Convergence of Y and non-Y channels onto single neurons in the superior colliculi of the cat

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Receptive field properties of single neurons in the cat superior colliculus were examined following selective conduction-block of Y-type fibers in contralateral optic nerve. Although the responses evoked by photic stimuli presented via the Y-blocked eye were significantly weaker than those evoked by stimuli presented via the normal eye, >85% of collicular cells were binocular. Furthermore, when binocular cells were stimulated via the Y-blocked eye their median upper cut-off velocity (100 °/s) was significantly lower than that (400 °/s) for stimuli presented via the normal eye. Thus, there is a substantial degree of excitatory convergence of Y- and non-Y-information channels on single collicular neurons and the responses to high velocity of motion appear to depend on the integrity of Y-type input.

Key words: Directional selectivity; Ocular dominance; Relative magnitudes of visual responses; Upper cut-off velocities

INTRODUCTION

The visual input to the retino-recipient layers of the cat superior colliculus (SC) originates either directly from the so-called W- and Y-type retinal ganglion cells (RGCs) in the contralateral or ipsilateral retinae, or is relayed to the SC via the dorsal thalamus and the ipsilateral visual cortical areas including primary visual cortices [1—5]. It has been reported that there is very little overlap in the laminar distribution of W- and Y-type retino-tectal terminals [1—4] and that only a small proportion of SC neurons which receives W-type retinal input receives also an indirect Ytype input relayed via the dorsal thalamus and corticotectal projections [5]. These results suggest, therefore, a very limited convergence of the W and Y channels on single neurons in the retino-recipient layers of the SC. On the other hand, our recent study of the velocity—response profiles of the SC neurons (6] revealed that a substantial proportion (43%) of SC neurons responds well over a wide range of stimulus velocities including both low velocities and high velocities > 200°/s. This result in turn suggests that in a substantial proportion of collicular neurons there is a convergence of W (good response to slowly moving stimuli and poor response to fast-moving stimuli) and Y (poor response to slowly moving stimuli and good response to fast-moving stimuli) channels. To assess more directly the extent of convergence of different information channels on single SC neurons and the contribution of the *Y* channel to the receptive field properties of collicular neurons, we have examined quantitatively several visual receptive field properties (e.g. eye dominance, velocity sensitivity, receptive field sizes, direction selectivity) of single neurons in the SC of the cats with selective conduction block of the Y-type fibers in one optic nerve (Y-blocked eye). Preliminary results have been presented in a form of an abstract [7].

MATERIALS AND METHODS

Six adult cats (three females, three males; weighing 2.8— 3.8 kg) were used. For the Y-blocking operation the cats were deeply anaesthetized with sodium pentobarbitone (40mg/kg, i.p). To maintain a surgical level of anesthesia small supplementary doses were added whenever necessary. The right optic nerve was compressed by a special cuff until the Y-type (t_1) component of the field response disappeared (for additional details see [8,9]). Antibiotic (ampicillin, 125mg, i.m.) was administered daily before, during and after the operation. Buprenorphine (0.03 mg) was also injected during recovery from the operation.

One to two weeks after recovery from the Y-blocking operation, initial surgery, including i.v. and tracheal cannulation, bilateral cervical sympathectomy and craniotomy, was carried out under a gaseous mixture of 1—1.5% halothane in $N_20/0_2$ (67%/33%). During the recording sessions, the animals were paralyzed with gallamine triethiodide (7.5mg/kg/h, iv.) in a mixture of sodium lactate (Hartmann's solution) and 5% dextrose (50% / 50%)

and artificially ventilated. Anesthesia was maintained with a gaseous mixture of $N_20/0_2$ (67%/33%) and 0.5—0.8% halothane. Body temperature was monitored continuously and automatically maintained with an electric heating blanket at about 37.5^0C. Expired CO_2 was maintained at 3.7—4.0% by adjusting the stroke volume of a pulmonary pump. Heart rate and electroencephalogram (EEC) were also monitored continuously and by adjusting, if necessary, the level of halothane in the gaseous mixture the heart rate was kept below 180 beats/mm while the EEC exhibited slow-wave synchronised activity. Antibiotic (amoxycillin trihydrate, 75mg), dexamethasone phosphate (4mg) and atropine sulphate (0.3mg) were injected daily i.m.

