ACTA NEUROBIOLOGIAE EXPERIMENTALIS

Acta Neurobiol Exp 2004, 64: 209-228

Motion sensitivity in cat's superior colliculus: contribution of different visual processing channels to response properties of collicular neurons

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Abstract. It is well established that neurons in the retinorecipient layers of superior colliculus (SC), the mammalian homologue of the optic tectum of other vertebrates, are extremely sensitive to moving stimuli. In our studies we have distinguished several functionally distinct groups of neurons in the retinorecipient layers of the SC of the cat on the basis of their velocity response profiles. Our data revealed substantial convergence of the Y and non-Y information channels on single SC neurons. Second, using the method of selective conduction block of the Y-type fibers in one optic nerve we have shown that responses of SC cells to high-velocity motion are dependant on the integrity of Y-type input. Third, in order to determine the degree of influence of the X- and W-type input on cellular responses we have examined spatial and temporal frequency response profiles of single collicular neurons using sinusoidal gratings drifting in the preferred direction. At any given eccentricity, most collicular neurons exhibited a preference for relatively very low spatial frequencies. The preference for low spatial frequencies combined with temporal frequency profiles of collicular neurons suggests that the Y- and W-type inputs constitute the major functional inputs to the retinorecipient layers of the SC and that the "top-down" X-type input from the visual cortex has only a minor impact on the spatio-temporal frequency response profiles of collicular receptive fields.

Minireview

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Key words: superior colliculus, cat, visual information channels, X-cells, Y-cells, W-cells, speed-tuning

INTRODUCTION

According to the concept of parallel processing, in the visual system of mammals and vertebrates in general, information about the visual world is extracted, processed and conveyed from retina to brain visual centers by distinct, largely parallel information channels (for reviews see Burke et al. 1998, Dreher et al. 1996, Livingstone and Hubel 1988, Rowe 1991, Stone 1983, Stone et al. 1979). In the cat these channels are traditionally called X, Y and W channels and they may correspond respectively to the so-called P (parvocellular), M (magnocellular) and K (koniocellular) channels in primates (Burke et al. 1998, Dreher et al. 1996, Leventhal et al. 1981, Rowe 1991, Stone 1983, Stone et al. 1979, for more recent review see Casagrande and Xu 2003, see however for an alternative point of view Kaplan 2003, Kaplan et al. 1990). The X, Y and W channels originate in different types of retinal ganglion cells. Thus, the X channel originates in morphologically identified β cells characterized by medium size somata, medium caliber axons and small, bushy dendritic trees (Boycott and Wässle 1974, Wässle et al. 1981). The Y channel originates in the morphological class of α cells, which at any eccentricity have the largest somata, large radially symmetric dendritic trees and large caliber axons (Boycott and Wässle 1974, Cleland et al. 1975, Peichl 1991, Peichl and Wässle 1981). Retinal W-cells constitute a very heterogeneous group of cells with small-to-medium somata of different dendritic morphologies (Berson et al. 1999, Isayama et al. 2000, Leventhal et al. 1985, Rowe and Dreher 1982, Stone and Clarke 1980).

Retinal ganglion cells which constitute the entrance point of X, Y and W channels differ not only in morphology, but also in many physiological features and are therefore postulated to play different functional roles in vision. For example, the X channel, characterized at any eccentricity by relatively high spatial resolution and poor temporal resolution, is postulated to be involved in processing information about high acuity pattern vision (Dreher et al. 1996, Rowe 1991, Stone 1983, Stone et al. 1979). By contrast, the spatial resolution of Y- and W-cells is much lower both in retina (Rowe and Cox 1993) and in the principal visual relay nucleus of the dorsal thalamus, the dorsal lateral geniculate nucleus (LGNd) (Saul and Humphrey 1990, Sireteanu and Hoffmann 1979, Stone 1983, Stone et al. 1979, Sur and Sherman 1982). The Y channel, characterised by high temporal resolution, good responsiveness at high stimulus velocities and nonlinear spatial summation within the receptive field appears to be involved in the processing of information about fast-moving photic stimuli (Burke et al. 1998, Dreher and Sanderson 1973, Dreher et al. 1993, 1996, Frishman et al. 1983, Hamasaki and Cohen 1977, Lee and Willshaw 1978, Stone 1983, Stone et al. 1979, Victor and Shapley 1979). By contrast, both X- and W-cells respond optimally to stimuli moving at low velocities (Cleland and Levick 1974a,b, Frishman et al. 1983, Lee and Willshaw 1978, McIlwain 1978, Stone and Hoffmann 1972). Finally, W-type retinal ganglion cells and their relay cells in LGNd have very heterogeneous receptive field properties and some common features including slow conduction velocity of their axons, "sluggish" responsiveness to photic stimuli and poor spatial resolution (Cleland and Levick 1974a,b, Fukuda and Stone 1974, Rowe and Cox 1993, Stone 1983, Stone et al. 1979, Wilson et al. 1976). It has been postulated that the W channel with its heterogeneous receptive field properties, slow axonal conduction velocity, "sluggish" responsiveness to photic stimuli and poor spatial resolution might underlie "ambient" vision, which includes perception of visual space, some low spatial resolution pattern vision and controlling the reflex direction of the gaze (Rowe and Cox 1993, Stone 1983, Stone et al. 1979). At least some W-cells (phasic W-cells, W-2 subclass) appear to be involved in detection of local movement in the environment (Rowe and Palmer 1995). It has also been proposed that the W channel as well as its primate equivalent K channel, plays a "modulatory" role in vision, at both the subcortical and cortical levels (Casagrande 1994, Casagrande and Xu 2003).

X, Y and W retinal ganglion cells differ in the pattern of projection to different subcortical retinorecipient nuclei (Leventhal et al. 1985, Rowe and Dreher 1982, Tamamaki et al. 1995). Thus, the main dorsal thalamic visual relay nucleus, the dorsal lateral geniculate nucleus, receives direct input from X-, Y- and W-type ganglion cells. It has been shown that, at least in the cat, all three information channels remain fairly neatly separated from each other not only in the LGNd (Saul and Humphrey 1990, Stone 1983, Stone et al. 1979, Sur and Sherman 1982, Wilson et al. 1976, cf. however for inhibitory interactions Burke et al. 1998, Wang et al. 1996) but also in its "satellite" ventral thalamic nucleus, the perigeniculate nucleus of the retinal thalamic nucleus (PGN) (Wróbel and Bekisz 1994). By contrast, there is a substantial excitatory convergence of Y and

non-Y channels in the visual cortex. This includes not only the cortical areas which belong to the so-called "form" pathway and are dominated by X-input (e.g., area 17 and area 21a) but also cortical areas constituting the so-called "motion" pathway dominated by Y-input (e.g., area 18, the posteromedial lateral suprasylvian area and the anterior ectosylvian visual area) (for review see Burke et al. 1998).

The superior colliculus (SC), the main retinorecipient nucleus of the mammalian mesencephalon and a presumed homologue of the optic tectum of other vertebrate groups, is involved in orientation response directing of the eye and head towards the object of interest and plays an important role in visually guided behavior as well as in integration of multimodal sensory information (Schiller and Tehovnik 2001, Schneider 1969, Stein and Meredith 1991, Stein et al. 2001, Wurtz and Albano 1980). In Figure 1 we present a simplified diagram of the cat visual system showing both direct (retino-tectal) and indirect (retino-geniculo-cortico-tectal) visual input to the SC.

The superficial retinorecipient layers of SC receive direct retinal input from only two information channels, that is, the W and Y channel (Berson 1988a, Berson et al. 1999, Hoffmann 1973, Isayama et al. 2000, McIlwain and Lufkin 1976, Leventhal et al. 1985, Stein and Berson 1995, Tamamaki et al. 1995; see however sparse X-type retinal projection to cat's SC reported by Wässle and Illing 1980 and Koontz et al. 1985). Retinal W-cell projections terminate in the most superficial cellular layer of the SC, the stratum zonale (SZ) and both the upper and the lower parts of the second cellular layer, the stratum griseum superficiale (SGSu and SGSl respectively). By contrast, projections of retinal Y-cells terminate in the lower part of SGS, the uppermost fiber layer, the stratum opticum (SO) and in the upper part of stratum griseum intermediale (SGI). So the overlap in the laminar distribution of the W-type and Y-type retino-tectal terminals appears to be limited to the SGSl, (Berson 1988a). Apart from the retinal input, the SC receives a strong visual input from lamina V cells in a number of visuotopically organized visual areas in the ipsilateral neocortex and this input is distributed throughout virtually all collicular layers (for reviews see Harting et al. 1992, Huerta and Harting 1984, Stein and Meredith 1991). Furthermore, a major cortico--tectal input to the retinorecipient collicular layers originates from layer V in areas 17 and 21a (for review see Harting et al. 1992), that is, areas dominated by the X-type input (for review see Burke et al. 1998). The great majority of collicular cells, which receive retinal W-input, are activated by cortical stimulation at latencies indicative of the convergence of retino-tectal afferents and Y- and non-Y-indirect cortico-tectal input onto single collicular neurons (Berson 1988b). It is not clear to what extent the spatial overlap of retino-tectal W- and Y-input and convergence of retino- and cortico-tectal input corresponds to the convergence of different information channels onto single collicular cells. In a present article we will try to further explore this issue by reviewing a series of experiments conducted by us in which we: (i) examined the velocity response profiles of collicular neurons located in different retinorecipient layers; (ii) carefully compared responses of binocular single SC neurons to stimuli presented *via* an eye with a selective block of Y-type optic nerve fibers with responses to stimuli presented *via* the normal eye, that is, the eye with an intact optic nerve. In addition, we present recently collected new data about the spatio-temporal frequency response profiles of collicular neurons.

VELOCITY RESPONSE PROFILE OF COLLICULAR NEURONS

It is well known that neurons in the retinorecipient layers of cat's superior colliculus are extremely sensitive to moving stimuli and a substantial proportion of them is sensitive to the direction of the stimulus movement (Dec et al. 2001, Dreher and Hoffmann 1973, Hashemi-Nezhad et al. 2003, Mendola and Payne 1993, Ogasawara et al. 1984, Stein and Meredith 1991, Waleszczyk et al. 1993, 1999). It has been shown earlier that some response properties of collicular neurons, such as the velocity response profile and selectivity for direction of stimulus movement were correlated with the type of retinal input they receive (Hoffmann 1973).

