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THE SPATIAL SUBSTRUCTURE OF VISUAL RECEPTIVE FIELDS IN THE CAT'S SUPERIOR COLLICULUS

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INTRODUCTION

Since the first recordings by Bell and colleagues *(5)* of the activity of visually driven single neurons in the superficial layers of cat's superior colliculus (SC) a considerable amount of data has been collected concerning the receptive field (RF) properties of these neurons (21, 29, 32, 46, 76, 77, 86). It has been well established that collicular neurons are extremely sensitive to moving visual stimuli and most of them exhibits a substantial degree of direction selectivity (29, 41, *45, 75).* According to a number of studies (17, 18, 23, 47, 60) the direction selectivity of collicular cells is a property intrinsic to the superior colliculus (see, however, Ref. *55,* 63, 79, 86). The simplest explanation for direction selectivity of collicular neurons would be the systematic variation of response latency across the receptive field as in simple cortical cells of cat area 17 *(52, 59).* Earlier experiments conducted in our laboratory (28, 87), however, failed to find any correlation between distribution of response latencies to stationary stimuli and type of response to moving stimuli in collicular receptive fields. In *1965* Barlow and Levick (4) proposed an explanation for directional selectivity of rabbit retinal ganglion cells which was based on asymmetry of inhibition in the preferred and opposite directions. According to the proposed model nondiscrimination for direction of movement should exist in the flank of the otherwise direction-selective receptive field which is first crossed for the motion in the preferred direction. The existence of such nondiscriminating zones for retinal ganglion cells in rabbit was shown by Barlow and Levick (4) and recently by He and his colleagues (30). In the case of a mechanism of direction selectivity which is based on asymmetry in the time course of excitation the nondiscriminating zone should be located on the opposite flank of the receptive field.

In the present study we focused on the spatial organization of RFs in relation to directional sensitivity in superior colliculus neurons of the cat and investigated movement-sensitive regions of collicular RFs by local movement of visual stimuli. We used an approach similar to that of Barlow and Levick (4) which attempted, on the basis of location of nondiscriminating zones, to distinguish between mechanisms of direction selectivity based on asymmetry of inhibition and asymmetry of excitation.

Some of these data have been presented in abstract form (19).

METHODS

The experiments were performed on adult cats of either sex weighing between *2.5* and *3.5* kg. The initial surgery was conducted under ether anesthesia and consisted of cannulation of cephalic vein for drug infusion, cannulation of femoral aorta for monitoring blood pressure and a tracheotomy to allow artificial respiration. The animals were then placed in a stere~tpxic frame and a pretrigeminal brainstem transection were performed under ether anesthesia. lui After the transection animals breathed regularly, the mean blood pressure was at 90-100 mm Hg and heart rate below 150 beats per minute. A small piece of bone and the underlying dura mater were removed to provide access to the SC through the overlying cerebral tissue (Horsley-Clarke coordinates A3-P1, Lat 0-4). The animals were immobilized with an intravenous infusion of Flaxedil (gallamine triethiodide, 8 mg/kg/h) and artificially ventilated with respiratory pump. The end-tidal CO2 level was kept at about 4%. Body temperature was maintained at 37^0-38^0C by means of a heating blanket with automatic control. Heart rate, electroencephalogram and blood pressure were continuously monitored during the experiment. The nictitating membranes were retracted and pupils dilated with topical application of drops of 10% Neosynephrine (phenylephrine hydrochloride) and *0.05%* atropine sulphate. Contact lenses of zero power were used to protect the corneal surfaces from drying. The optic discs were back-projected on the screen using a reverse-projecting ophthalmoscope and the area centrales were estimated by the method of Bishop and colleagues (13).

Single unit activity was recorded using varnished tungsten Hubel-type microelectrodes, 2-4 MW impedance. Action potentials were conventionally amplified, displayed on an oscilloscope and monitored over a loudspeaker. The stimuli from a light projector were presented on the concave screen situated 75 cm from the cat's eyes. The screen could be positioned anywhere in the visual field of the cat (see Ref. 29 for details). The usage of concave rather than a tangent screen and the projector positioned above the cat's head allowed movement of visual stimuli with a steady velocity independent of the position of the tested region in the receptive field and the location of the receptive fields of the unit. The responsiveness of a neuron to the visual stimulation and the location of the receptive fields were determined using dark and light stimuli moved by hand. All test recordings were made for each eye separately or only for the dominant eye. The eye not being tested was always occluded. The RFs were examined by using a *0.5* deg x 1 deg light bar moving along the horizontal axis. Speed of stimulus movement chosen for detailed investigation of RF was usually 70 deg/s, a value which is close to the mean optimal velocity for SC units from the superficial layers reported in some other studies (66, 69).

Neuronal spike responses to 32 repetitions of stimuli were averaged in the time domain as peristimulus time histograms (PSTHs). Bin width was kept constant for a given velocity, so that one bin covered always not only the same time and but also the same dimension of the receptive field independent on the amplitude of stimulus movement.

Direction selectivity index (DSI) was calculated using the following formula:

DSI = (Rpref-Rnpref)/Rmax(pref, npref)

where Rpref corresponds to the response (peak discharge rate after subtraction of spontaneous activity) to a stimulus moving in the preferred direction, i.e. direction of stimulus movement eliciting the greatest response, Rnpref corresponds to the response to a stimulus moving in the direction opposite to preferred one (null or nonpreferred) and Rmax(pref, npref) corresponds to the larger value in the set of Rpref, Rnpref. Preferred and nonpreferred direction refer to the preference for the movement across the whole RF and corresponding DSI will therefore be called global DSI. Cells were considered direction-sensitive if the the global DSI was ≥ 0.5 (i.e, the magnitude of its response to the preferred direction was at least twice that to the opposite (nonpreferred) direction), and directionally biased when $0.3 \geq$ DSI < 0.5. The local DSI was determined for small movements within subregions of the cell's receptive field. Values ranged from -1 to 1. Negative scores indicate the local direction preference was opposite the global value, whereas positive scores indicate agreement between local and global direction preference.