The corneas were protected with zero-power, air-permeable plastic contact lenses. Pupils were dilated and accommodation paralysed with 1% atropine sulphate solution. The nictitating membranes were retracted with 0.128% phenylephrine hydrochloride. Artificial pupils (3 mm in diameter) were placed in front of the contact lenses. Optics of the animals were further corrected with additional lenses bringing the eyes to a focus on a tangent screen located 57cm in front of the animals. The locations of the optic discs and the areae centrales were plotted daily.

A plastic cylinder was mounted and glued around the craniotomy (Horsley—Clarke coordinates P2—A4 and LU—5). A platinum/iridium glass-coated microelectrode was inserted through a smaller dural opening to 14mm below the cortical surface and the cylinder was filled with 4% agar gel and sealed with warm wax (melting point 40^0C). The microelectrode was advanced further with an hydraulic micromanipulator. Action potentials of single collicular neurons were recorded extracel lularly, conventionally amplified and then used to trigger standard pulses which were fed to the microcomputer for on-line analysis and data storage. The excitatory receptive fields (discharge fields) of recorded neurons were plotted with light slits and spots from a hand-held projector and remapped with black bars and spots [10,11]. The computer-controlled light slits from a slide-projector, with a luminance of 15 cd/rn^2 against a background luminance of 0.9 cd/rn^2, were used for quantitative study of receptive field properties of recorded cells. The peristirnulus 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 condition. The responses were then smoothed using a Gaussian weighted average over five neighbouring bins. The mean direction selectivity index (MDI) [12] of a given cell was calculated according to the following formula:

$$MDI = \left| \frac{\sum_{i-1}^{n} RiDIi}{\sum_{i-1}^{n} Ri} \right|$$

where ***n*** is the number of velocities tested; Ri is the magnitude of the responses in the preferred direction at each stimulus velocity while DI is the direction selectivity index (at each stimulus velocity) calculated by the following formula:

$$DI = [(R_p - R_{np})/R_p] \times 100\%$$

where R_p and R_{np} are the peak discharge rates at the preferred and non-preferred direction respectively [8,131.

Spike discharge rates and direction selectivity indices are expressed as means ± s.e. The χ^2 test, the Wilcoxon matched-pairs signed ranks test or Mann-Whitney U test [14] were used to assess statistical differences in the sample data. Statistical differences were considered significant when p at two-tailed criterion was <0.05.

At the end of the recording sessions the animals were deeply anaesthetized and perfused transcardially with warm (37^0C) Hartmann's solution (sodium lactate) followed by 4% solution of paraformaldehyde in 0.1 M phosphate buffer (pH 7.4). The electrode tracks were reconstructed from 50 µm coronal sections stained with cresyl violet.

RESULTS

In two of the six experimental animals the pressure used produced a complete loss of the Y-type (t_1) component of response. In the remaining four cats the magnitude of the Y-type (t_1) component of response was reduced to 4 -13% of the original response. In all but one cat there was also a small (9-11o/o) reduction in the amplitude of the X-type (t_2) component of the response. In all but one cat the level of block of the Y-component was maintained throughout the experiment. In one cat, however, on the third day of the acute experiment there was a substantial (25%) recovery of the t_1 potential in the right (Y-blocked) optic nerve. The data collected after the partial recovery of the t_1 potential were not included in the present analysis. The question of recovery of conduction from pressure-block has been discussed previously [9]. In particular, we have considered whether the pressure-block might allow at least some Y fibers to conduct at slower velocities and have given reasons why this is unlikely.

Of 83 cells recorded from the left SC of the Y-blocked cats, only in 51 cells were the receptive field properties tested quantitatively. In the analysis of the ocular dominance classes apart from these 51 cells we included an additional ten cells for which we had only qualitative data.

As in our previous study [6], all our electrode penetrations went through the central part of the SC where the binocular part of the visual field is represented [15]. Furthermore, all neurons tested quantitatively were recorded from the retino-recipient layers, in particular, the lower part of stratum griseum superficiale or from the stratum opticum.