We have distinguished several functionally distinct groups of collicular neurons on the basis of velocity response profiles to photic stimuli (Waleszczyk et al. 1999). Single unit activity was recorded extracellularly in anesthetized and paralized animals. Action potentials of collicular neurons were conventionally amplified. Triggered standard pulses were fed to microcomputer for on-line analysis and data storage. The peristimulus time histograms (PSTHs) were constructed by summing the responses to 10-100 successive stimulus sweeps (number of sweeps related positively to stimulus velocity) at each test conditions. The temporal base of PSTH

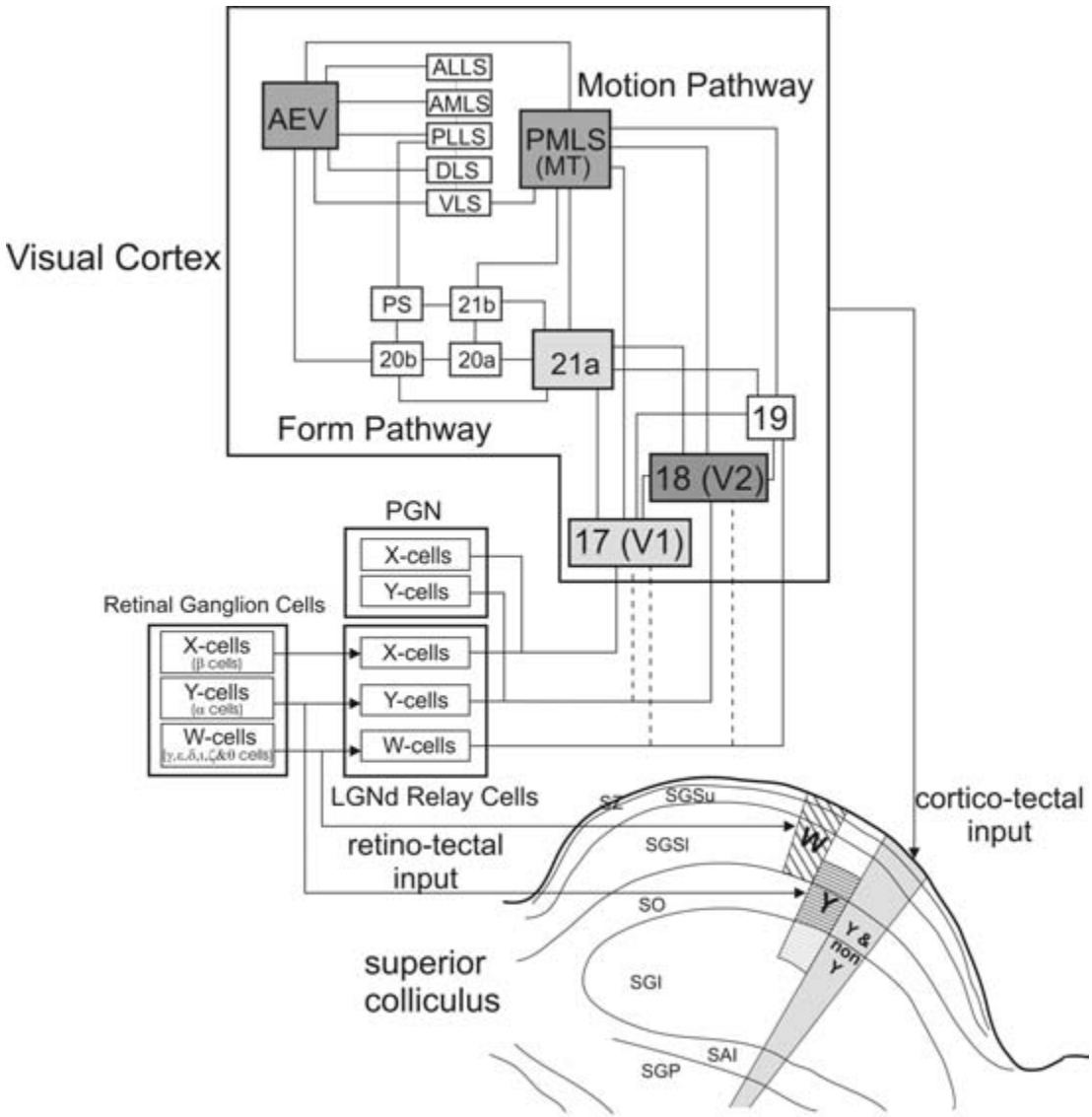

Fig. 1. Simplified diagram of the visual system of the cat showing direct (retino-tectal) and indirect (retino-geniculo-cortico--tectal) visual input to the superior colliculus. (SZ) Stratum zonale; (SGSu) upper part of the stratum griseum superficiale; (SGSl) lower part of the stratum griseum superficiale; (SO) stratum opticum; (SGI) stratum griseum intermediale; (SAI) stratum album intermediale; (SGP) stratum griseum profundum. Hatched areas marked by W or Y correspond to the laminar distribution of retinal W and Y ganglion cells terminals (retino-tectal input, Berson 1988a). Grey-filled area corresponds to laminar distribution of the cortico-tectal input originating in a number of the ipsilateral visual cortical areas (Harting et al. 1992). (PS) posterior suprasylvian area; (ALLS, AMLS, PLLS, PMLS, DLS, VLS) lateral suprasylvian areas: anterolateral, anteromedial, posterolateral, posteromedial, dorsal, ventral; (AEV) anterior ectosylvian visual area. Figure has been modified from Fig. 1 of Burke et al. (1998) and Fig. 9 of Waleszczyk et al. (1999) with some additional changes.

was divided into 150 bins. The bin width varied depending on stimulus velocity, the amplitude of the sweep and the time the stimulus remained stationary outside the receptive field. The PSTHs were smoothed using Gaussian weighted average over five neighboring bins. The smoothed values were used for presentation of responses and evaluation of peak discharge rates. Peak discharge rate was defined as the maximum in the PSTH during the time of stimulus presentation or shortly after for high stimulus velocities.

In Figure 2 we illustrate typical responses of three groups of SC cells excited by moving stimuli.

The first group is constituted by cells which give excitatory responses but only to stimuli moving at

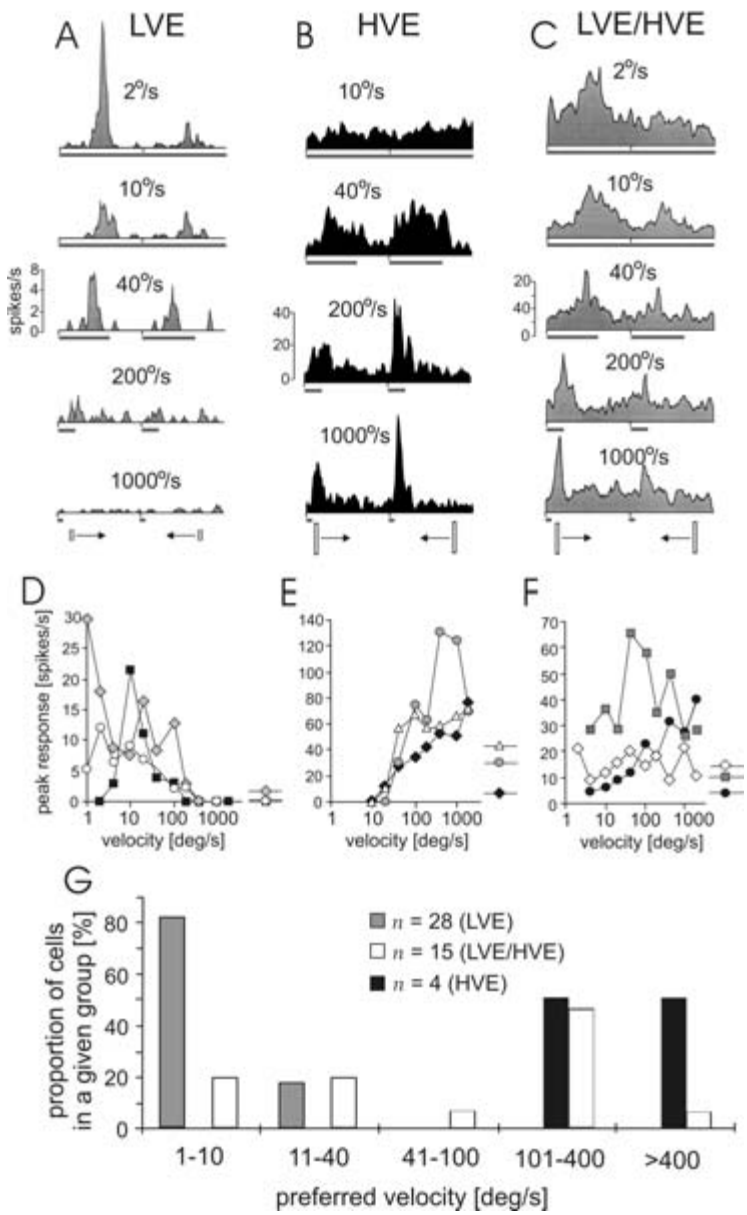

Fig. 2. Responses of collicular neurons to stimuli moving at different velocities. (A), (B) and (C) Peristimulus time histograms of responses for three neurons excited by moving stimuli. The velocity of moving stimulus (a light bar) is indicated above each histogram. The left half of each histogram shows the response to the stimulus moving in one direction across the receptive field, the right half of histogram shows the response for movement in the opposite direction. Directions of movement are indicated beneath the bottom histograms. The stimulus moved during the time indicated by thick grey lines beneath each histogram and for velocities above 40 deg/s remained stationary for a certain time outside the receptive field before moving back in the opposite direction. In (A) are shown responses of a cell excited only by slowly moving stimuli (low-velocity-excitatory or LVE cell), in (B) responses of a cell excited by stimuli moving at moderate and high velocities but not at low velocities (high-velocity-excitatory or HVE cell) and in (C) are shown responses of a cell excited by stimuli moving at all velocities tested (low-velocity-excitatory/high-velocity-excitatory or LVE/HVE cell). (D) Graphs of peak response vs. velocity for three other LVE cells; (E) graphs of peak response vs. velocity for three other HVE cells; (F) graphs of peak response vs. velocity for three other LVE/HVE cells. The peak responses plotted in (D), (E) and (F) have been corrected for background ("spontaneous") activities. Level of background activity is indicated at the bottom right of each graph. (G) Percentage histogram of preferred velocities of LVE and HVE neurons. Figure has been modified from Fig. 2 and 5 of Waleszczyk et al. (1999) with some additional changes.

