VELOCITY RESPONSE PROFILES OF COLLICULAR NEURONS: PARALLEL AND CONVERGENT VISUAL INFORMATION CHANNELS

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Abstract—We have recorded from single neurons in the retinorecipient layers of the superior colliculus of the cat. We distinguished several functionally distinct groups of collicular neurons on the basis of their velocity response profiles to photic stimuli. The first group was constituted by cells responding only to photic stimuli moving at slow-to-moderate velocities across their receptive fields (presumably receiving strong excitatory W-type input but not, or only subthreshold, Y-type input). These cells were recorded throughout the stratum griseum superficiale and stratum opticum and constituted 50% of our sample. The second group of cells exhibited excitatory responses only at moderate and fast velocities (presumably receiving excitatory Y-type but not W-type input). These cells constituted only about 7% of the sample and were located principally in the lower stratum griseum superficiale. The third group of cells was constituted by cells excited over the entire range of velocities tested (1 — 200°/s) and presumably received substantial excitatory input from both W- and Y-channels. These cells constituted almost 26% of our sample and were located in the lower stratum griseum superficiale, stratum opticum and the upper part of the stratum griseum intermediale. Overall, cells receiving excitatory Y-type input, i.e. the sum of group two and group three cells, constituted about a third of the sample and their excitatory discharge fields were significantly larger than those of cells receiving only W-type input. A fourth distinct group of collicular neurons was also constituted by cells responding over a wide range of stimulus velocities. These cells were excited by slowly moving stimuli, while fast-moving photic stimuli evoked purely suppressive responses. The excitatory discharge fields of these cells (presumably, indicating the spatial extent of the W-input) were located within much larger inhibitory fields, the extent of which presumably indicates the spatial extent of the Y-input. These low-velocity-excitatory/high-velocity-suppressive cells were recorded from the stratum griseum superficiale, stratum opticum and stratum griseum intermediale and constituted about 17% of the sample. The existence of low-velocity-excitatory/high-velocity-suppressive cells in the mammalian colliculus has not been previously reported. Low-velocity-excitatory/high-velocity-suppressive cells might play an important role in activating “fixation/orientation” and “saccade-” premotor neurons recorded by others in the intermediate and deep collicular layers. Overall, in the majority (57%) of collicular neurons in our sample there was no indication of a convergence of W- and Yinformation channels. However, in a substantial minority of collicular cells (about 43% of the sample) there was clear evidence of such convergence and about 40% of these (low-velocity-excitatory/high-velocity-suppressive cells) appear to receive excitatory input from the W-channel and inhibitory input from the Y-channel. © 1999 IBRO. Published by Elsevier Science Ltd.

Key words: cat’s superior colliculus, excitatory responses, suppressive responses, superficial and intermediate layers, parallel channels, convergence of W- and Y-channels.

The superior colliculus (SC), the principal retinorecipient nucleus of the mammalian mesencephalon, plays an important role in the selection of targets for visually guided behaviour, integration of sensory information and initiation of goal-directed orientation responses towards novel sensory stimuli (for reviews see Refs 81, 82 and 93). The superficial layers of the SC (stratum zonale; stratum griseum superficiale, SGS; and stratum opticum, SO) receive massive visual inputs which originate either directly in the retinas or are relayed mainly, but not exclusively, via the dorsal lateral geniculate nuclei (LGNd) and a number of visual cortical areas, again mainly but not exclusively in the ipsilateral hemisphere (for reviews see Refs 34, 42 and 82). In the cat, the species in which the connectional and functional organization of the superficial collicular layers has been studied most thoroughly, these layers receive their direct retinal input from only two (the so-called W- and Y-channels) of the three principal parallel information channels present in the visual system of this species. 11,14,20,38,52,71,83,87 The W-type retinal ganglion cells (RGCs), especially the W-2 subtype, which provide the principal retinal input to the SC, 9,12,35 may be involved in the detection of local motion in the environment but respond poorly or not at all to fast-moving photic stimuli, 18,19,50,57,88 Although Y-type RGCs, like the W-2 subgroup of the RGCs, are presumed to be mainly involved in processing information about motion, unlike W-cells they exhibit good responsiveness to photic stimuli moving at high velocities and poor responsiveness to slowly moving photic stimuli. 18,32,50,59 There is very little overlap in the laminar distribution of W-type and Y-type retinotectal terminals. 11,28,38,55,77,87 Furthermore, although there is a strong excitatory convergence on single collicular neurons of retinal W-type input and corticotectal input from the primary visual cortices, only a small proportion of collicular neurons which receive W-type retinal input also receives Y-type input via the corticotectal projection. It is not clear therefore to what extent, if any, the convergence of retinal and corticotectal inputs onto single collicular neurons represents the convergence of different visual information channels. Indeed, despite clear-cut differences in the receptive field properties of W-type and Y-type RGCs (especially in the velocity sensitivity profiles) it has been claimed in numerous studies that