The relative magnitude of responses and ocular dominance profiles: Analysis of our unpublished data collected in normal cats indicates that the mean magnitude of responses (measured as peak discharge rates) of binocular neurons to visual stimuli presented via the contralateral eye (31.0 ± 7.2 spikes/s) was significantly ($p < 0.05$, $n = 20$; Wilcoxon test) greater than that of responses evoked by visual stimuli presented via the ipsilateral eye (19.1 ± 2.9 spikes/s). By contrast, in binocular cells recorded from the SC of cats with one Y-blocked eye, the mean magnitude of responses to visual stimuli presented via the Y-blocked (contralateral) eye (24.3±3.8 spikes/s) was significantly

smaller (p 0.02, $n = 44$; Wilcoxon test) than that (32.1 + 5.0 spikes/s; Fig. la) of responses evoked by visual stimuli presented via the normal (ipsilateral) eye. Despite substantially lower mean peak discharge rate to stimuli presented via the contralateral (Y-blocked) eye in the Y-blocked cats than that to stimuli presented via the contralateral eye in the normal cats, the difference was not significant ($p = 0.14$; Mann-Whitney U-test). Similarly, despite clearly higher mean peak discharge rate to stimuli presented via the ipsilateral (normal) eye in the Y-blocked cats than that

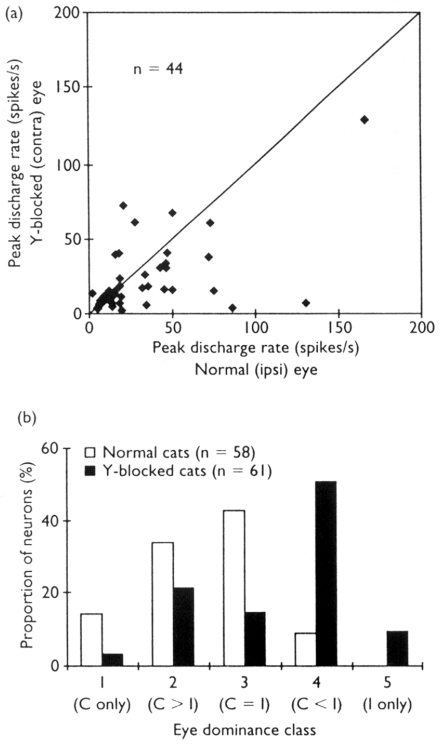

Fig. 1. (a) Graph of peak discharge rates of responses of the SC cells to stimuli presented via the Y-blocked eye vs those to stimuli presented via the normal eye. The mean peak discharge rate (24.3 ± 3.8 spikes/s) for stimuli presented via the Y-blocked eye was significantly lower than that (34.0 ± 5.0 spikes/s) for stimuli presented via the normal eye ($p < 0.01$; Wilcoxon test). (b) Percentage histograms of eye dominance classes of neurons recorded from the SC of normal [6] and Y-blocked cats (present sample). Class I cells and class 5 cells are monocular neurons which respond only to photic stimuli presented via the contralateral eye and ipsilateral eye, respectively; class 2 cells are binocular neurons which give stronger excitatory response when stimulated via the contralateral eye; class 3 cells are binocular neurons which are excited equally strongly when stimulated through either eye; class 4 cells are binocular neurons excited more strongly when stimulated via the ipsilateral eye. Note that the collicular neurons recorded from the Y-blocked cats unlike those recorded from the normal cats tend to be dominated by the ipsilateral (normal) eye. The distribution of eye dominance classes of the SC neurons recorded in Y-blocked cats is highly significantly different ($p < 0.0001$, χ^2 test) from that of the SC neurons recorded in the normal cats.

to stimuli presented via the ipsilateral eye in the normal cats, the difference was not significant ($p = 0.31$; Mann-Whitney U-test).

As indicated in Fig. lb (black bars), and consistent with the significantly lower magnitude of the responses to stimuli presented via the Y-blocked eye, most binocular cells in our sample were class 4 cells, that is, they were dominated by the ipsilateral (normal) eye (31/61; 51%) with less than a quarter of the cells (13/61; 21.5%) dominated by the contralateral (Y-blocked) eye (class 2 cells). Furthermore, a substantial proportion of cells (6/61; 1O%) were monocular class 5 cells, that is, they could be activated exclusively by stimuli presented via the ipsilateral (normal) eye. This result contrasts sharply with the distributions of eye dominance classes in the sample of the SC cells recorded by us in normal cats [61 where there was a complete absence of monocular class 5 cells, only a small minority of cells (5/58; 8.5% of the sample) was dominated by the ipsilateral eye (class 4 cells), over a third of the sample (20/58; 34%) was dominated by the contralateral eye (class 2 cells) and there was a substantial proportion (8/58; 14%) of monocular class I cells, that is, cells which could be exclusively activated via the contralateral eye (Fig. lb, white bars). Not surprisingly, the difference in distributions of the eye dominance classes between the normal and the Y-blocked cats is highly significant ($p = 0.0001$; χ^2 test).