Statistical significance of differences was assessed using non-parametric tests: the Wilcoxon

matched-pairs signed-ranks test and sign test (71). Statistical differences were considered significant when P at two-tailed criterion was 0.05 or less.

At the end of each penetration the recording site was marked by making a lesion with a current of 20 μA, electrode negative, applied for 30 s through the electrode. At the end of the experiment the animal was deeply anaesthetized with an intravenous injection of 150 mg of sodium pentobarbitone (Nembutal) and perfused with 10% formol saline solution. The brain was postfixed for about two weeks. The brains were frozen, sectioned (coronal sections cut at 50 μm) and the recording sites were verified on Nissl-stained sections.

All experimental procedures were approved by the Animal Care Committee at the Nencki Institute.

RESULTS

Thirty three out of 60 *(55%)* cells recorded from SC were considered to be direction-sensitive, since their global DSI value was ≥ 0.5. In all neurons the responses to a large (70 deg) amplitude of movement of the light bar along the horizontal axis of the RF were obtained first. To avoid problems with response qualification, neurons having a "spontaneous" firing rate above *5* spikes/s and/or peak discharge rate for optimal stimulation below 90 spikes/s were discarded from detailed investigation of the spatial organization of their receptive fields. For the remaining neurons the responses to the smaller amplitude movements in the center of the RF were investigated. The smallest amplitude of the stimulus movement which was still effective for evoking a response of the cell was estimated and then the receptive field was tested with this small amplitude of motion positioned spatially side-by-side along the horizontal axis of the RF (Fig. lA). Twelve collicular units were recorded from for sufficient time to allow systematic investigation of the whole RF. Six of them were classified as direction-selective (DS neurons) when tested with the maximal movement range covering the whole horizontal dimension of the RF, while the other six were classified as direction-nonselective (nDS neurons). For one of DS neurons receptive fields of ipsi- and contralateral eye were completely analyzed.

The minimum displacement of moving stimulus which was effective in generating a direction-selective response was 0.5 deg. However, some cells were not sensitive to a short amplitude of stimulus movement and required at least 15 deg of summation distance in the center of the RF for generation of a motion-sensitive response. We did not find any correlation between eccentricity of RF and the dimension of summation region for movement detection. Furthermore, in the group of DS neurons, the value of DSI was significantly lower ($p \leq 0.01$, Wilcoxon matched-pairs signed-ranks test, $n = 9$) for the small amplitude of movement for the stimulus placed in the center of the RF (central DSI) than that obtained for the amplitude of movement covering the whole dimension of the RF (global DSI). On the other hand, there was no significant difference between central and global DSIs in the group of nDS neurons ($p = 0.5$, sign test, $n = 6$) (Fig. 1B). The means of DSIs obtained for the small amplitude movements in subregions situated along the horizontal axes of the RF were both for the group of direction-selective and for the

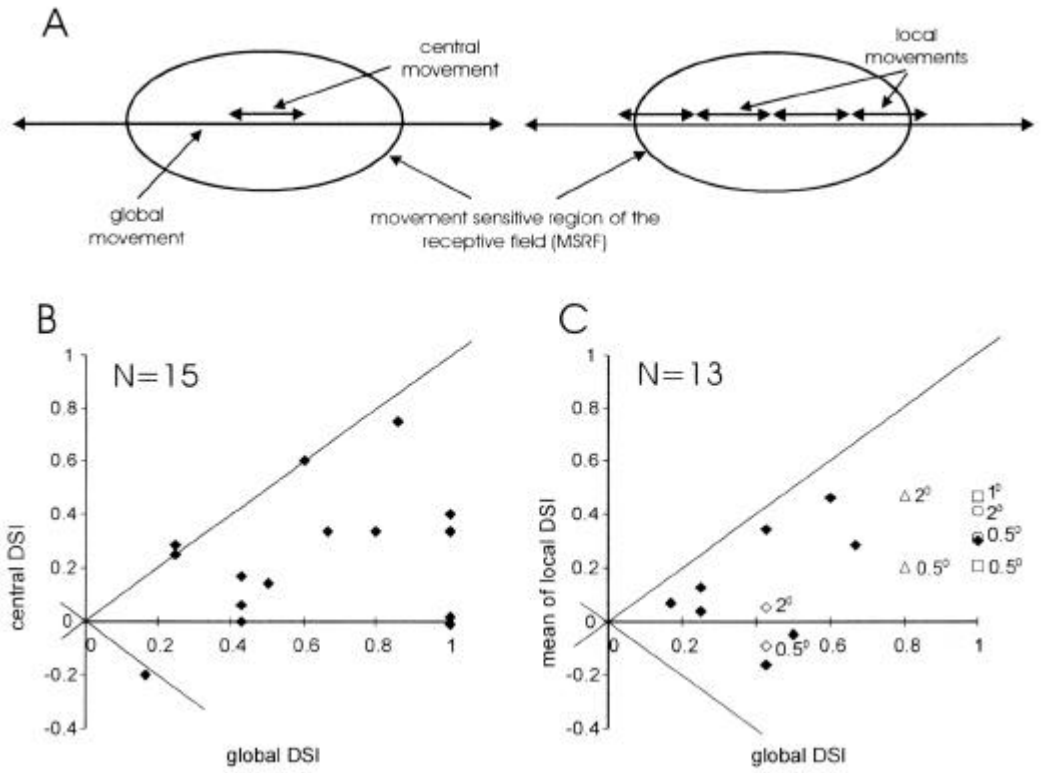

Fig. 1. - *Relation of local direction selectivity index (DSI) to global DSI.*

A: Explanation of the experimental procedures. B: Graph of central DSI (DSJ in the center of the receptive field (RF) obtained with the smallest tested amplitude of motion) versus global DSI (DSI obtained for the maximal amplitude of motion (70 deg) covering at least twice the dimension of the movement-sensitive region of the receptive field (RF)). Points located between diagonals represent cells for which DSI in the central region of the RF for the motion of small amplitude was smaller than the global DSI. C: mean DSI calculated for all subregions located along horizontal axis versus global DSI. For four cells marked with open symbols DSIs were calculated for two small amplitudes of motion. The amplitude of motion is shown on the right side of each open symbol. Notice that all points are located between diagonals. N - number of RFs tested.

direction-nonselective cells, significantly lower ($p < 0.01$ for DS neurons ($n = 7$), $p \leq 0.02$ for nDS neurons ($n = 6$), Wilcoxon matched-pairs signed-ranks test) than the respective global DSIs (Fig. 1C). Accordingly, for the three DS cells for which receptive fields were tested with two different amplitudes of movement (Fig. 1C, open symbols) the mean DSI was smaller for the smaller amplitude of stimulus movement.