Abbreviations: HVE, high-velocity-excitatory cells; HVS, high-velocity-suppressive; LGNd, dorsal lateral geniculate nucleus; LGNv, ventral lateral geniculate nucleus; LP, lateral posterior nucleus; LyE, low-velocity-excitatory cells; RGCs, retinal ganglion cells; RRZ, retinorecipient zone of the pulvinar; SC, superior colliculus; 5g. suprageniculate nucleus; SGI, stratum griseum superficiale; SO, stratum opticum.
the receptive field properties of collicular neurons throughout the retinorecipient layers are rather homogeneous (for review see Ref. 82).

It has been shown recently that contrary to previous assertions there is a substantial degree of excitatory convergence of different information channels in different visual cortical areas of mammals with well-developed visual systems such as cats and macaque monkeys (for review see Ref. 16). In the present study, in order to assess the proportion of collicular neurons in which there is convergence (or lack of convergence) of different visual information channels we have examined quantitatively the velocity response profiles of single neurons in the retinorecipient layers of the cat’s SC to photic stimuli. Our results indicate that in almost half of the collicular neurons there is a detectable convergence of different visual information channels.

A preliminary report of this work has been published in abstract form.26

EXPERIMENTAL PROCEDURES

Animals, anesthesia and surgical procedures

All efforts were made to minimize animal suffering and to reduce the number of animals used. Experiments adhered strictly to the guidelines of the National Health and Medical Research Council of Australia and all procedures were approved by the Sydney University Animal Care and Ethics Committee. Five adult, normally pigmented, female cats weighing from 2.2 to 3.5 kg were provided by the Laboratory Animal Services of the University of Sydney. The initial surgery which included intraventricular and tracheal cannulation, bilateral cervical sympathectomy and craniotomy was carried out under 1.5% halothane in N20/02 (67%/33%) gaseous mixture. During the recording sessions, the animals were paralysed with gallamine triethiodiate at the rate of 7.5 mg/kg/h in a mixture of equal parts of 5% dextrose and sodium lactate (Hartmann’s) solutions and artificially ventilated. Anaesthesia was maintained with a gaseous mixture of N20/02 (67%/33%) and halothane (0.5%). Expired CO2 was maintained at 3.7–4.0% by adjusting the rate of the pulmonary pump. Body temperature was maintained at about 37.5°C. Heart rate and electroencephalogram were monitored continuously. Each day antibiotic (amoxycillin trihydrate, 75 mg), dexamethasone phosphate (4 mg) and atropine sulphate (0.3 mg) were injected intramuscularly. Antibiotic (amoxycillin trihydrate, 75 mg), dexamethasone phosphate (0.5%) and halothane (0.5%) were injected intravenously.

The corneae 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. Correcting lenses were used, if required, to focus the eyes on a tangent screen located 57 cm in front of eyes. The locations of the optic discs and the areae centrales were plotted daily using a fibre-optic projector.

Recording

Craniotomy for recording the activity of single neurons in the superior colliculus was made at Horsley-Clarke coordinates P2-A4 and L0-5. A plastic cylinder was mounted around the opening and glued to the skull with dental acrylic to form a well around the hole. A small opening in the dura was made above the recording site. A plastic cylinder was mounted around the opening and glued to the skull with dental acrylic to form a well around the hole. A plastic cylinder was mounted around the opening and glued to the skull with dental acrylic to form a well around the hole. A plastic cylinder was mounted around the opening and glued to the skull with dental acrylic to form a well around the hole. Artificial pupils, 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. Correcting lenses were used, if required, to focus the eyes on a tangent screen located 57 cm in front of eyes. The locations of the optic discs and the areae centrales were plotted daily using a fibre-optic projector.

Photic stimulation and data analysis

The excitatory receptive fields (discharge fields) of recorded units were first plotted with a hand-held light slit projector and remapped with hand-held black bars and spots. The size of the excitatory discharge field was defined as the area of visual space within which moving bars, lighter or darker than the background elicited an increase in the cell’s firing rate which was detectable by ear.21 The positions and dimensions of receptive fields were corrected for tangential distortion. The relative magnitude of the responses to photic stimuli presented separately through either eye (ocular dominance class) was evaluated quantitatively by the analysis of the peristimulus time histograms3 Computer-controlled light slits or spots from a slide projector, used for studying, quantitatively, the properties of the receptive fields. had a luminance of 15 cd/m2/m2 against a background luminance of 0.9 cd/m2/m2. The peristimulus time histograms were usually constructed by summing the responses to 30 successive stimuli sweeps at each test condition. The temporal base of each histogram 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 (see Figs 2, 3, 4, 6, 7). The responses were then smoothed using a Gaussian weighted average over five neighbouring bins. The smoothed values were used for peristimulus time histograms and evaluation of the peak discharge rates.