Velocity sensitivity: Despite the fact that in normal cats binocular SC cells are frequently dominated by the contralateral eye (class 2 cells, Fig. 1b) both the median optimal velocities (10˚/s) and the median upper cut-off velocities (400˚/5) were the same for the stimuli presented via the contralateral and the ipsilateral eyes (insets in Fig. 2a,b) and there were no significant differences between the eyes in the optimal ($p = 0.44$; Wilcoxon test) or upper cut-off velocities ($p > 0.2$; Wilcoxon test).

In Fig. 2a the optimal velocities for stimuli presented via the contralateral (Y-blocked) eye are graphed against the optimal velocities for stimuli presented via the ipsilateral (normal) eye. Although the median optimal velocity for stimuli presented via the normal eye at 15˚/s was higher than that (10^0/s) for stimuli presented via the Y-blocked eye, the difference was not statistically significant ($p > 0.5$; Wilcoxon test).

By contrast, the ability of the SC neurons to respond to stimuli moving at high velocity (exceeding 200˚/5) appeared to be substantially impaired when the stimuli were presented via the Y-blocked (contralateral) eye (Fig. 2b; Fig. 3a—c). Thus, while the clear majority of the binocular SC cells in our sample (24/41; 58.5%), exhibited upper cutoff velocities exceeding 200˚/s when stimulated via the normal eye, a substantial majority of these neurons (30/41; 73%) did not respond to the stimuli moving at velocities exceeding 2000/s when stimulated via the Y-blocked eye (Fig. 2b; Fig. 3a—c). Furthermore, all six monocular class 5 cells in our sample responded well to stimuli moving at the velocities exceeding 200˚/s. Indeed, the median upper cut-off velocities for photic stimuli presented via the Yblocked and normal eye were respectively 75˚/s and 300˚/s and the difference is highly significant ($p < 0.0001$; Wilcoxon test).