Structure of the movement-sensitive receptive fields of direction-selective neurons.

In 5 out of 6 DS cells most of the test-zones in the receptive fields showed preference for the same direction of movement as for the stimulus moving across the whole RF. In these fields the arithmetic mean of the local DS preference agreed with

the global directionality (Fig. 1C). Examples of the responses of such a cell are shown in Figs 2 and 3. Consecutive histograms in Fig. 2A show responses of the cell, stimulated via the ipsilateral eye, to different amplitudes (from 70 deg, the uppermost histogram, to *0.5* deg, the lowermost histogram) of horizontal movements around the RF center. Even the movement of the smallest amplitude *(0.5* deg) was still effective in evoking the response of this cell. However, the response was clearly direction-selective only when the bar movement extended through a large portion of the receptive field (amplitudes of movement 20 deg and 70 deg, Fig. 2A). The 20 deg motion elicited stronger responses than the maximal (70 deg) amplitude movement of the bar along the RF horizontal axis. This observation may indicate the presence of a suppressive surround. When the amplitude of the motion was reduced to *5* deg of visual angle, discharges in the null direction were also elicited. This in turn resulted in a substantial loss of direction selectivity. The movements of 2 deg and *0.5* deg of visual angle were still effective in exciting the cell, but the corresponding DSI decreased further (Fig. 2A, two bottom histograms) as compared to the stimulus movement covering the whole RF. A detailed exploration of ipsilateral eye RF was provided by moving the light bar within consecutive test zones along the horizontal axis of the RF with 2 deg amplitude of motion (Fig. 2C). The movement restricted to the left flank of the receptive field revealed clear-cut selectivity for the same direction as that for movement covering the whole RF (Figs 2C, 3A and D). Movements restricted to other test zones resulted in excitatory responses also to the nonpreferred direction of motion. However, in most of the tested regions the direction preference was maintained. Responses which were not selective for direction of movement were detected in *25%* out of 20 tested zones (Fig. 3D) and were located mainly on the right flank of the RF. Thus in this cell the distribution of directional preference in the RF is in agreement with Barlow and Levick (4) hypothesis; nondiscriminating for direction of movement zone is located on the flank of the receptive field which was first crossed when motion was in the preferred direction.

With the local movement of yet smaller amplitude *(0.5* deg) we observed an increase in the number of zones where the response to a moving stimulus did not show direction selectivity *(55%* out of 22 tested points, Fig. 3E) as compared to the 2 deg amplitude. Nondiscriminating zones were rather irregularly distributed over the tested region. Decrease in asymmetry for the opposite directions in response for this small *(0.5* deg) amplitude of movement in the test-zones of the RE accompanies decrease in the magnitude of response in the preferred direction (compare Figs 3 A and B). The response to stimulation with the movement extending throughout the whole receptive field irrespective of the eye through which the cell was stimulated showed preference for the same direction. When stimulating this cell with small amplitude of movement via the contralateral eye, in most of the test-zones we observed preference for the same direction of movement (Figs 2D, 3C and F) as for stimuli presented via the ipsilateral eye. In this case, however, the nondiscriminating zone appeared to be located on the left flank of the receptive field which was first crossed when movement was in the nonpreferred direction, This result is inconsistent with the Barlow and Levick model (4).

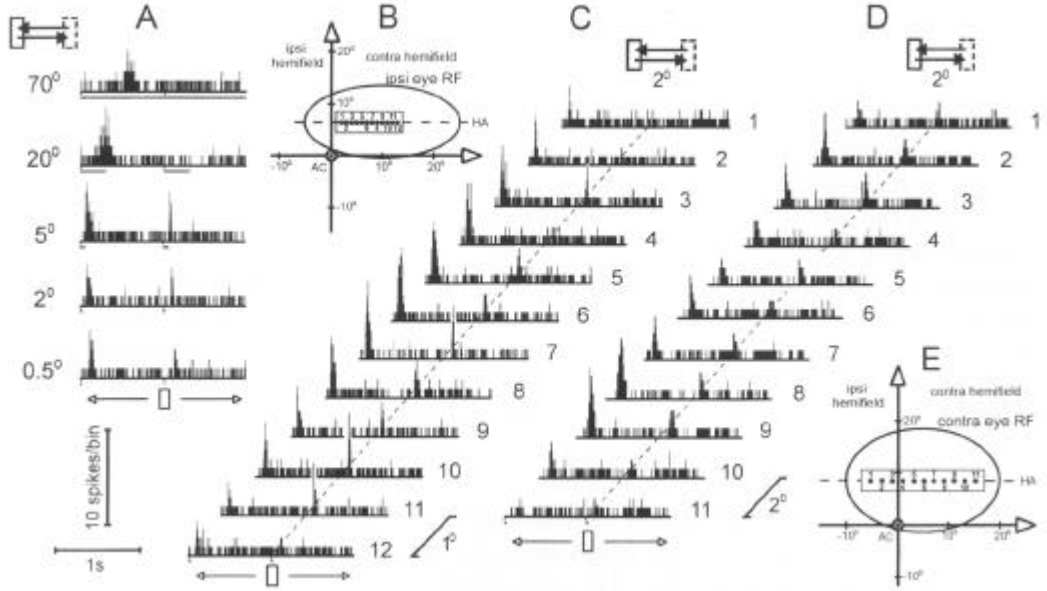

Fig. *2. - Structure of the receptive field of one of the directionally selective collicular neurons.*