low-to-moderate velocities. Indeed, these low-velocity-excitatory or LVE cells do not respond to stimuli moving at velocities exceeding 200 deg/s (Fig. 2A,D). All LVE cells responded optimally to photic stimuli moving at velocities not exceeding 40 deg/s and over 80% of them responded optimally at velocities not exceeding 10 deg/s (Fig. 2G). Following velocity response profiles based classification of neurons in mammalian visual cortices (Orban 1984) our LVE cells could be identified as either low-velocity-tuned cells or, when no attenuation of response is observed at very low velocities, as low-pass cells. LVE cells constituted about 50% of collicular neurons and all of them were recorded from SGSu, SGSl or from SO. Cells in the second group gave excitatory responses to photic stimuli moving at moderate and high velocities, and did not respond to slowly moving stimuli (Fig. 2B,E). All high-velocity-excitatory (HVE) cells responded optimally to velocities exceeding 100 deg/s and for half of them the maximal response was evoked by stimuli moving at velocities exceeding 400 deg/s (Fig. 2G). HVE cells constitute less than 25% of collicular neurons (Hashemi-Nezhad et al. 2003, Waleszczyk et al. 1999) and according to Orban's (1984) velocity profile classification most of them could be identified as velocity high-pass cells.

Cells constituting the third group gave clear-cut excitatory responses to photic stimuli moving at a very wide range of velocities (Fig. 2C,F). These low-velocity-excit-

atory/high-velocity-excitatory (LVE/HVE) cells, or velocity broad-band cells according Orban's classification, constitute about a quarter of collicular neurons. About half of our sample of LVE/HVE cells responded optimally at low or moderate stimulus velocities (<100 deg/s), while the other half of the sample displayed maximal response at velocities exceeding 100 deg/s (Fig. 2G).

Cells responding well to fast-moving stimuli (belonging to HVE or LVE/HVE group) were recorded mainly from the lowermost part of SGSl or from SO. Only very occasionally HVE and LVE/HVE cells were recorded above and below this region, that is, from the upper part of the SGSl and the upper part of SGI.

A fourth group of collicular cells was also constituted by cells responding over a wide range of stimulus velocities. However, these cells were excited by slowly moving stimuli, while fast-moving stimuli evoked suppression of their "spontaneous" activity (Fig. 3). Low-velocity-excitatory/high-velocity-suppressive (LVE/HVS) cells constituted about 15% of collicular neurons in our sample and were recorded in the lower part of SGS, SO and SGI (Waleszczyk et al. 1999).

Similar velocity response profiles showing excitation at low velocities and suppression at high velocities has been observed for stimulation of the contralateral and ipsilateral eyes (Fig. 4). Figures 4B and 5 show the organization of receptive fields of LVE/HVS neurons. The middle two peristimulus time histograms in Fig. 4B show responses obtained to stimulation of the contralateral eye with the bar moving across the excitatory discharge field (shown as a hatched oval in the center of the diagram) embedded in much larger suppressive field (grey oval). Note that the huge suppressive field extended into both the contralateral and the ipsilateral visual fields. The outer boundary of the suppressive field of LVE/HVS neurons could not be accurately determined. The two uppermost and the two lowermost peristimulus time histograms show responses of the neuron to bar movement outside the excitatory discharge field. No excitation was elicited for

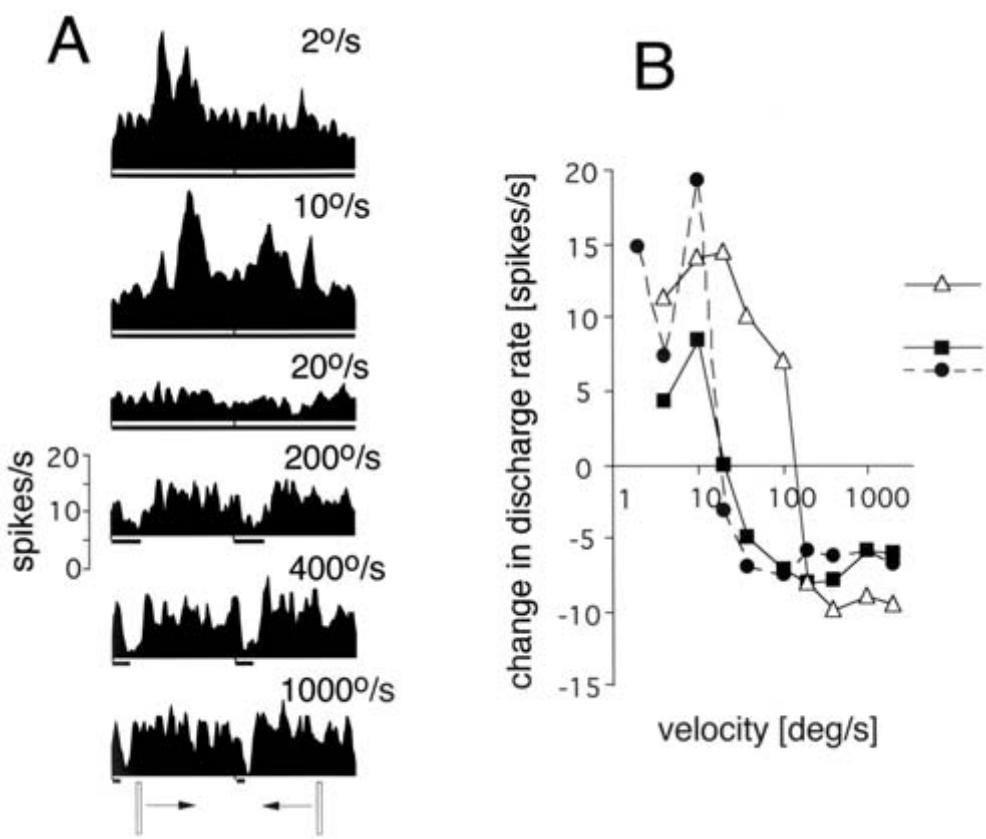

Fig. 3. Responses of collicular neuron excited by slowly moving stimuli but suppressed by stimuli moving at high velocity. (A) Peristimulus time histograms of responses for a low-velocity-excitatory and high-velocity-suppressive (LVE/HVS) neuron; (B) graphs of changes in discharge rate relative to the background activity vs. velocity of stimulus movement for three LVE/HVS cells. Note the high level of "spontaneous" activity of LVE/HVS cells indicated at the right of the graph. Other conventions as in Fig. 2. Figure has been modified from Fig. 7 of Waleszczyk et al. (1999).

stimuli moving at low velocity, but clear suppression at high velocity of movement was observed. No preference for direction or axis of the stimulus motion was apparent in suppressive responses to fast-moving stimuli (Fig. 5).

To our knowledge, ours (Waleszczyk et al. 1999) is the first description of collicular neurons excited by slowly moving stimuli and suppressed by fast-moving stimuli. However, neurons with similar properties have been described in the pretectal nucleus of the optic tract and the dorsal terminal nucleus of the accessory optic system of eutherian mammals such as the domestic cat (Hoffmann and Schoppmann 1981) and macaque monkey (Hoffmann and Distler 1989) as well as in marsupials such as the tammar wallaby (Ibbotson et al. 1994). LVE/HVS cells most likely correspond to the "fixation" neurons, a group of premotor neurons recorded in behaving mammals from the rostral SC (where high acuity, "fixation" parts of the retina are represented). The "fixation" neurons increase their discharge rates during active visual fixation and reduce their activity before the saccade's onset and pause for most of the saccade (Bergeron and Guitton 2001, Guitton and Munoz 1991, Munoz and Guitton 1991, Munoz and Wurtz 1993a,b, Peck and Baro 1997).

CORRELATION BETWEEN THE VELOCITY RESPONSE PROFILES AND OTHER RECEPTIVE FIELD PROPERTIES OF COLLICULAR NEURONS

Collicular cells of these four classes differ from each other not only in the velocity response profiles but also in other receptive field properties. Neurons which were excited by fast-moving stimuli, that is, HVE and