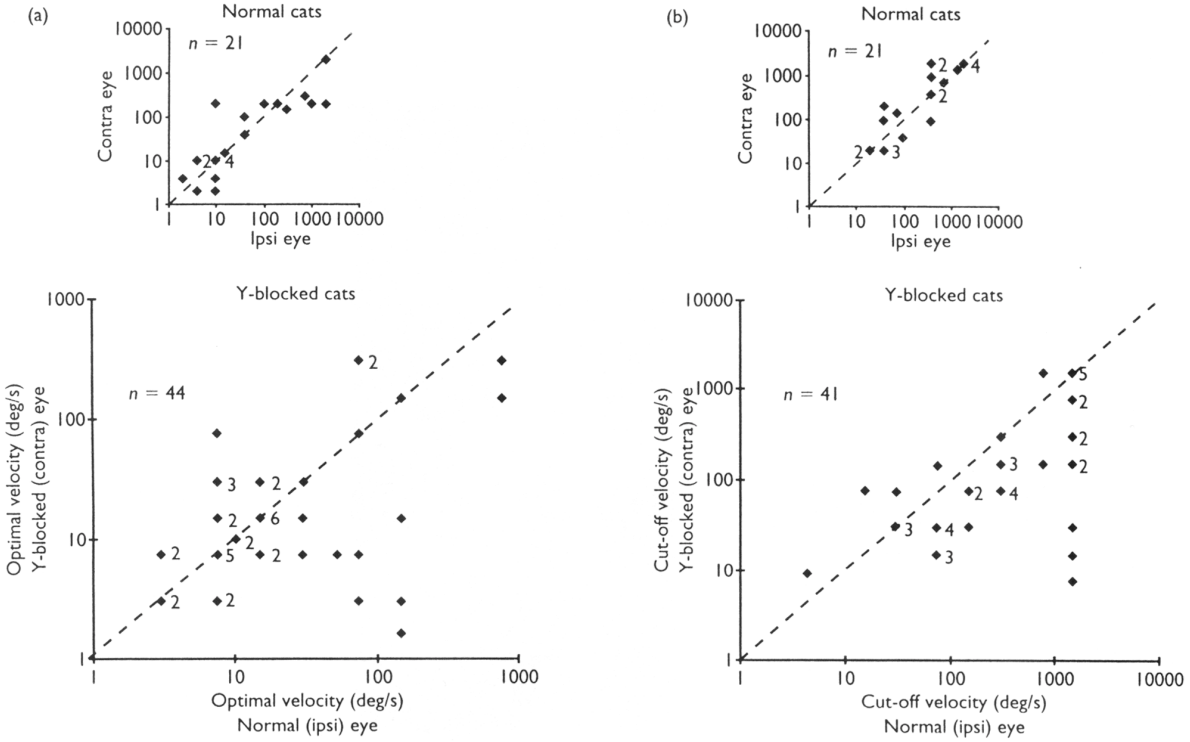

Fig. 2. Velocities of binocular neurons recorded from the SC of normal cats (insets) and cats in which the contralateral optic nerve has been Y-blocked. Velocities determined via the contralateral eye are graphed (in logarithmic scale) against the velocities determined via the ipsilateral eye. (a) Preferred velocities. Note that in normal cats (inset data collected earlier in our laboratory) preferred velocities for stimuli presented through either eye tend to be the same ($p = 0.44$; Wilcoxon test). Note also that in the cats with Y-blocked contralateral eye there is a greater scatter of preferred velocities for stimuli presented via each eye than in the normal cats. Nevertheless, the differences in the optimal velocities were not statistically significant ($P > 0.5$; Wilcoxon test). (b) Upper cut-off velocities. Note that in normal cats (inset data collected earlier in our laboratory) upper cut-off velocities for stimuli presented through either eye tend to be the same ($P > 0.2$; Wilcoxon test). By contrast, in cats with the Y-blocked contralateral optic nerve the upper cut-off velocities for stimuli presented via the contralateral eye are substantially and significantly ($p < 0.0001$; Wilcoxon test) lower than those for the stimuli presented via the normal ipsilateral eye. The numbers attached to some points in all graphs indicate several values at those points.

Velocity profiles: As in our previous study [6] we distinguished several classes of collicular neurons on the basis of the velocity profiles of their responses to visual stimuli, The contribution of the Y channel to responsiveness to fast-moving (>200˚/s) stimuli was especially apparent in cells which when stimulated via the normal (ipsilateral) eye did not respond to slowly moving (<20˚/s) stimuli but gave clear-cut excitatory responses to moderate (50-100˚/s) and high (200—2000˚/s) velocities. These high-velocity excitatory cells (HVE cells; 7% of cells in sample in ref. [6]) constituted almost 10% of the present sample (5/51). Three of the HVE cells were monocular class 5 cells while the remaining two although binocular, were class 4 cells, that is, they responded more strongly to the stimuli presented via the ipsilateral, normal eye. Both class 4 HVE cells exhibited much lower cut-off velocities (200˚/s) when stimulated via the Y-blocked contralateral eye (Fig. 3a,b).

The contribution of the Y-channel to responsiveness to fast-moving stimuli was also apparent in cells which gave clear-cut excitatory responses over the entire range of stimulus velocities employed by us (l—2000˚/s). When stimulated via the normal, ipsilateral eye these low velocity excitatory/high velocity excitatory cells (LVE/HVE cells in ref. [6]) constituted over a quarter of our sample (14/51; 27.5%; 26% of the sample in ref. [6]). Half of the LVE/HVE cells (7/14) exhibited substantially lower upper cut-off velocities when stimulated via the contralateral, Y-blocked eye (Fig. 3c). Furthermore, one LVE/HVE cell was a monocular class 5 cell.

We also recorded two cells (2/51; 4%) which were excited by the slowly moving (2-10˚/s) bars, responded poorly to stimuli moving at moderate (20—50˚/s) velocities, while fast-moving (>100˚/s) stimuli evoked purely suppressive responses. Both of these low velocity excitatory! high velocity suppressive cells (LVE/HVS; 17% of the sample in ref. [6]) were monocular class 5 cells.