A: Responses of the neuron to stimulation of the ipsilateral eye with a light bar *(0.5* deg x 1 deg). The stimulus was positioned in the center of the RF and moved along the horizontal axis with different amplitudes but at the same velocity of 70 deg/s. As indicated by arrows beneath the lowermost histogram each peristimulus time histogram (PSTH) represents the responses to stimulus motion from right to left and back. The stimulus moved during the time indicated by length of the bar below each histogram and remained stationary until moving again in the opposite direction. Amplitudes of stimulus motion (indicated on the left side of each histogram) varied from *0.5* deg to 70 deg. B:
Schematic plot of the ipsi eye RF in the visual field. An outline of the RF was revealed by using a hand-held dark stimulus. Filled circles indicate positions of the centers of 12 testzones. C: Spatial distribution of responses of the neuron during stimulation via the ipsilateral eye by moving stimulus at 2 deg amplitude. Numbers on the right side of each histogram indicate the position of test-zone within the RF. D: Spatial distribution of responses of this neuron during stimulation via the contralateral eye. E: Schematic plot of the contra eye RF in the visual field.
Centers of the consecutive test-zones were separated by 1 deg for ipsi eye and by 2 deg for contra eye. HA - horizontal axis of the RF, AC - area centralis indicated by Velocity of the stimulus motion 70 deg/s. Time and spike rate calibration applies to both A, C and D.

Distribution of zones discriminating or nondiscriminating direction of movement in the RFs of three other DS cells support the Barlow and Levick hypothesis that observed direction selectivity based on asymmetry in inhibition in the preferred and opposite directions. In RFs of these neurons the nondiscriminating zone was located on the side of the RF where the movement in the preferred direction began. In two of them an additional nondiscriminating zone was located in the center of the RF. However, the distribution of discriminating and nondiscriminating zones in the RF of two other DS cells does not support the Barlow and Levick model. In one of these cells the nondiscriminating region was located in the flank of the RF which was first crossed during movement in the nonpreferred direction. In the

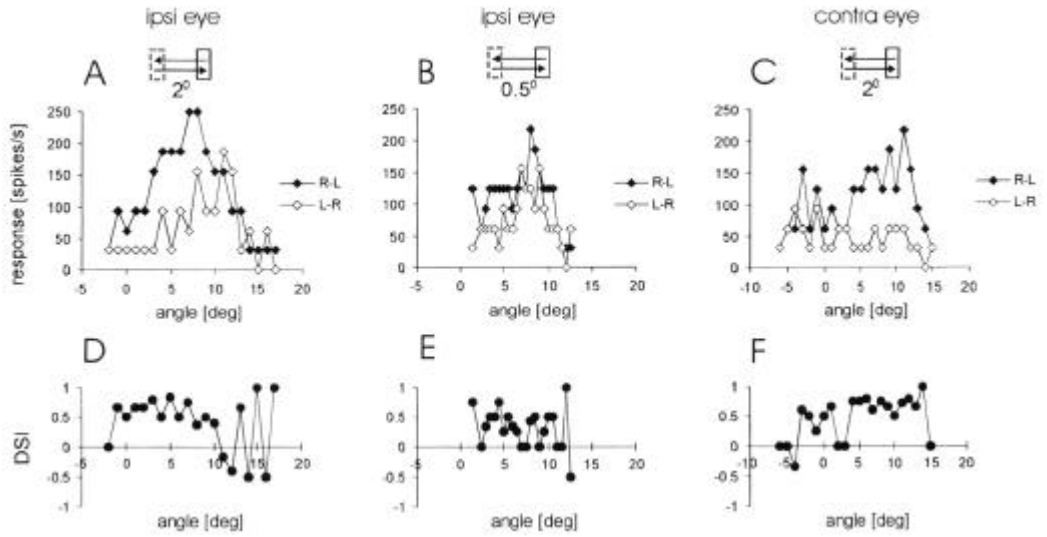

Fig. 3. - *Spatial distribution of responses and DSJs for the directionally selective neuron whose responses are illustrated in Fig. 2.*

A: Distribution of peak responses in the RF to stimulation via the ipsilateral eye with a light bar *(0.5* deg x 1 deg) moving with 2 deg amplitude. PSTHs of these responses are shown in Fig. 2 C. B: Spatial distribution of peak responses to stimulation of the ipsilateral eye, amplitude of stimulus movement *0.5* deg. C: Spatial distribution of peak responses to stimulation via the contralateral eye, amplitude of stimulus movement 2 deg. PSTI-Is of these responses are shown in Fig. 2 D. D, E and F: Spatial distributions of DSIs along the horizontal axis calculated on the basis of responses shown in A, B, C, respectively. DSI values above zero indicate the same directional preference for local and global movement, DSI values below zero opposite directional preference. R-L indicates the direction of movement from the right to left; L-R, from left to right. The velocity of stimulus motion was always 70 deg/s.

second cell, whose receptive field structure is described in detail below, the single nondiscriminating zone was located in the center of the RF (Fig. 4B and D). The response of the neuron to stimuli presented via the contralateral (dominant) eye was direction-selective when tested with the maximal amplitude of movement of the light bar along the horizontal axis of the RF, with the preferred direction from right to left (Fig. 4A). Reducing the amplitude of the movement to 3 deg revealed the heterogeneous structure of the receptive field of this neuron. Nine test zones separated by 2 deg distances along the horizontal axis of the receptive field were tested with a bar moving over 3 deg (Fig. 4B). The distribution of the DSIs, calculated for these nine test zones (Fig. 4D), reveals organization of the RF into two subregions with responses characterized by opposite preference of the direction of movement. Positions of the maximum of the responses to the motion to right and left were displaced in this RF. Such property makes this receptive field ideal for perception of expanding or approaching objects.