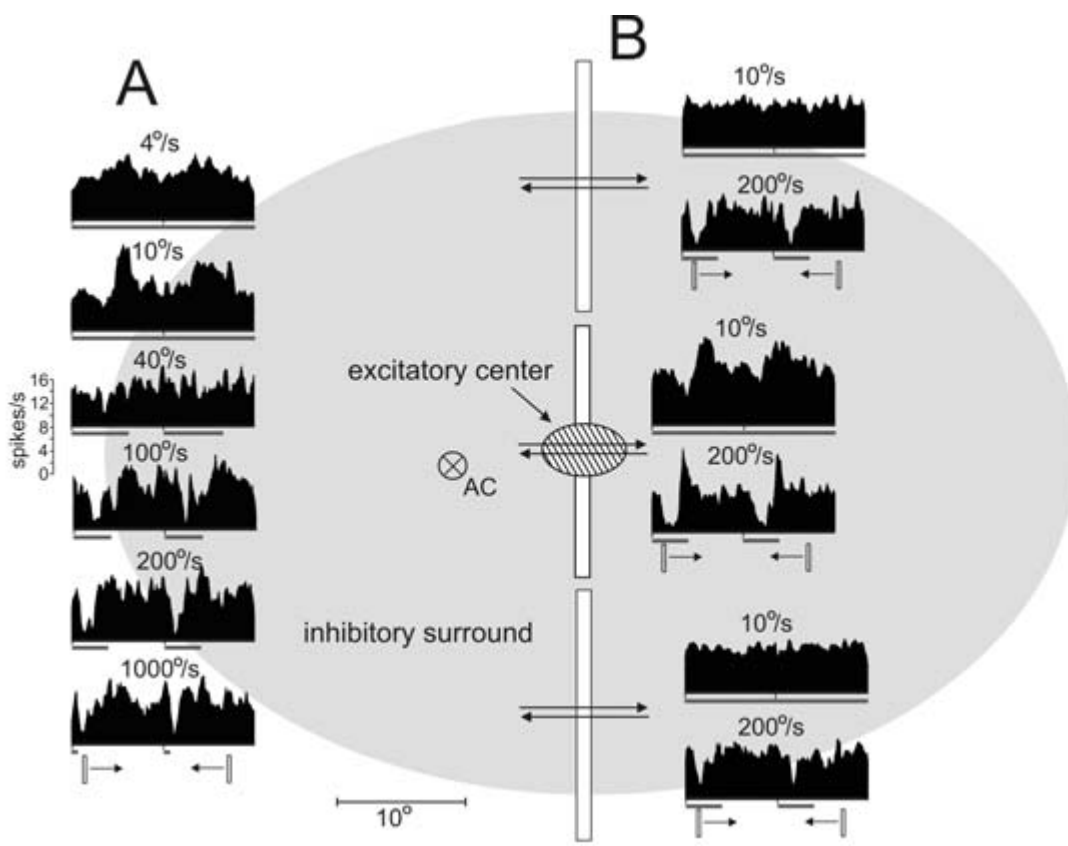

Fig. 4. Receptive field organization of LVE/HVS cells. (A) Peristimulus time histograms of responses of LVE/HVS neuron to stimulation *via* the ipsilateral eye with the bar moving forwards and backwards across the receptive field. Note the excitation at low velocities (4 deg/s and 10 deg/s) and a clear suppression at high velocities (100 deg/s and more) with virtually no response at intermediate velocities (40 deg/s). (B) Peristimulus time histograms of responses obtained to the stimulation of the contralateral eye with the bar moving across the excitatory discharge field shown as a hatched oval in the center of the diagram (the middle two histograms) and outside the excitatory discharge field (the two uppermost and two lowermost histograms). The grey oval represents the large suppressive field. X marks the position of the area centralis (AC). Other conventions as in Fig. 2. Figure has been modified from Fig. 6 of Waleszczyk et al. (1999) with new histograms in part B.

LVE/HVE cells, had large receptive fields (mean diameter ± SEM, (11.7 ± 7.5 deg) – significantly larger (P<0.002; Mann-Whitney U-test) than those of LVE cells (mean diameter ± SEM, 6.0 ± 3.0 deg) (Fig. 6A). Similarly the peak discharge rates and "spontaneous" activities of HVE and LVE/HVE cells were also significantly higher than the respective values for LVE cells (P<0.0001; Mann-Whitney U-test, in both cases). Small receptive fields, relatively low spontaneous activity, weak responses to visual stimuli and sensitivity to slowly moving stimuli are characteristic features of the W channel (Cleland and Levick 1974a,b, Fukuda and Stone 1974, Irvin et al. 1986, McIlwain 1978, Stone and Hoffmann 1972, Wilson et al. 1976). Location of LVE neurons with these properties in, and below collicular layers which are the site of termination of retino-tectal W-input, suggests strongly that LVE cells receive excitatory input from W-type retinal ganglion cells.

Large receptive fields, relatively high peak discharge rates and relatively high "spontaneous" activities are, apart from good responses to fast-moving stimuli, the typical features of cells in the Y channel, both in the retina and in the LGNd (Dreher and Sanderson 1973, Frishman et al. 1983, Hamasaki and Cohen 1977, Lee and Willshaw 1978, Orban 1984, Saul and Humphrey 1990, Wilson et al. 1976), as well as in cortical area 18 cells dominated by Y-input (Dreher 1986, Orban 1984, Stone and Dreher 1973). Laminar localization of collicular cells responding well to fast-moving stimuli overlaps with the laminar distribution of Y-type retino-tectal terminals. Both the properties of receptive fields and the localization of cells constituting HVE and LVE/HVE groups in the collicular laminae innervated by Y-input strongly suggest that responses of these cells to high-velocity movement are dependant on Y-input (see also next section).

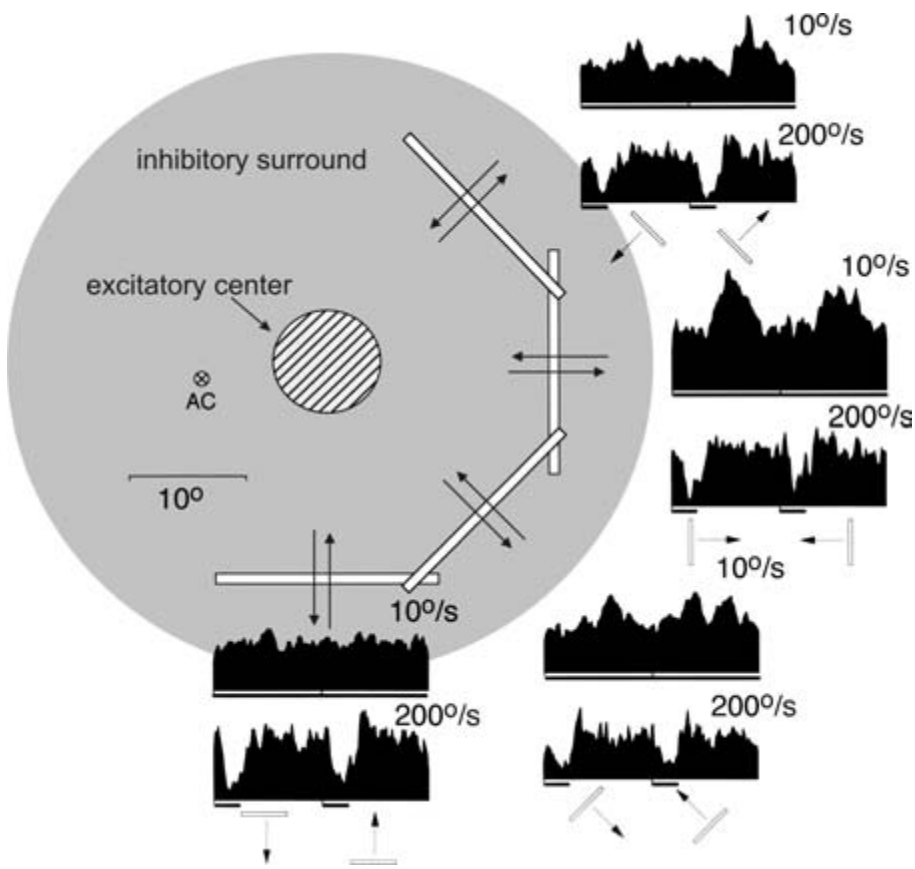

Fig. 5. Receptive field organization of LVE/HVS neuron. Peristimulus time histograms show responses of an LVE/HVS neuron to stimuli moving at low (10 deg/s) and high (200 deg/s) velocity along different axes across the receptive field. Note clear excitatory response evoked by vertical bar moving horizontally at low velocity across the receptive field and virtually no response to bar moving slowly up and down across the receptive field. Note also that the suppressive responses to stimuli moving at high velocity are not direction- or axis-of-movement dependent. Conventions as in Figs. 2 and 4. Figure has been modified from Fig. 7B of Waleszczyk et al. (1999).

LVE and HVE cells together constituted almost 60% of collicular neurons in our sample. Response properties of these cells indicate that they receive a strong excitatory input from only one channel, the W channel in the case of LVE cells and the Y channel in the case of HVE cells. The remaining cells, LVE/HVE and LVE/HVS cells constituting together about 40% of our sample, appear to receive convergent input from at least two visual information channels.

EFFECTS OF SELECTIVE BLOCK OF CONDUCTION IN Y OPTIC NERVE FIBERS

We have used the method of selective conduction block of Y optic nerve fibers to examine in which way elimination of Y-input modifies the velocity response profiles of collicular neurons. To selectively inactivate Y-fibers we used the method of pressure blocking (see Burke et al. 1998 for detailed description of the method). The Y optic nerve fibers, which are the thickest, are the most susceptible to applied pressure.

Figure 7 illustrates the basic outline of the pressure blocking method. The pressure device is placed over the right optic nerve exposed by a dorsal approach. Three implanted electrodes, one placed on the nerve just behind the right eyeball (1), the second in the intracranial right optic nerve (2) and the third in the left optic tract (3), allow for monitoring of the procedure of selective conduction-block of Y-fibers (Fig. 7A). In the control situation, before compressing the nerve, when the field potential is recorded from the left optic tract following an electrical pulse delivered to the optic nerve just behind the eyeball two biphasic waves are observed. The first, the so-called t_1 component of the response is generated by impulses traveling along the Y-fibers while the second, the so-called t_2 component corresponds to slower transmission along X-fibers. Consistent with selective block of conduction in Y-fibers following repeated application of appropriate pressure to the optic

