoded in broad terms. Upon exposure to novel discrete sensory stimuli, neural discharge becomes more localized and directly relevant to the presence of the novel stimuli. The following discussion explores the possiblity that the superior colliculus may importantly contribute to navigation because of the requirement for spatial attention to stimuli in the environment.

GENERAL DISCUSSION

Our initial hypothesis was that the superior colliculus may provide important spatially-relevant information to the limbic system for use in continually updating spatial mnemonic representations. Various limbic structures (e.g., hippocampus and associated neocortex, subicular complex, limbic thalamus) are known to encode information concerning an animal's location and heading direction. Both Experiments 1 and 2 of this study demonstrate for the first time the existence of location and directional movement neural representations in superior colliculus in freely behaving rats. Extended tests of collicular neuron responses to environmental manipulation revealed that their spatial correlates only superficially resembled those of the limbic portion of the tectolimbic circuit.

Comparisons With Spatial and Movement Representations in the Limbic System

Hippocampal place cells require visual information to establish but not to maintain location-specific firing (Leonard and McNaughton, 1990). The maintenance of place fields despite the removal of room lights suggests that these cells are involved in spatial mnemonic processes. In contrast, location coding by a subset of superior collicular neurons showed a significant decrease in reliability when animals were tested in darkness. This suggests that location codes in superior colliculus are dependent on the immediate visual sensory environment and, unlike hippocampal place cells, do not show mnemonic properties. Therefore, despite the initial similarity of the location coding in these two structures, their respective contributions to active navigation are likely fundamentally different. The differences in visual sensitivity of spatial correlates recorded across structures demonstrates that cellular activity which correlates with the current location of the animal could reflect different aspects of spatial memory processing. With careful environmental manipulations and probe trials, the relative contributions of different brain structures to navigation can be determined. Although the superior colliculus may not be involved in mapping mnemonic features of the environment, it likely contributes information that can be used by hippocampal and thalamic afferents for establishing and maintaining cellular representations of space.

Findings from testing animals in a novel environment in the present study suggested that the overall geometry of the room plays an important role in spatial coding by superior collicular neurons. Margules and Gallistel (1988) have demonstrated that rats utilize the overall environmental shape to establish their directional heading. Thus, the coding of overall room geometry by superior collicular neurons may importantly contribute to active navigation in rats. Similar to superior collicular cells, geometry of the testing room also plays a particularly important role in maintaining hippocampal place fields (O'Keefe and Burgess, 1996). Part of the superior colliculus contribution to hippocampal representations of space may be information about the geometric structure of the room via the tectocortical pathway. Unlike the

superior collicular location coding in familiar environments, many place cells in hippocampus are controlled by the location of the visual cues (O'Keefe and Speakman, 1987). Information about the constellation of distal cues may arrive in hippocampus via geniculostriate pathway rather than the tectocortical system. Integrating information about the relationship of the distal visual cues and room geometry likely provides hippocampus with stable representations of the environment. The absence of well localized spatially selective discharge in superior colliculus, compared to hippocampus, may be a result of the type of spatial information being integrated to form the spatial firing pattern. Because the hippocampus integrates information about both room geometry and distal visual cues, more precise fields may be formed. In contrast, only general features of the environment may be encoded by superior colliculus resulting in cellular coding of locations that is less specific.

LDN head direction cells show qualitatively similar mnemonic properties as place cells in hippocampus; they are maintained for short periods of time in darkness, and require visual information to establish the preferred directional firing (Mizumori and Williams, 1993). In contrast to heading direction codes in LDN, the superior collicular directional cells fired in response to movement either toward or away from the center platform. Thus, instead of coding a particular direction in absolute space, superior collicular directional cells appear to be guided by the local geometry of the behavioral testing apparatus. The findings of directional coding in superior colliculus irrespective of lighting conditions, and the fact that superior colliculus projects to LDN, suggests that maintenance of LDN directional activity in the dark may be derived in part by superior colliculus input. Consistent with this view, lesion data and the current experiments indicate that superior colliculus can importantly contribute to knowledge of directional heading within an environment and that this information can be used by efferent structures to mediate active navigation (Lines and Milner, 1985; Foreman and Stevens, 1987).