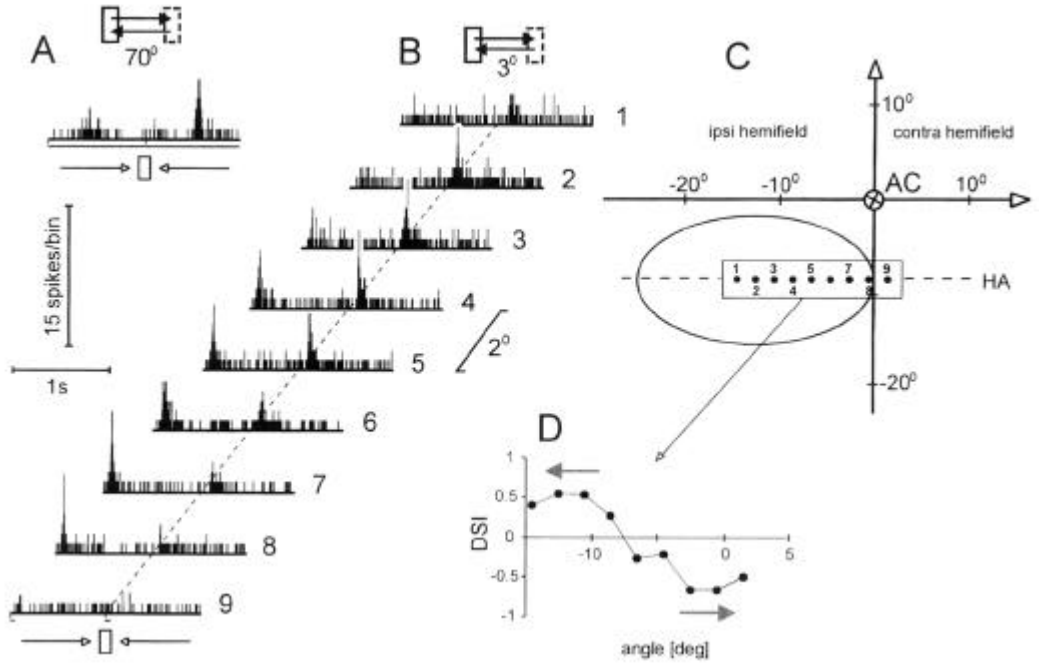

Fig. *4. - Directional substructure of the RE of an another direction-selective neuron.*

A: P5TH of response to the light bar *(0.5* deg x 1 deg) moving with maximal amplitude along the horizontal axis of the RF. B: PSTHs of responses of the neuron to 3 deg amplitude movement of a light bar. Numbers on the right side of each histogram indicate the positions of test-zones in the RF. In both A and B responses to the stimuli presented via the contralateral (dominant) eye. Velocity of stimulus motion in both A and B 70 deg/s. C: Position of the contralateral RF in visual field. An outline of the hand-plot of the RF with black stimulus. D: Spatial distribution of DSIs along the horizontal axis of RF. Arrows show local directional preference. Other explanations as for Figs 2 and 3.

Structure of the movement-sensitive receptive fields of direction-nonselective neurons.

Based on the structure of the receptive fields in the group of nDS units we could distinguish two subcategories of cells. Half of nDS neurons (3 of 6) had homogeneous structure of the receptive field, i.e. they did not show direction selectivity (DSI < *0.5)* in the response to a stimulus moving across the whole RF nor in their responses to small amplitude movement in any of the tested regions of the receptive field. An example of responses of a nDS cell with a uniform structure of the RF is shown in Figs. 5A and SB. The neuron showed weak preference for movement from right to left in response to the stimulus moving across the whole RF (Fig. *5A*, DSI = 0.43). In all tested subregions of the receptive field the cell responded to a stimulus moving over 2 deg in both directions with relatively small differences in the magnitude of responses (low values of DSIs). The spatial distribution of the DSIs calculated on the basis of responses to stimuli moving with 2 deg amplitude is shown in Fig SC. The values of DSI ranged between *-0.5* and *0.5* with the mean 0.04. Non-DS responses were registered also with 0.5 deg amplitude of movement (not shown).