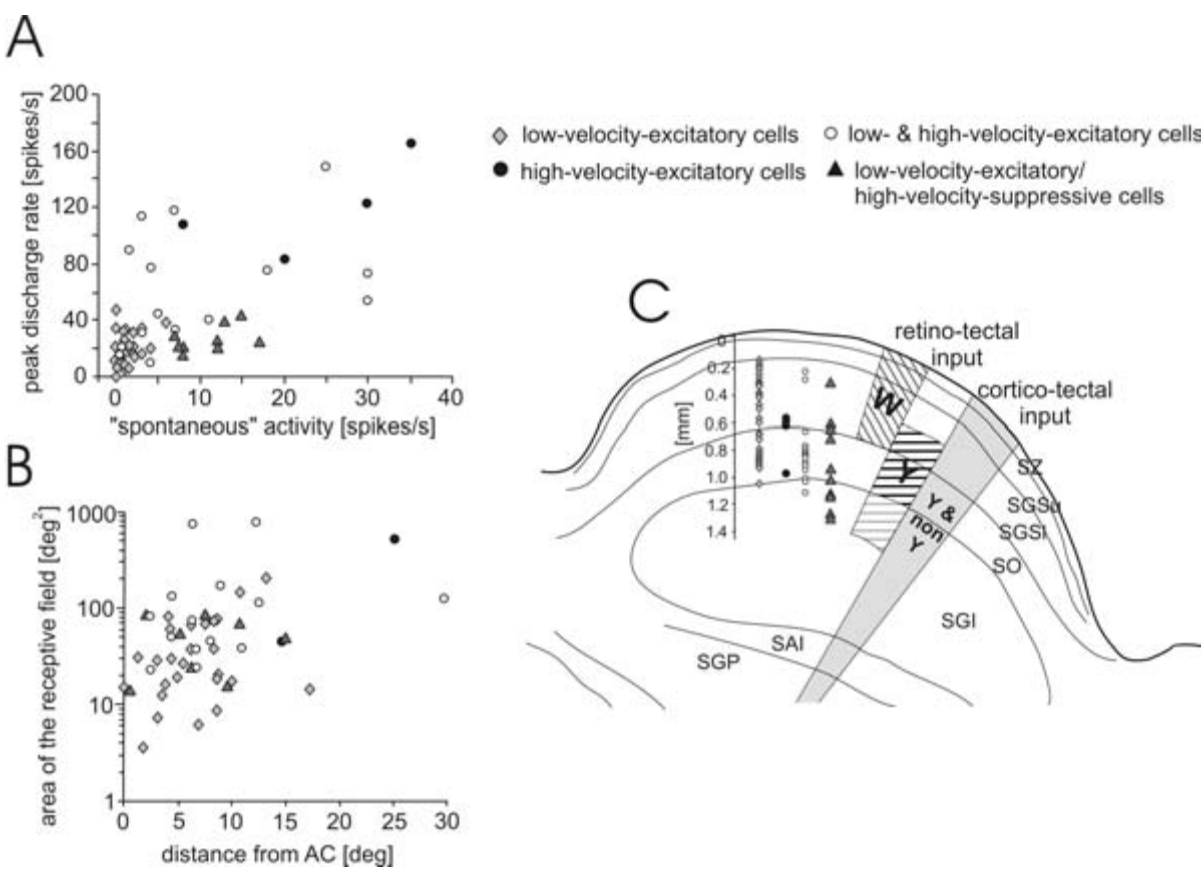

Fig. 6. Receptive field properties of collicular neurons of different classes. (A) Peak discharge rate obtained for optimal stimulus vs. "spontaneous" activity; (B) area of excitatory receptive field plotted against the distance of the receptive field center from area centralis (AC). Data obtained for stimuli presented via the dominant eye. (C) Depth and laminar distribution of collicular neurons of different classes. Conventions as in Fig. 1. Figure has been modified from Figs. 5 and 9 of Waleszczyk et al. (1999).

nerve the t_1 component of the field potential disappears while the t_2 component remains largely unaffected (Fig. 7B). Overall, the selective block of conduction results from a mixture of demyelination and degeneration of Y optic nerve fibers and is maintained for about two weeks and sometimes longer (Cottee et al. 2003). In the case of "heavy" degeneration block, when the field potential is recorded shortly after Y-block in the intracranial optic nerve (electrode 2 in Fig. 7) following stimulation of the contralateral optic tract the t_1 component of the response is still present, but it disappears after few days due to progressive degeneration of the Y-fibers (Burke et al. 1998).

The majority of neurons in the SC responds to visual stimulation *via* either eye, i.e., they are binocular. By selectively blocking conduction in Y-fibers of only one optic nerve we could compare responses to photic stimulation *via* the normal eye with responses to photic stimulation *via* the eye with selective block of conduction in Y-fibers (Y-blocked eye) and, in this way determine the contribution of the Y-input to the response properties of collicular neurons. Figure 8 shows velocity response profiles of collicular neurons obtained by independent stimulation of each eye following Y-block of the eye contralateral to the site of recording. In the case of cells sensitive to high velocity movement (LVE/HVE cells) responses to high velocity stimuli presented *via* the Y-blocked eye were either absent (Fig. 8, the middle row) or much weaker than those to stimuli presented *via* the normal eye (Fig. 8, the lowermost row). The presence of weak responses to fast-moving stimuli presented *via* the Y-blocked eye suggests incompleteness of Y-block. The recording session commenced about one week following block induction and lasted for 4-5 days. Recovery of conduction starts about two weeks after pressure block (Cottee et al. 2003) and during the course of recording sessions we occasionally observed some recovery of the t_1 component of response which was invariably accompanied by recovery of some responsiveness to fast-moving stimuli presented *via* the Y-blocked eye. Y-blocking affected also the velocity response profiles of some LVE cells reducing their upper cut-off velocity and/or peak discharge rate to stimuli presented *via* Y-blocked eye (Fig. 8, the uppermost row). This suggests that at least some LVE cells might receive a weak subthreshold Y-input, which by itself is not able to generate responses to fast-moving stimuli (cf. Hoffmann 1973).

Figure 9 (A, B and C) summarize for our sample of collicular neurons the effect of selective Y-block on the upper cut-off velocities, i.e., the highest velocities of

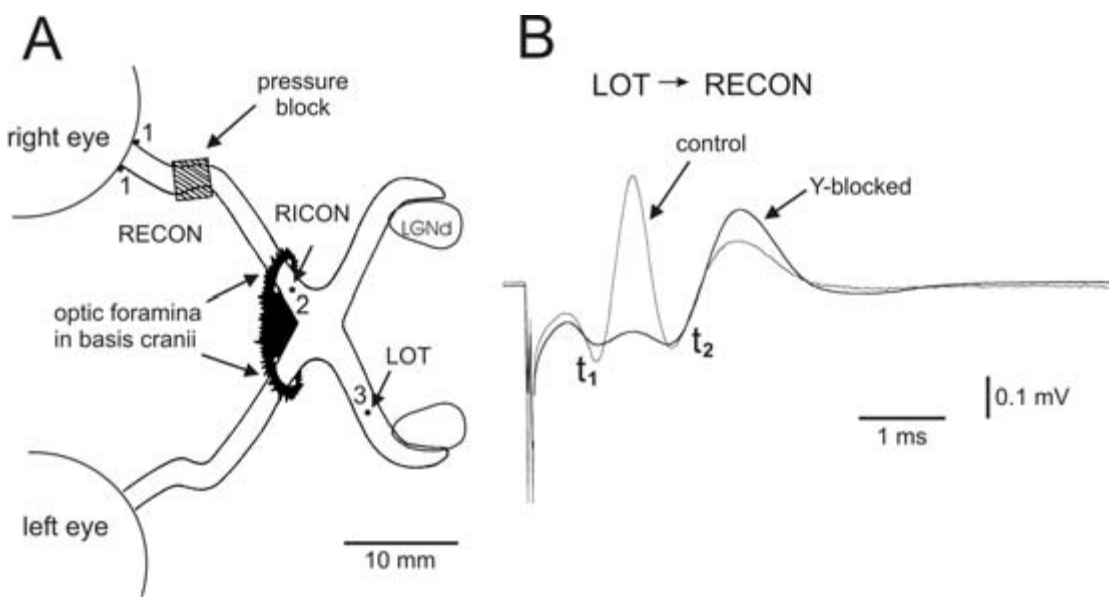

Fig. 7. Selective pressure block of conduction in Y-fibers of cat optic nerve. (A) Diagram of the peripheral visual system in the plan view showing location of the pressure cuff (hatched area) and positions of electrodes used both for stimulation and recording. One electrode is located in the right extracranial optic nerve near the eyeball (1, RECON), the second in the right intracranial optic nerve (2, RICON) and the third in the left optic tract (3, LOT), (LGNd) dorsal lateral geniculate nucleus. (B) Response recorded from right extracranial optic nerve (1, RECON) to stimulation of the left optic tract (3, LOT). Dark trace is the response recorded after application of the pressure, the faint trace is the pre-block control (cat LB164). Notice reduction of the t_1 response after the block. Figure has been modified from Fig. 1 of Burke et al. (1998), potentials in B are new.

moving photic stimuli at which any response could be evoked. In control cats, the upper cut-off velocities for stimuli presented *via* the ipsilateral eye were usually very similar or slightly lower than those for stimuli presented *via* the contralateral eye (Fig. 9A,C). By contrast, the upper cut-off velocities for stimuli presented *via* the ipsilateral (normal) eye were significantly higher ($P<0.0001$, Wilcoxon test) than those for stimuli presented *via* the Y-blocked, contralateral eye (Fig. 9B,C). There was, however, no difference between the upper cut-off velocities of collicular neurons for stimuli presented *via* the ipsilateral eye in control cats and the upper cut-off velocities for stimuli presented *via* the ipsilateral eye of Y-blocked cats ($P>0.05$, Mann-Whitney U test). On the other hand, as indicated in Figure 9C, the upper cut-off velocities for stimuli presented *via* Y-blocked contralateral eye were significantly lower than these for stimuli presented *via* normal contralateral eye ($P<0.005$, Mann-Whitney U test). Apart from impairment of responsiveness to fast-moving stimuli presented *via* the Y-blocked eye, the peak discharge rates for stimuli presented *via* the Y-blocked eye were also significantly lower than those for stimuli presented *via* the normal eye (Wang et al. 2001). This in turn, resulted in the changes in proportions of collicular cells dominated by the input from the contralateral eye and those dominated by the input from the ipsilateral eye. Thus, consistent with other reports (cf. Schoppmann and Hoffmann 1979) in normal cats almost 15% of collicular cells responded exclusively to stimuli pre-