The majority of the cells in the present sample (30/51; 59%) when stimulated via the normal eye could be classified as LVE cells since they gave strongest excitatory responses at stimulus velocities not exceeding 40˚/s and responded poorly, if at all, at velocities > 200˚/s. LVE cells constituted 48% of cells in the sample of Waleszczyk *et al.* [6]. Although the principal visual input to the LVE cells is likely to originate from the W-channel [6] in the substantial

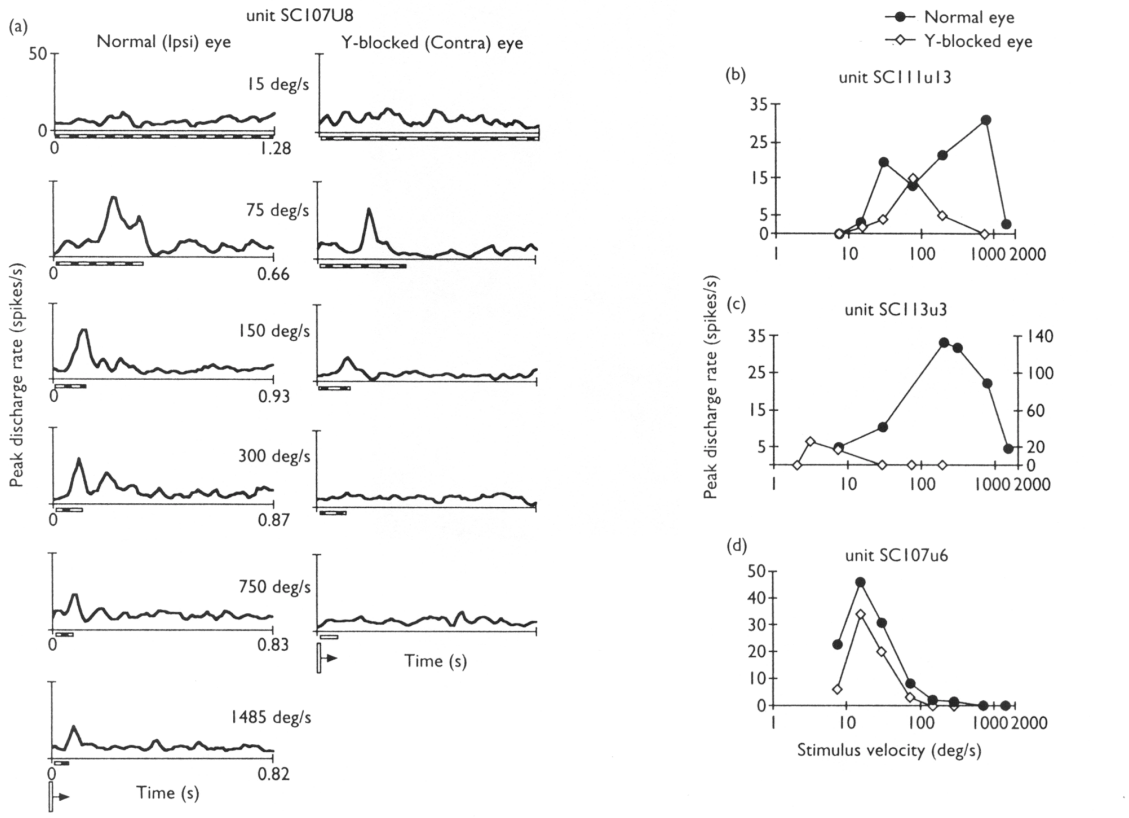

Fig. 3. (a) Peristimulus time histograms (PSTHs) of responses of a binocular direction-selective HVE neuron recorded from the SC of a cat with Y-blocked contralateral optic nerve. In each histogram the stimulus (a vertically oriented 6 X 1˚ light bar) moves from left to right across the cell's receptive field (icons beneath the bottom histograms). The velocity of movement of the bar is indicated above each histogram. The bar moves only during the time indicated by the filled rectangles beneath the histograms and then remains stationary for 400 ms (at 75˚/s) or 800 ms (at velocities >100^0/s) outside the receptive field before moving back in the opposite direction (not indicated). The period of time necessary to complete single sweeps (in one direction) plus delays is indicated on the right of each histogram. Each PSTH was compiled from responses to 20—100 successive stimulus sweeps (number of sweeps related positively to stimulus velocity) at each test condition. Note that irrespective of the eye through which the stimuli were presented the cell did not give a clear response to stimuli moving at 15˚/s. Note also that the cell responded well to fast-moving stimuli presented via the normal ipsilateral eye but did not respond to stimuli moving at velocities > 150˚/s when stimulated via the Y-blocked, contralateral eye. (b) Graphs of the velocity response (peak discharge rates) curves for another binocular HVE cell. Note that when stimulated via the normal eye this cell responds clearly to stimuli (vertically oriented 6.5 X 1˚ light slits) moving at velocities in the range of 40 to almost 2000˚/s but does not respond to stimuli moving at velocities > 300˚/s when stimuli are presented via the Y-blocked eye. (c) Graphs of the velocity response curves of a binocular collicular neuron which exhibits excitatory responses over a wide range of velocities when the stimuli are presented via the normal eye (LVE/HVE cell) but responds only to slowly moving (< 10˚/s) stimuli (vertically oriented 3.8 X 0.5˚ light slits) when they are presented via the Y-blocked eye. Note different scales for the responses to stimuli presented via Y-blocked eye (left scale) and those to stimuli presented via the normal eye (right scale). (d) Graphs of the velocity response curves of binocular collicular neuron which irrespective of the eye through which the stimuli (horizontally oriented 3 X 1˚ light slits) are presented exhibits strong excitatory responses to stimuli moving at low and moderate velocities but no responses to fast-moving stimuli (LVE cell). Note however that the upper cut-off velocity is lower when the stimuli are presented via the Y-blocked eye.