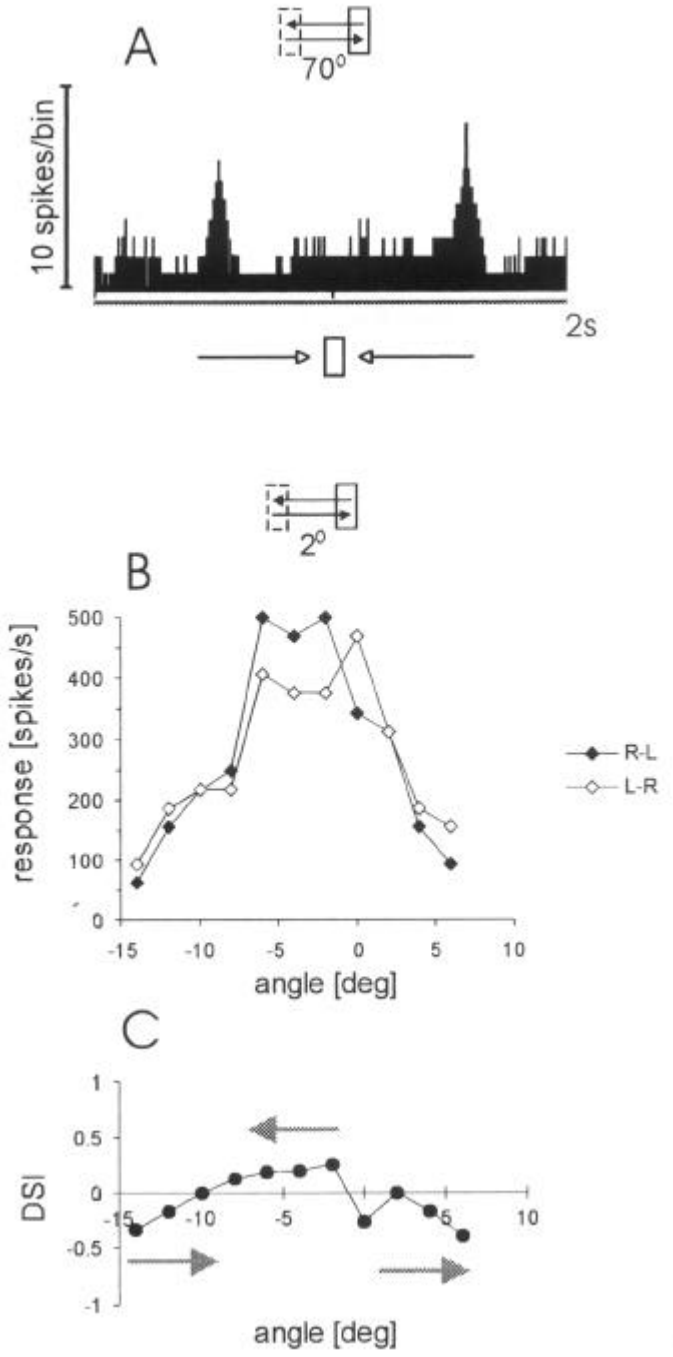

Fig. 5.- *Example of nondirection selective collicular neuron with homogeneous structure of RE.*

A: PSTH of response to movement across the whole receptive field, B: spatial distribution of responses and C: DSIs. The stimuli (presented through the ipsilateral, dominant eye) were 70 deg (A) or 2 deg (B) excursions of the light bar *(0.5* deg x 1 deg) moving at 70 deg/s along the horizontal axis of the RF. Other explanations as for Figs 2, 3 and 4.

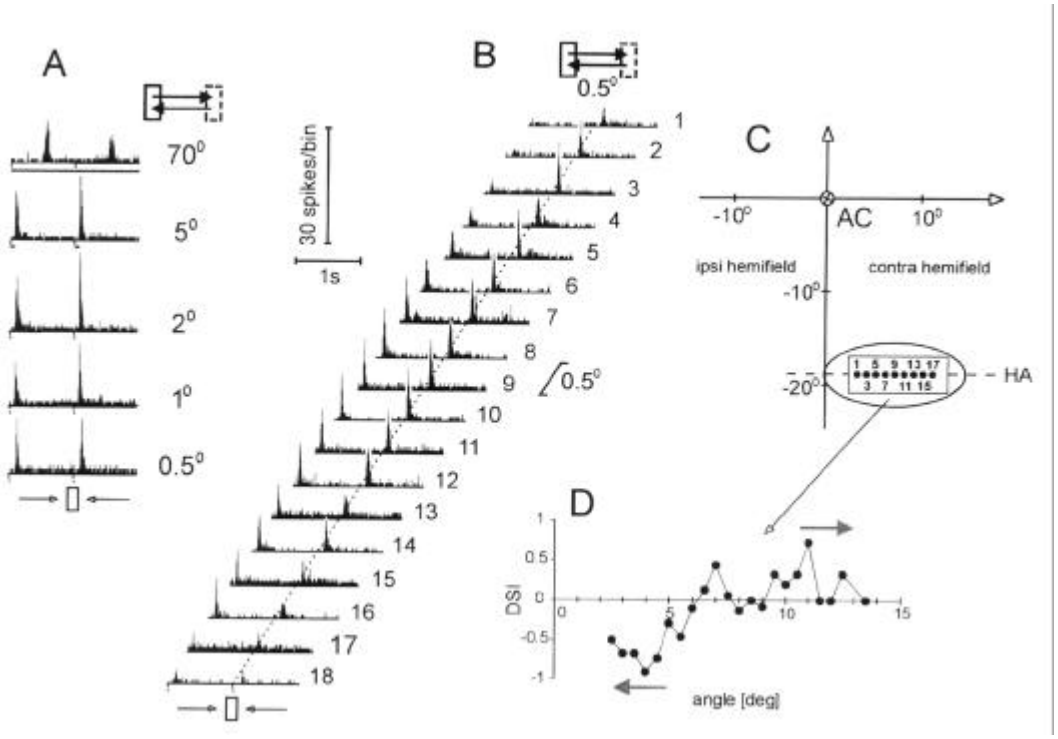

Fig. *6.- Heterogeneous structure of the RF of a non-direction-selective neuron with a high sensitivity to small amplitudes of motion.*

A: PSTHs of responses in the center of the RF to gradually decreasing amplitudes of motion of the light bar *(0.5* deg x 1 deg) moving along the horizontal axis of the RF at a velocity of 70 deg/s. The amplitude of the stimulus motion is shown on the right side of each histogram. B: PSTHs of cell responses recorded in 18 test zones consecutively positioned in the RF. The amplitude of motion of light bar *(0.5* deg x 1 deg) was *0.5* deg, velocity 70 deg/s. In both A and B responses to the stimulation via the contralateral (dominant) eye are illustrated. C: Position of the contralateral RF in the visual field. D: Spatial distribution of DSIs along the horizontal axis of the RF. Other explanations as for Figs 2, 3 and *4*.

The other three nDS units had heterogeneous structure of the RF, i.e. depending on the tested position in the receptive field the cell could show directional selectivity (DSI ~ *0.5)* in some test zones and no directional sensitivity in the other test regions.

The responses of a directionally nonselective cell with high sensitivity to a small amplitude *(0.5* deg) of the stimulus movement are presented in the Fig. 6. The, large amplitude of movement (70 deg) of the light bar evoked a response of the cell with a slight preference for motion from left to right (DSI = 0.43, Fig. 6A, the uppermost histogram). However, the movement of the same light bar but with a smaller amplitude limited to the central region of the RF elicited a response with no preference whatsoever (Fig 6A, lower histogram). With *0.5* deg amplitude of motion as a test stimulation, the central region of the RF was tested in *22* consecutive spatial regions. Fig. 6B illustrates the characteristics of cell responses from each

of 18 test zones situated in the centre of RF (Fig. 6C). In test zones situated in the left flank of the RF directionally sensitive responses were elicited although the preferred direction of the movement was opposite (DSI < 0, Fig. 6D) to that when the maximal range of movement was used (Fig. 6A, the uppermost histogram). Positions in the central region of the RF revealed directionally nonsensitive responses. The responses to movements restricted to the right flank of the RF show preference for the motion in the same direction as that when the maximal range of the stimulus motion was applied. The distribution of DS indices along the horizontal axis of the receptive field is shown on Fig. 6D. Regions with a preference for opposite directions of stimulus movement are located on the opposite edges of the RF with a nondiscriminating zone situated in the RF center. As for the DS cell whose responses are illustrated on Fig. 4 this receptive field might contribute to perception of expanding or approaching objects.