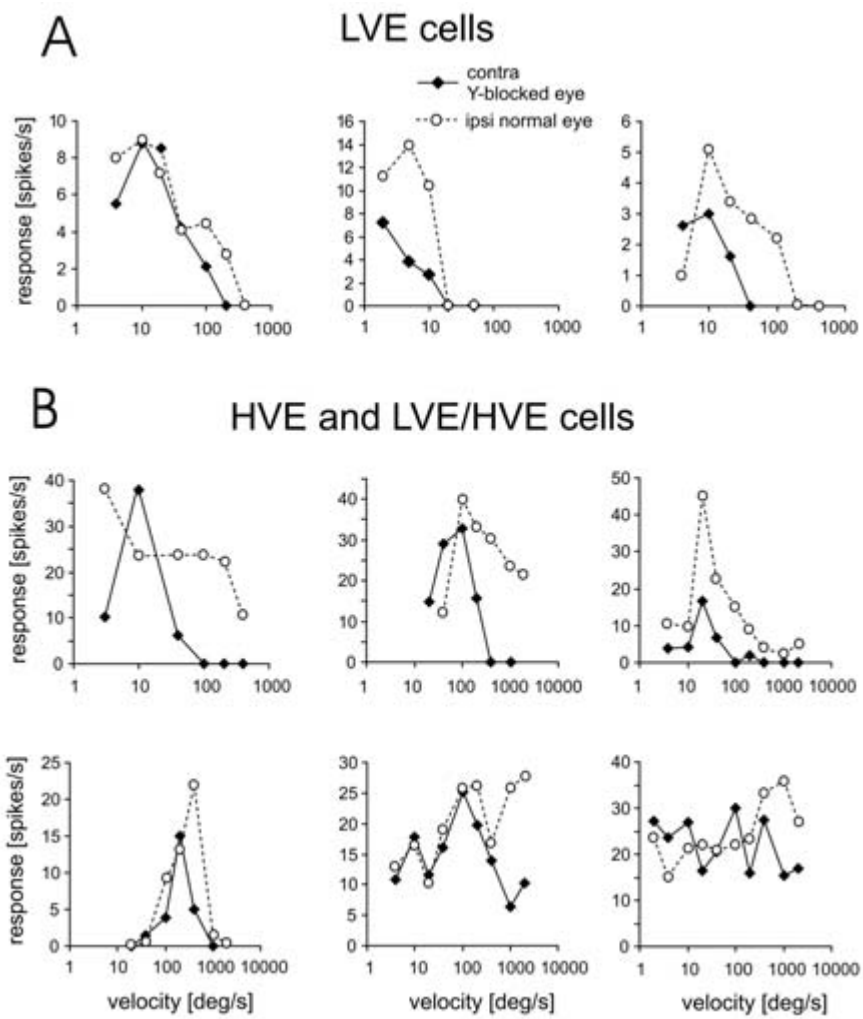

Fig. 8. (A), (B) Velocity response profiles obtained for stimulation *via* the normal (ipsilateral) and Y-blocked (contralateral) eye for a group of collicular neurons excited only by slowly moving stimuli (A, LVE cells) and for a group of neurons which exhibited excitatory responses to fast-moving stimuli presented *via* the normal eye (B, HVE and LVE/HVE cells). Figure based on the set of data presented in paper by Wang et al. (2001).

sented *via* the contralateral eye (class 1 cells; Fig. 9D) and close to 35% of collicular neurons, although binocular, responded more strongly to stimuli presented *via* the contralateral eye (class 2 cells; Fig. 9D). By contrast, in cats with selective conduction block of Y-fibers in the contralateral optic nerve the distribution of eye dominance classes was clearly shifted towards the ipsilateral - normal eye with about 50% of neurons either dominated or exclusively driven by stimuli presented *via* the ipsilateral eye (class 4 and 5; Fig. 9E). Indeed, the difference in the distributions of the eye dominance classes between the normal and Y-blocked cats is highly significant ($P<0.0001$, χ^2 test, Wang et al. 2001).

The above results support the earlier findings indicating that there is substantial degree of excitatory convergence of Y- and non-Y-inputs onto single collicular neurons (cf. Waleszczyk et al. 1999) and indicate that responses to high velocity of movement are dependant on the presence of Y-input.

SPATIOTEMPORAL FREQUENCY RESPONSE PROFILES OF COLLICULAR NEURONS

With use of the method of selective block of conduction in Y-fibers of the one optic nerve we have shown that sensitivity of collicular neurons to high-velocity movement depends on the presence of Y-input. However, the question arises to what extent the responses of SC neurons to slowly moving stimuli depend on W-input and to what extent, if any, they depend on the indirect X-input relayed *via* retino-geniculo-cortico-tectal pathway. Although neurons in both W and X channels respond well to slowly moving stimuli (Cleland and Levick 1974a,b, Frishman et al. 1983, Lee and Willshaw 1978, McIlwain 1978, Stone and Hoffmann 1972), they differ in the spatial properties. Indeed, at any eccentricity, retinal and geniculate neurons in the X channel exhibit relatively high spatial resolution, while

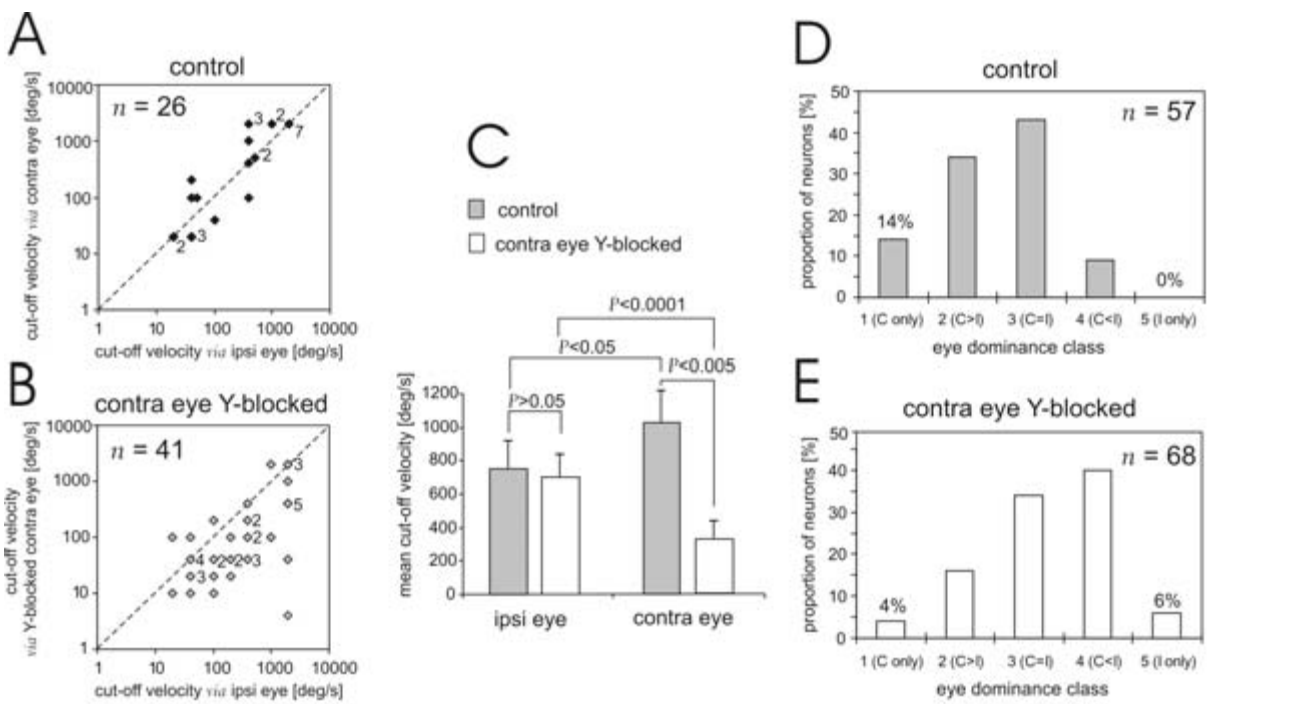

Fig. 9. (A), (B) Graphs of the upper cut-off velocities of binocular neurons recorded from the superior colliculus of normal (A) and Y-blocked cats (B) for stimulation *via* the ipsilateral eye vs. stimulation *via* the contralateral eye. (C) Summary of the statistical comparison of the upper cut-off velocities of binocular collicular neurons recorded in normal and Y-blocked cats. (D), (E) Distributions of eye dominance classes of neurons recorded from superior colliculus of normal cats (D) and cats with conduction block of Y-fibers in the optic nerve contralateral to the recording site (Y-blocked cats) (E). Class 1 and class 5 cells are monocular cells which responded only to stimuli presented *via* the contralateral or *via* the ipsilateral eye, respectively; class 2 and class 4 cells are binocular neurons which responded more strongly to stimuli presented *via* the contralateral eye or *via* the ipsilateral eye, respectively; class 3 cells are binocular neurons which give response of the similar magnitude when stimulated *via* either eye. Figure based on the set of data presented in paper by Wang et al. (2001).

neurons in the W channel are not sensitive to high spatial frequencies (Rowe and Cox 1993, Saul and Humphrey 1990, Sireteanu and Hoffmann 1979, Stone 1983, Stone et al. 1979, Sur and Sherman 1982).

Thus, in order to further analyse the issue of W channel and/or X channel contributions to responses of collicular neurons we have examined spatial frequency properties of cells in the SC using sinusoidal gratings drifting at different temporal frequencies in the preferred direction and mapped out spectral receptive fields plotting spatial against temporal frequency (Waleszczyk et al. 2003a,b). When a cell is tested with drifting gratings of different spatial and temporal frequencies, its response profile plotted as a function of spatial and temporal frequencies can "form" different shapes (Clifford and Ibbotson 2003). In the case of spatial tuning, when the cell is sensitive to a particular spatial frequency the response profile "forms" an elongated ridge over a wide range of temporal frequencies. The ridge of peak sensitivity is elongated parallel to the temporal frequency axis. On the other hand, in the case of temporal tuning the response profile is elongated parallel to the spatial frequency axis. For speed-tuned cells the ridge of peak sensitivity is elongated along the iso-speed line oriented relative to the spatial and temporal frequency axes. Thus, the speed-tuned cells respond selectively to a particular combination of