A large percentage of behaviorally correlated neurons in superior colliculus were related to the movement state of the animal. Cells that fired in response to forward movement, stopping, and turning were identified, particularly in the intermediate and deep layers. Similar movement-related activity in neurons has been observed in posterior cortical areas (McNaughton et al., 1994) and caudate nucleus (Mizumori and Cooper, 1995; Mizumori, et al., 1996). Although the correlates are similar across these structures, it is not clear that the sensory control of these cells is the same. For example, a posterior cortical neuron that fired in response to turning behavior was modulated by a combination of visual and vestibular input (McNaughton et al., 1994). For the one superior collicular turn cell tested with passive body bends, vestibular input did not play a particularly important role in controlling the turn-related activity, and many turn-related cells recorded in superior colliculus did not require visual information to maintain the behavioral correlate. As with the location and direction codes of superior colliculus, the movement correlates recorded in this structure may share similarities and exhibit differences in processing sensory information when compared to other structures. In the case of the turn correlates, superior colliculus activity co-occurs with movement, whereas some posterior cortical neurons appear to be modulated by vestibular–visual interactions.

A Possible Role for Superior Colliculus in Active Navigation

The present data combined with previous reports on the sensory control of spatial coding in limbic structures argue strongly that a broad neural systems analysis is required in understanding how navigation is accomplished. In addition to the differences in sensory-dependent processing across brain structures of spatial information, there are also differences in the role of experience on spatial processing. On several occassions it was demonstrated that a manipulation would change a correlate, but the correlate would either return after 20 min of testing; or, in other cases, not until the next day. Thus, following restoration of original environmental conditions, the time course of representational reorganization varies substantially from midbrain to cortical structures.

Consistent with the finding that collicular location codes require prolonged periods of time to become reliable after major disruption in an expected environment is the result that one spatial cell tested in the novel environment did not become active until the third day of testing. Although the preferred firing field was first observed at this time, the cell did not show a consistent pattern of change in location specificity across subsequent test days. It appears that experience-dependent changes in superior colliculus neural activity are fundamentally different than those occurring in thalamus and hippocampus where spatial representations become stable in at most tens of minutes (Wilson and McNaughton, 1993).

The superior colliculus is classically viewed as part of an orientation system mediating approach and avoidance behaviors to stimuli in the environment. In cats the multisensory integration that occurs within the intermediate and deep layers of superior colliculus is dependent on cortical input (Wallace and Stein, 1994). Importantly, cortical input is also critical for multisensory approach behaviors (Wilkinson, et al., 1996). In the present study multisensory integration was observed in several cells, as was multimodal integration. It seems likely, therefore, that in the rat multisensory integration serves a similar purpose and is controlled by similar mechanisms as it is in cats.

Based on these data we postulate that upon exposure to a new environment, the superior colliculus is initially sensitive to specific features of the environment. Our novel environment data support this view since, in contrast to location fields recorded in a familiar environment, the location fields in the novel environment were selective to single maze arms. With continued exposure, animals soon learn to attend to only a subset of available cues. Perhaps the superior collicular neurons function in a similar way; that is, collicular neurons become tuned to more general, rather than specific environmental features. This form of experience-dependent modulation may occur because of (top-down) cortical influences. Thus, cue removal in a familiar environment had no effect on cell firing, and the location cells exhibited comparatively

broad fields during asymptote performance in a familiar environment. Despite this rather broad spatial code, the colliculus remains adapted to detecting potentially significant changes in its sensory surround. In support of this argument, the location and direction coding of one cell could be controlled by the presence of new stimuli introduced into the familiar environment. Such data imply that the superior colliculus may provide current visual information that can be used by limbic structures to update spatial representations. If the environmental change is sufficiently great (e.g., sudden darkness), cells may reorganize their coding properties in an attempt to adapt. Stabilization of the location fields following dark testing may take time because it depends on cortical input to guide the experience-dependent collicular representations of space.

In conclusion, a main functional contribution of the superior colliculus to navigation may be to continually update limbic cortical structures with significant information concerning the current sensory surround. Its neural codes do not, however, passively reflect the available sensory cues. Rather, there is likely important cortical modulation of collicular responsiveness to familiar cues. In the absense of this modulatory influence (i.e., when not in a familiar environment), the superior colliculus defaults to a function of "detecting" novel stimuli.

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