DISCUSSION

The main conclusions of the present study are: 1) The direction selectivity of collicular cells in superficial layers is not an invariable feature of the receptive field but depends on the amplitude of stimulus movement and varies between subregions of the receptive field; 2) Decrease of the amplitude of motion results in a decrease of direction-selective response both in the group of direction-selective cells and in the group of cells classified as direction nonselective, but with a directional bias; 3) Decrease of direction selectivity for small amplitude movement results mainly from increase in the magnitude of response in the nonpreferred direction of movement.

In the following sections we argue for the collicular origin of the mechanisms responsible for directional tuning in collicular cells and we discuss possible mechanism of direction-selective response on the collicular level.

Origin of the directional selectivity in the superior colliculus.

The visual information is relayed to the superficial layers of the cat superior colliculus directly from the retina (6, 8-11, 26) and indirectly via the retino-geniculo-cortico-collicular pathway (31). Both retinal ganglion cells and cortical cells can be a potential source of directionally selective responses in the superior colliculus. This property can be also generated by a network intrinsic to the superior colliculus. The directionally selective ganglion cells have been described in the rabbit (2, 14, 40, *56,* 84, 88), cat *(15, 64, 65,* 81, 82) and monkey retina (20). Since the central projection of DS retinal cells is fully crossed (see Ref. 38) they cannot be responsible for the presence of collicular directionally selective responses revealed by stimulation via the ipsilateral eye (see example in Fig. 2). Furthermore, we observed that a decrease in the amplitude of movement resulted in a decrease of selectivity for direction of stimulus movement even if the amplitude of the stimulus movement was large enough to cover the whole receptive field of single

DS W-type ganglion cells (< 2 deg) (15, 65, 82). Input from DS W-type ganglion cells cannot explain all phenomena related to collicular direction selective responses; however, convergent projection from the DS and/or non-DS W-type and/or Y-type, including directionally biased Y-type (70), ganglion cells could underlie the heterogeneous substructure of collicular RFs with diverse local DS indices. This convergent projection could form global directionally biased excitatory input to the cell, which is shaped by collicular mechanisms into a high-degree directional response.

Some previous studies indicate that primary visual areas (area 17 and 18) which send dense projection to the superficial layers of the superior colliculus (27) can play an important role in the directional selectivity of the collicular neurons. Thus in the cat elimination of the cortical input, either by lesion (7, *51*, *63*, 78, 86) or by cooling (55) substantially reduces the proportion of collicular neurons selective for direction of movement. The origin of the collicular directional selectivity was attributed to the directional selectivity of complex cells in layer 5 of primary visual cortex projecting to stratum griseum superficiale *(57)*. A number of other studies indicated, however, that in cats (17, 18, 31, 46, 60) selectivity for direction in collicular responses was preserved after elimination of cortico-tectal input. More recently Mendola and Payne (47) reported no differences in direction selectivity of collicular neurons in normal adult cats or in cats with ablation of primary visual areas (either neonatally or as adults) provided that poorly responsive neurons were eliminated from the analysis. They observed a substantial reduction in responsiveness of collicular neurons. Taken together, all these contributions suggest that cortical input enhances the direction-selective response of collicular neurons rather than imposes this property onto the SC. The results of Fortin and colleagues (23), showing the presence of direction-selective responses in the superior colliculus of young rats before maturation of the visual cortex, strongly indicate an extracortical origin of the collicular direction selectivity in these animals. Assuming a similarity in general mechanisms among mammalian species, this finding supports the suggestion that directional selectivity in the superior colliculus is independent of the cortical input.

Possible mechanism of collicular direction selectivity.

Two simple models have been proposed to explain direction selectivity of visual neurons. The first, proposed by Reichardt *(58)*, was based on spatiotemporal asymmetry of excitatory inputs to a cell to explain motion detection in the fly. The second model, introduced by Barlow and Levick (4) for direction-selective ganglion cells in rabbit retina, was based on asymmetry of the inhibition in two directions of movement. Both models have been further developed for explanation of directional sensitivity of cortical neurons (1, 12, 16, 22, 24, *25*, *36*, 43, *52*, 59, 67, 72, 83) and it has been shown that both mechanisms could contribute to direction selectivity either independently or in cooperation (42, *53)*.

The attenuation in response magnitude and reduction in directional indices of responses with decrease of amplitude of stimulus movement observed by us indicates

that spatiotemporal asymmetry of the excitatory input to a cell can underlie the collicular directional selectivity. In the linear version of the model consecutively shorter excitatory response latencies across the receptive field are responsible for reinforcing the response in the preferred direction of movement. For a small amplitude of movement the stimulus remains in the RF region with similar response timing and therefore very small differences in the magnitude of the responses to stimuli moving in opposite directions can be observed. For movement across the whole RF the shift in the time course of the response in the distant parts of the receptive field is big enough to allow for optimal summation of the responses in the preferred direction. Earlier studies in our laboratory (28, 87) showed that a directional response to moving stimuli can coexist with homolatency of responses to stationary stimuli. This in turn would suggest that simple spatiotemporal maps may not be useful for prediction of directional tuning. Similar conclusions were reached in relation to direction-selective cortical cells of layer 6 of cat's area 17 with non-oriented spatiotemporal maps and in contrast to over half of layer 4 cells for which orientation of the spatiotemporal maps is correlated with observed directional tuning (see Ref. 33). It is likely that in collicular neurons nonlinear facilitatory and/or suppressive interactions dependent on temporal offset of responses evoked at different spatial positions can account for directional response. Furthermore, the model based on differences in the excitatory response timing within the RF and presumed to underlie differences in the magnitude of the response to both directions of movement, cannot explain lack of cell firing to large amplitude movement in the nonpreferred direction in those cells which responded to the small amplitude of movement. Thus the lack of response in the null direction for the global movement may be caused by either suppressive interaction between elements of the receptive field or a spatial summation of inhibition (cf. Refs *54,* 67 for cortical neurons).