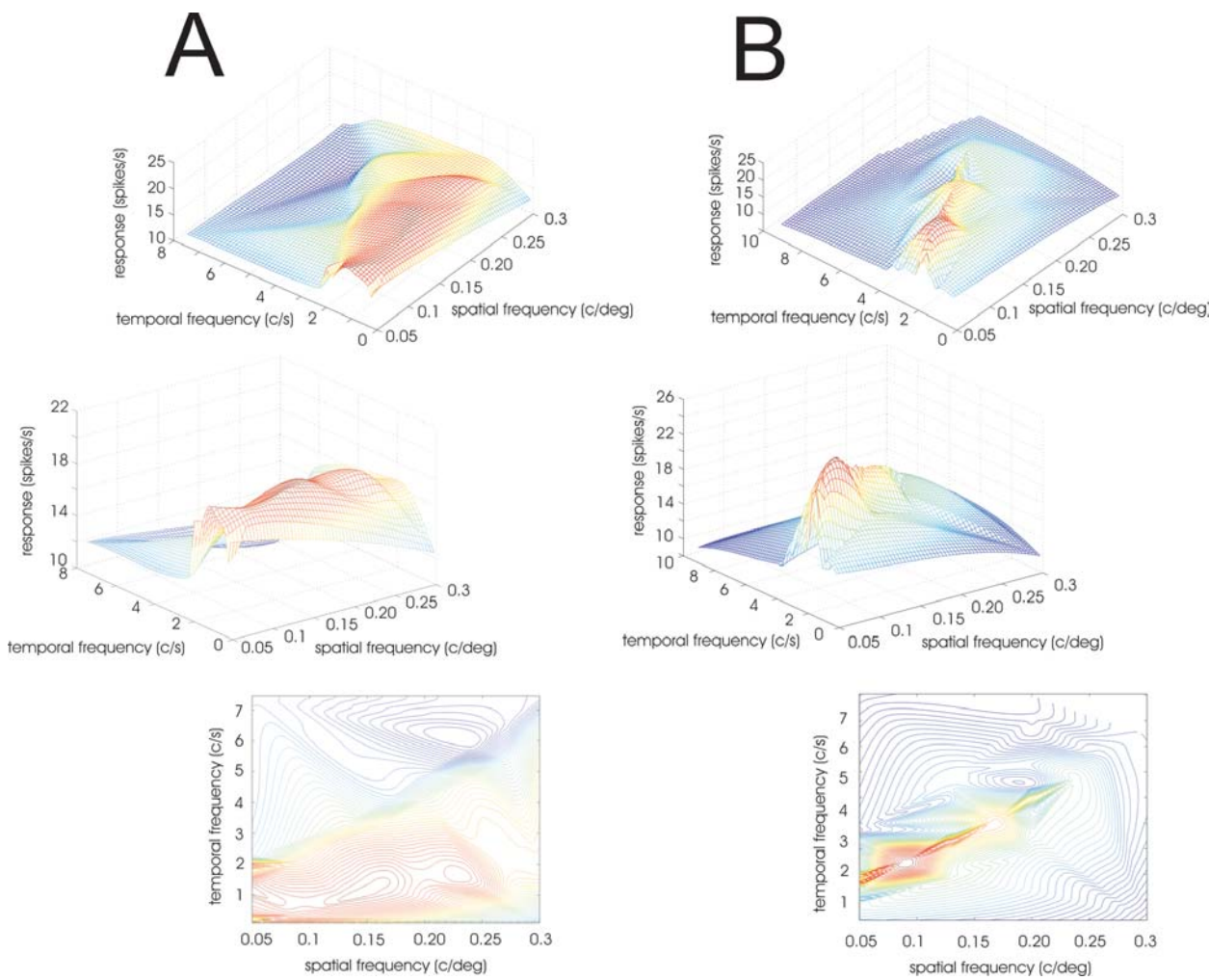

Fig. 10. Spatio-temporal frequency response profiles of two neurons (A, B) recorded from superficial layers of cat's superior colliculus. Plots in one column show spectral receptive field of one neuron, the two upper are perspective plots, the lower ones are contour plots. The plots of spectral receptive fields were created from responses of the neuron to a sinusoidal grating moving in the preferred direction. Twenty-four to forty different spatio-temporal frequency combinations were used to determine the response profile of the neuron. Each spatio-temporal combination was presented 12 times in pseudo-random order. Mean firing rate during the stimulus presentation was taken as a measure of the response. Contrast 50%. Waleszczyk, Nagy, Eördegh, Wypych and Benedek, unpublished results.

spatial and temporal frequencies, that is, to a certain speed of stimulus motion.

Figure 10 shows spatio-temporal frequency response profiles of two collicular neurons recorded in the upper part of SO. The three diagrams in each vertical column show from different points of view the spectral receptive field of one neuron. For both neurons, the response to spatial frequency varies with the temporal frequency of the stimulus indicating speed-tuning. The ridge of peak sensitivity is elongated and oriented relative to the spatial frequency axis. The steeper the line along which the response is located the higher the optimal velocity. The difference in the angle of orientation of the ridge of peak sensitivity between these two spectral receptive fields indicates the difference in the optimal speed.

Spatio-temporal frequency response profiles of more than half of the collicular neurons in our sample indicate that these cells are speed-tuned (Fig. 11 A,B). To our knowledge, until now, the existence of speed-tuned cells has been reported only in: (i) the middle temporal cortical visual motion area (MT area) of macaque monkeys (Perrone and Thiele 2001, 2002, Priebe et al. 2003); (ii) the pretectal nucleus of the optic tract of a marsupial, the tammar wallaby (Ibbotson and Price 2001); (iii) nucleus lentiformis mesencephali of the pigeon, an avian homologue of the mammalian nucleus of optic tract (Ibbotson and Price 2001, Wylie and Crowder 2000); and (iv) in some area 18 neurons in the visual cortex of the cat (Friend and Baker 1993). We have also recorded cells with spectral receptive fields showing suppression at high velocities (Fig. 11C). Such a profile would correspond to the velocity response profile of our low-velocity-excitatory and high-velocity-suppressive cells (LVE/HVS cells). As in the case of LVE/HVS cells, the activity of the cell, whose spatio-temporal frequency profile is shown in Fig. 11C, was suppressed by the movement of grating in any direction. Cells with similar spatio-temporal frequency characteristics have been found also in the nucleus of the optic tract and dorsal terminal nucleus of the accessory optic system of the marsupial tamar wallaby (Ibbotson et al. 1994). Some collicular cells in our sample had receptive field profiles which were difficult to classify (Fig. 11D). In the MT area of primates, cells with this type of spectral receptive field respond well to fast-moving stimuli (Perrone and Thiele 2001), and cells with such spectral receptive fields could

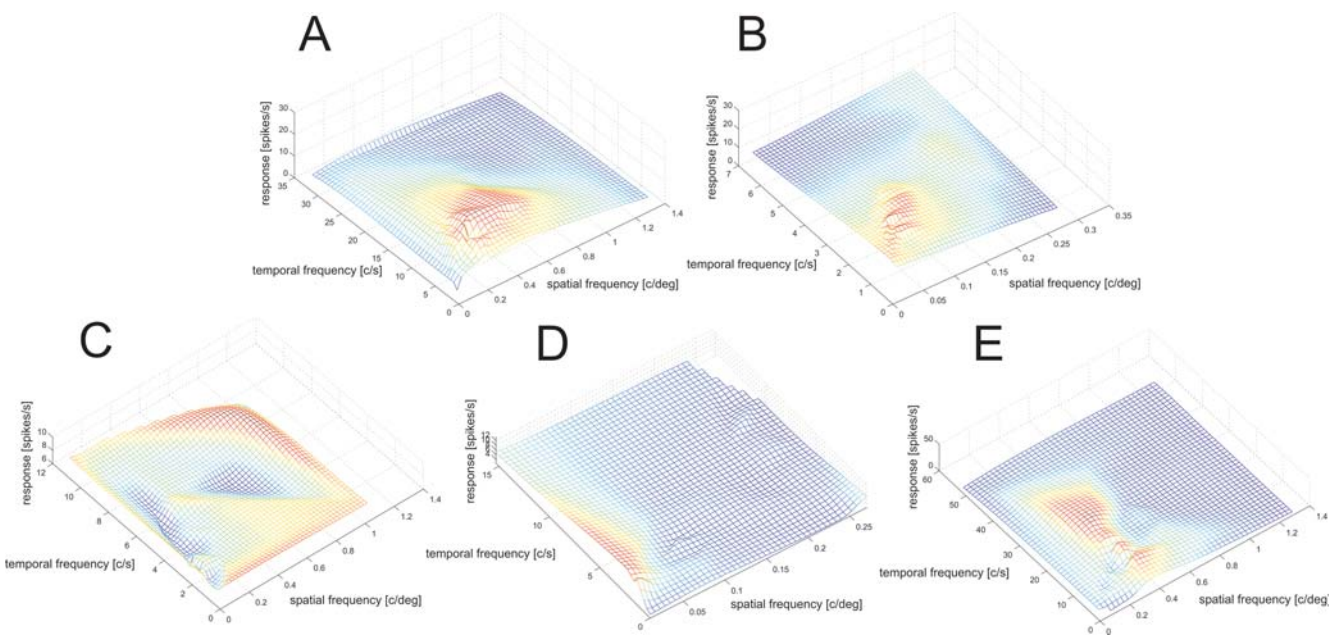

Fig. 11. Types of spectral receptive fields of collicular neurons. (A, B) Spectral receptive field of speed-tuned cells. Response profile in (A) shows broad tuning, that in (B) more narrow tuning. (C) Spatio-temporal response profile showing suppression of neuron's activity in the region of the spatial and temporal frequencies corresponding to high speed of the moving stimulus. (D) Spectral receptive field of spatial frequency low-pass cell. Location of the region of peak sensitivity indicates good responsiveness of the neuron at high velocity. (E) Spectral receptive field showing spatial tuning. The region of peak sensitivity is parallel to the temporal frequency axis. Waleszczyk, Nagy, Eördegh, Wypych and Benedek, unpublished results.

correspond to HVE cells. Finally, some collicular cells had spectral receptive fields which displayed spatial tuning (Fig. 11E). This type of tuning is a characteristic feature of neurons in cat's primary visual cortex (areas 17 and 18). Indeed, for most of the neurons in area 17 (Bisti et al. 1985, Friend and Baker 1993, Tolhurst and Movshon 1975) and in area 18 (Friend and Baker 1993), optimal spatial frequency is invariant with the temporal frequency (see however Bisti et al. 1985, Galli et al. 1988 concerning spatio-temporal frequency separability in area 18). Whenever we tested the responses of a cell with a grating moving in the preferred and anti-preferred direction the spatio-temporal frequency response profiles obtained for both directions of movement were very similar.