majority (21/30; 70%) of LVE cells in the present sample, the upper cut-off velocities for stimuli presented via the Y-blocked eye were lower than those for stimuli presented via the normal eye (Fig. 2b, Fig. 3d). Indeed, for the entire sample of LVE cells the difference in upper cut-off velocities for stimuli presented via the normal eye (median upper cut-off velocity 100˚/s) and those presented via the Y-blocked eye (median upper cut-off velocity 50˚/s) was highly significant (p = 0.0003; Wilcoxon test).

The size of the discharge fields and direction selectivity: Although for many binocular SC neurons the sizes of the discharge fields revealed by photic stimulation through each eye could be quite different, the mean size of the discharge fields mapped via the normal (ipsilateral) eye (44.6deg^2 ± 7.7; n=45) was not significantly different (p 0.54; Wilcoxon test) from that (38.2deg^2 ± 5.7; *n* = 45) of the discharge fields mapped via the Y-blocked eye.

There was also no significant difference (p = 0.52; Wilcoxon test) in the mean direction selectivity indices (MDI; see Materials and Methods) of responses to stimuli presented via the Y-blocked eye (0.44 + 0.04) and those for stimuli presented via the normal eye (0.45 ± 0.04). Furthermore, for the binocular HVE/LVE and HVE cells which

responded poorly or not at all to fast-moving stimuli presented via the Y-blocked eye and thus presumably lost their Y input from the Y-blocked eye, the MDI for stimuli presented via the Y-blocked eye (0.58 ± 0.11) was not significantly different ($p = 0.91$; $n = 9$; Wilcoxon test) from that (0.56 ± 0.12) for stimuli presented via the normal eye.

DISCUSSION

In the present study we have found that, unlike normal cats, in the cats with a Y-blocked contralateral optic nerve a substantial proportion (almost 10%) of collicular neurons could be activated exclusively via the ipsilateral eye (monocular, class 5 cells). The majority of binocular collicular cells were class 4 cells, that is, they responded more strongly to the stimuli presented via the ipsilateral eye and the median upper cut-off velocity for stimuli presented via the Y-blocked eye was substantially and significantly lower than that for the stimuli presented via the normal eye.

The lack of a significant effect of blockade of the Y-input on the direction selectivity of the SC cells appears to be in conflict with results obtained by Crabtree and his colleagues [16], who reported that the percentage of collicular cells exhibiting strong directional preferences was dramatically reduced following binocular injections of high dosages of antibodies raised against large (Y-type) retinal ganglion cells (RGCs). The discrepancy might be related to the fact that our measure of the direction selectivity indices was a graded one whereas that used by Crabtree and his colleagues [16] was all-or-nothing (cells were defined as directionally selective if they gave a response to movement in one direction that was at least twice as great as the response to movement in the opposite direction). Furthermore, in view of the fact that even after binocular injections of high doses of the antibodies against the large RGCs about a quarter of collicular cells exhibited strong directional preferences [116] we conclude that the direction selectivity of SC cells is not critically dependent on the Y-type input.