Dreher and Hoffman (21) presented results, which strongly indicate participation of inhibition in generation of directional response in cat's collicular neurons and support Barlow and Levick model (4). They observed suppression of background firing during stimulus motion in the null direction (an observation confirmed for some of our DS cells, see Fig. 2A, 20 deg amplitude). Dreher and Hoffman (21) suggested directionally selective cortical complex cells acting via collicular inhibitory interneurons as the source of the observed suppression. Indeed, numerous intrinsic GABAergic neurons in superior colliculus (49, *50)* might participate in generation of a directional response. It is possible that spatial asymmetry of inhibition could be responsible for the spatial shift of the time course of the excitatory response unifying the two basic models proposed to account for directional response (see Ref. *53* for discussion of GABAA and spatiotemporal structure of cortical DS neurons).

The other mechanism underlying direction selectivity may make use of an inhibition that is uniform over the whole RF and nonselective for stimulus movement resulting in an increase of threshold for spike generation and in that way enhancing any existing differences in forward and reverse direction generated by the excitatory inputs. Such a mechanism underlying directional selectivity has been proposed by

Sato and colleagues *(67)* for direction-selective neurons (except for those in layer 6) in the primary visual cortex of the macaque. A smaller intensity of response to movement of large amplitude than expected from intensive responses in subregions of RF found by us suggests the existence of delayed suppression or suppression that does not only overlap the excitatory receptive field but extends well beyond it or requires a greater summation region for inhibition than excitation. The presence of such an inhibitory field overlapping or extending beyond the excitatory one and/or inhibitory interactions within collicular receptive fields was revealed by decrease of the response to a moving stimulus with increase of stimulus size (21, 46, 80, *85)* or suppression of the response to a first stimulus by introduction of a second stimulus (37, 61, 62).

We conclude that control of firing threshold by an inhibition that is nonselective for direction of stimulus movement can accentuate a directionally biased response based on excitatory and inhibitory input. Other nonlinear mechanisms such as inhibitory interactions between elements of the receptive fields are also very likely to play an important function in generation of directional selectivity in superior colliculus neurons. The role and nature of the inhibitory mechanisms in the response properties of collicular neurons and their connection with directional selectivity will require further investigations.

Existence and function of subunits.

It is commonly accepted that the superior colliculus is involved in the central processing of visual information (cf. Refs 3, 68, 79) including motion perception, visual attention and orientation behaviour (29, 44, 48, 66, *73-75).* However, the spatial organization of RFs of collicular neurons have not been previously investigated in detail. In this study we have shown that the RFs of superior colliculus neurons are composed of subregions with different response profiles. For example, cells with high DS index (when tested by full-length movement along the horizontal axis of its receptive field) appear to often contain subregions with direction-nonseflsitive responses, or subregions characterized by preference for the opposite direction.

The question arises why the responses in the subregions differ, particularly in the occurrence of a response in the preferred direction opposite to the direction for the whole RF. In our experiments (unlike, in experiments of Barlow and Levick (4) or He and colleagues (30) with the use of an aperture) the stimulus in the time between local movements remained stationary in the receptive field. Such an approach excluded the contribution of a phasic component of the response to stimulus onset and offset. At the same time this approach did not exclude the effects of the local adaptation to the stimulus. The presence of a response in the nonpreferred direction could be the result of disinhibition caused by adaptation to the stationary stimulus before its movement. Such an explanation would be consistent with the suggestion about the importance of inhibition in the mechanism of direction selectivity.

The functional significance of multiple subregions within single receptive fields is not clear. They may render the cells more responsive to small movements within

a relatively large RF and underlie the integration of motion signals. Lack of directional selectivity for local movements in subunits combined with the presence of a response in the nonpreferred direction indicates that collicular cells can be involved in detection of local motion. For the price of information about properties of the motion such as directional component of the motion the gain is increase of probability of response during any movement in any direction. A function of detection of local movement in the environment has been already proposed for the W-2 subtype of retinal ganglion cells *(65)*. Both anatomical and physiological data indicate that this group of cells forms the bulk of the projection to the SC (8, 10, *35*, 39).

Existence of subunits with different directional response profile within single receptive fields suggests another function of collicular neurons. They may play an important role in the extraction of spatial component of information about motion. Depending on the arrangement of the direction-selective and nonselective zones within their receptive fields collicular cells may function as detectors of approaching and expanding objects when the direction preference of neighboring subunits is opposite and oriented outside of their common border (see Fig. 4 for example of the receptive field profile of such cell). When the direction preferences of neighboring subunits are opposite but oriented towards each other the cell can serve for the detection of withdrawing or contracting objects.

Finally, neurons with subregions having different properties can be involved in multiple synchronized networks participating in the detection of diverse stimulus properties.

SUMMARY

Although the direction selective properties of the superficial layer cells of the cat's superior colliculus have been extensively studied, the mechanisms underlying this property remain controversial. With the aim to understand the mechanism(s) underlying directional selectivity of collicular neurons we examined the substructure of their visual receptive fields.

1. The strength of cell responses and the direction selectivity indices varied in relation to the location of the tested region within the receptive field and the amplitude of stimulus movement.

2. Decrease of the amplitude of motion resulted in a decrease of direction selectivity index both in the group of direction-selective cells and in the group of cells classified as direction nonselective but with a directional bias.

3. The decrease of direction selectivity for small amplitude movement resulted mainly from increase in the magnitude of response in the nonpreferred direction of movement.

4. These results suggest that the receptive fields of most collicular cells are composed of subregions with different response profiles and indicate that inhibitory mechanisms dictate direction selectivity of collicular cells.

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