The clear majority (over 70%) of cells in our sample of collicular neurons exhibited band-pass spatial frequency tuning while some cells exhibited low-pass tuning. Figure 12A shows spatial frequency tuning curves for two collicular neurons, the upper one displays spatial band-pass characteristic, the lower shows low-pass characteristic. Consistent with earlier report of Pinter and Harris (1981) the distribution of optimal spatial frequencies, shown in Fig. 12B, indicates that most collicular cells responded optimally at very low spatial frequencies. For our sample of collicular neurons the mean optimal spatial frequency was 0.14 cycles/deg (range: 0.03-0.83), mean spatial bandwidth was 2.8 octaves. Since receptive fields of most neurons were located in the central part of the retina, (mean distance between center of receptive field and area centralis was 5.1 deg, range: 0.7-20 deg) it seems unlikely that the low optimal spatial frequency of collicular neurons obtained in this study was the result of high eccentricity of their receptive fields. Thus, the mean optimal spatial frequency obtained for our sample of SC neurons was very similar to the optimal spatial frequencies reported in the literature for: (i) W-type cat's retinal ganglion cells (Rowe and Cox 1993; optimal spatial frequency between 0.2 and 0.3 as estimated from graphs in their Figs. 1 and 2 for tonic and phasic W-cells); (ii) Y-cells in cat's LGNd (Saul and Humphrey 1990; 0.12, 0.13 cycles/deg, respectively means for the so-called "lagged" and the so-called "nonlagged" Y-cells); (iii) neurons in those cortical areas of the cat which are presumed to belong to the motion- rather than pattern-processing

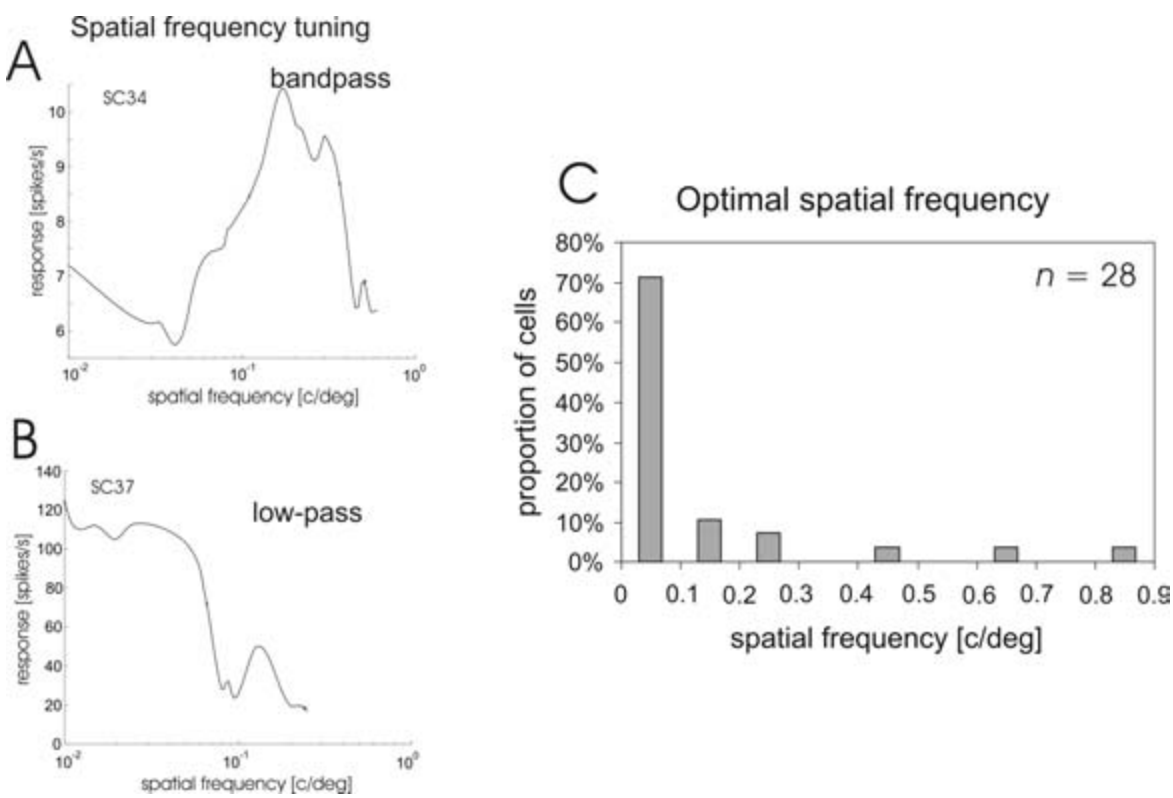

Fig. 12. Spatial frequency properties of SC neurons. (A, B) Two examples of the spatial frequency tuning curves. Upper (A) is the tuning curve of a spatial frequency band-pass cell, below (B) is example of the tuning curve of a spatial frequency low-pass cell. (C) Distribution of the optimal spatial frequencies.Waleszczyk, Nagy, Eördegh, Wypych and Benedek, unpublished results.

stream dominated by Y-input (e.g., area 18, about 0.2 cycles/deg (Movshon et al. 1978); the posteromedial lateral suprasylvian or PMLS area, 0.16 cycles/deg (Zumbroich and Blakemore 1987); the anterior ectosylvian visual or AEV area, 0.2 cycles/deg (Nagy et al. 2003)); and (iv) cells in cortical areas of the cat dominated by W-input (area 19, 0.16 cycles/deg (Bergeron et al. 1998, Tardif et al. 1997)). On the other hand, the mean optimal spatial frequency of our sample of SC neurons is much lower than that of: (i) LGNd X-cells (0.58, 0.43 cycles/deg, means for "lagged" and "nonlagged" X-cells, respectively, (Saul and Humphrey 1990)); (ii) that of neurons in area 17 dominated by X-input (0.86 cycles/deg for simple cells and 0.93 cycles/deg for complex cells (Movshon et al. 1978)); or even (iii) that of population cortico-tectal cells in area 17 (0.7 cycles/deg (Casanova 1993)). Interestingly, the mean optimal spatial frequency for our sample of collicular neurons is only slightly lower than that (0.26 cycles/deg (Morley and Vickery 1997)) of cells in area 21a, that is, another cortical area which belongs to the "form" pathway dominated by X-input (Burke et al. 1998, Dreher 1986, Dreher et al. 1993, 1996) and like area 17 (Ogasawara et al. 1984, Rosenquist and Palmer 1971, Wickelgren and Sterling 1969) strongly influences the magnitude of responses of SC neurons and the spatial properties of their receptive fields (Hashemi-Nezhad et al. 2003). Despite the fact that the spatio-temporal frequency response profiles of collicular neurons do not appear to be influenced by the X-type input, the X-input to the SC relayed *via* the visual cortex might be implicated in reported involvement of the SC in pattern discrimination (Lomber 2002, Sprague 1991, Sprague et al. 1970, Tunkl and Berkley 1977, 1985).

GENERAL DISCUSSION

Already very early lesion studies indicated that superior colliculus is involved in spatial localization and orienting response suggesting that this nucleus is an essential part of the visual system which deals with a question "Where is it?" and not "What is it?" (Schneider 1969, see also Spraque 1996). We have shown that in most collicular neurons their response properties are strongly dependent on Y-input. Similar dependence has been found for neurons in area 18, the posteromedial lateral suprasylvian area and the anterior ectosylvian visual area, cortical areas which belong to the part of the visual system involved in motion perception and action (Benedek et al 1988, Mucke et al. 1982, for review see Burke et al. 1998). Both the similarity of response properties indicating the great influence of Y-input and the connections of the superior colliculus with extrastriate cortical areas (the posteromedial lateral suprasylvian area and the anterior ectosylvian visual area) *via* the lateral posterior-pulvinar complex indicate that the SC belongs to the part of the visual system involved in action and motion perception. Speed-tuning suggesting the specialization of collicular cells in extraction of information about the velocity of moving objects strongly supports this notion.

Convergence in superficial layers of the superior colliculus of excitatory input from different visual information channels with complementary temporal properties and velocity response profiles (W and Y channels), can be regarded as a first step to a more global integration of multimodal sensory information in the deeper layers. One of the reasons of this convergence is most likely the strong participation of the SC in visuomotor behavior, particularly in reflex adjustment of head and eyes, which often has to be performed in shortest possible time. Collicular cells which appear to receive excitatory input from both Y and W channels (LVE/HVE cells) presumably innervate saccade-related neurons ("saccadic" neurons) located in deep layers of the SC. On the other hand, collicular cells which appear to receive excitatory input from W channel and suppressive input from the Y channel (LVE/HVS cells) most likely constitute the group of "fixation" neurons. Both "saccadic" and "fixation" neurons project to premotor circuitry in the brainstem reticular formation involved in visual fixation and saccadic eye movement (for review see Munoz 2002). The pathway from retina through the superficial layers and then the deep layers of the SC to the oculomotor nuclei contains relatively few synapses, is relatively short and therefore appropriate for fast orientation response to visual stimuli. By contrast, the time may not be the critical factor in the LGNd and the part of the cortex primarily concerned with form perception and the separation of the different visual information processing channels for longer distances may be needed for elaboration of sensation.

Collicular cells which receive convergent input from different visual information channels located in SO and the upper part of SGI most likely constitute also the output to the extrageniculate dorsal thalamic structures, to the ventral division of lateral posterior nucleus (vLP) and the suprageniculate nucleus (Sg) (Abramson and

Chalupa 1988, Hicks et al. 1986, Katoh and Benedek 1995). Indeed, similarly to LVE/HVE cells in the SC substantial proportion of Sg neurons are responsive to visual stimuli moving at a very wide range of stimulus velocities (Benedek et al. 1997). Therefore, it is very likely that convergence of different visual information channels is a feature which characterizes not only the SC, but also the extrageniculate dorsal thalamic visual pathway as well.

CONCLUSIONS

The clean separation of the visual information processing channels seems to be the unique feature of retinal and geniculate components of the mammalian retino-geniculo-cortical pathway. By contrast, at least in the cat, there is a substantial degree of convergence of Y and non-Y visual information channels in the main mesencephalic retinorecipient nucleus, the superior colliculus. Relatively low spatial frequency sensitivity of collicular neurons indicates that Y- and W-type inputs (direct retino-tectal or indirect retino-geniculo--cortico-tectal) constitute the major functional input to retinorecipient layers of SC. The "top-down" (*via* cortico-tectal projection) X-type input to the SC appears to exert only a minor (if any) influence on spatio-temporal frequency response profiles of neurons in the retinorecipient layers of the SC.

ACKNOWLEDGEMENTS

We thank, Gabriella Eördegh, Zsuzsanna Paroczy, Antal Berenyi and Attila Nagy of Albert Szent-Györgyi Medical and Pharmaceutical Center for their participation in some of the experiments described here. Thanks are also due to Marek Wypych of the Nencki Institute of Experimental Biology and Peter Liszli of Albert Szent-Györgyi Medical and Pharmaceutical Center for computer programming. The work was financially supported by the grants from the National Health and Medical Research Council of Australia, Polish State Committee for Scientific Research (KBN) grant no. 3P04C08222, and grant no. T042610 from OTKA of Hungary.

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Received 21 February 2004, accepted 2 April 2004