Evidence for parallel information channels in superior colliculi: Consistent with previous studies of the SC in normal cats [1—6,17], only a minority of the SC cells recorded in the present study exhibited strong responses to fast-moving ($>200^0$/s) stimuli presented via the normal eye and thus presumably receive strong Y-type input [1,6]. However, most of these cells (HVE cells and LVE/HVE cells in ref. [6]), either could not be activated by stimuli presented via the Y-blocked eye (monocular, class 5 cells) or responded poorly to fast-moving stimuli. The fact that all but two HVE cells in the present sample were monocular cells activated exclusively through the normal eye, is consistent with our previous suggestion [6] that these cells receive their principal excitatory input through either eye from the Y-channel. It is also worth pointing out in this context that the percentage of SC cells responding to fast-moving stimuli was dramatically reduced in cats in which high dosages of antibodies raised against large (Y-type) RGCs were injected into both eyes [16].

Evidence for convergence of different information channels: Convergence of Y- and non-Y-channels on single SC cells is clearly indicated by the fact that although most LVE/HVE cells in our sample were binocular, many of them responded poorly to fast-moving stimuli presented via the Y-blocked eye. The presence of a substantial proportion of LVE/HVE cells responding well to fast-moving stimuli presented via either eye might be related to the incompleteness of the Y-block in all but two of the cats tested by us. Indeed, in these two cats all LVE/HVE cells responded poorly to fast-moving stimuli presented via the Y-blocked contralateral eye. Furthermore, although the clear majority of binocular SC cells which when stimulated via the normal eye, responded only to stimuli moving at low to moderate velocities (25/41; 61.0%; LVE cells in ref. [6]), a proportion of such cells exhibited substantially lower peak discharge rates and lower upper cut-off velocities when stimulated via the Y-blocked eye. Indeed, for our sample of the binocular LVE cells we found that the peak discharge rates of the responses to stimuli presented via the normal (ipsilateral) eye were significantly higher *($p=O.02$)* than those to stimuli presented via the Y-blocked (contralateral) eye. This result seems to argue against our earlier suggestion [6] that LVE neurons do not receive excitatory input from the Y channel. However, although virtually all collicular cells which receive Y-type input directly from the retina appear to respond well to fast-moving visual stimuli [1] the absence of responses to fast-moving visual stimuli does not necessarily imply the absence of Y-type input [1,11]. Thus, at least some of the LVE cells, might receive a small proportion of their input from the Y channel. This input by itself might he subthreshold and not able to generate discharges to fast-moving stimuli. Furthermore, about 10% of collicular cells which receive Y-type excitatory input not directly from the retina but rather via the retino-geniculo-cortical relays [1,4,5] do not respond to fast-moving stimuli [1,16]. Consistent with this, 20—25% of cells in areas 17 and 18 of cat primary visual cortices which receive excitatory Y-type input (as indicated by the high conduction velocities of their retinogeniculate afferents) responded poorly to photic stimuli moving at velocities >100°/s [11]. This poor responsiveness to fast-moving stimuli of some cortical neurons receiving Y-type excitatory input might be related to the fact that 40% of layer V cells recorded from area 17 (and presumably projecting to the SC; for reviews see [5,18,19]) responded to high-velocity visual stimuli only after inactivation of visuotopically corresponding parts of layer V of area 18 [20].

CONCLUSION

In the present study we have demonstrated that contrary to previous claims, in the cat a substantial proportion of the SC cells receives excitatory convergent inputs from Y-type and non-Y-type (presumably mainly W- type) channels. In the SC cells receiving convergent Y-type and non Y-type excitatory inputs the direction selectivities are not determined by the Y-inputs. Good responsiveness of collicular cells to fast-moving visual stimuli, like that of the cortical neurons [see for review 9] appears to be invariably dependant on the presence of a Y-type excitatory input to the cell. However, it is possible that a substantial proportion of the SC cells which do not respond well to fastmoving visual stimuli receive Y-type retinal input via the geniculo-cortical relays.

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