Localization of recording sites

At the end of long penetrations microlesions were made with 20 µA current passing through the microelectrode for 20 s (electrode negative). At the end of the recording session (lasting four to six days) the animal was deeply anaesthetized with an intravenous injection of 120 mg of sodium pentobarbionate and perfused transcandially with warm (37°C) Hartmann’s solution followed by a 4% solution of paraformaldehyde in 0.1 M phosphate buffer (pH 7.4). The midbrains were stereotaxically blocked and sectioned coronally at 50–100 µm. Artificial pupils, 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. Correcting lenses were used, if required, to focus the eyes on a tangent screen located 57 cm in front of eyes. The locations of the optic discs and the areae centrales were plotted daily using a fibre-optic projector.

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The corneae 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. Correcting lenses were used, if required, to focus the eyes on a tangent screen located 57 cm in front of eyes. The locations of the optic discs and the areae centrales were plotted daily using a fibre-optic projector.

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Statistics

Statistical significance of differences between different groups of cells was assessed using non-parametric tests: the Mann—Whitney U-test or χ2-test.80 Statistical differences were considered significant when P at two-tailed criterion was 0.05 or less.

RESULTS

Binocular and spatial characteristics of collicular neurons

All our electrode penetrations were through the central part of the SC where, in the superficial layers at least, the binocular part of the visual field is represented (Fig. 1A; see Refs 9, 27 and 49). Consistent with this, as indicated in Fig. 1B, the great majority of cells (50/58; about 86%) in our sample were binocular cells, that is, they could be activated by stimuli presented via either eye. All monocular cells (8/58; about 14%) in our sample could be activated by photic stimuli presented via the contralateral, but not the ipsilateral, eye (class I cells). Furthermore, the majority of binocular cells was either dominated by the contralateral eye (class 2 cells) or responded equally well to photic stimuli presented through either eye (class 3 cells). Thus, the eye dominance distribution in our sample is very similar to those reported in previous studies of the cat’s collicular visual neurons, with receptive fields located within the binocular part of the visual field (see Refs 4, 9, 20, 36, 38, 56, 79 and 85). For all binocular cells the velocity response profiles were virtually the same irrespective of the eye through which the stimuli were presented.

Consistent with numerous previous reports27–38 all neurons but one in our sample were characterized (at least at some velocities, see further) by the presence of excitatory discharge regions in their receptive field. Thus, as the narrow slit of light (or a light spot of small diameter) crossed the
excitatory discharge region there was a clear increase in the cell’s firing rate (Figs 2A, B, C, 3B, D, F, 4B, D, F). This increase in firing rate often consisted of a single peak in the peristimulus time response histogram (Fig. 2A and B, top and bottom histograms, respectively; Figs 3B, D, F, 4B, D, F). For most cells, however, at least at certain stimulus velocities, the peristimulus time response histograms comprised two or more distinct peaks (Figs 2B, C, 4F; see Ref. 22) suggesting that there were several discharge subregions that were partly or completely separated from one another.

Most cells in our sample exhibited a degree of direction selectivity, that is, they responded more vigorously to stimuli moving across their receptive field in one (preferred) direction than to stimuli moving in the opposite direction. However, for a given cell the degree of direction selectivity was usually velocity-dependent (Figs 2A, B, C, 3D, 4D, F; see Refs 22, 56, 85 and 89). Furthermore, at a given velocity some cells exhibited a substantial degree of direction selectivity only when short stimuli, not extending beyond the excitatory discharge region, were applied (Fig. 3B, D) but not when the photic stimuli extended well into the parts of the suppressive regions of cells responding poorly to fast-moving stimuli (Fig. 3F; see Refs 22, 36 and 85). Indeed, in all neurons constituting this group (28/58 cells, about 48% of our sample) light bars much shorter than the width of the excitatory discharge region evoked stronger responses than stimuli approximating the width of the excitatory discharge region (Fig. 3B; G; see Refs 22, 36 and 85).

Low-velocity-excitatory (LVE) cells responded well (as indicated by a substantial increase in firing rate) to short-to-medium size (1–6”) bars moving at slow-to-moderate (1–100/s) velocities, but poorly, if at all, to fast-moving short or long bars or spots (over 100/s; Figs 2A, D, 3B, C, D, F, G). Furthermore, most of the LVE cells (23/28 about 82%) gave their strongest responses to short bars, or small diameter spots, moving at velocities not exceeding 100/s (Figs 2A, D, 3D, G, 5A). Indeed, the mean preferred velocity for LVE cells was 9.60/s (± 8.80/s). Consistent with the velocity—response profiles based classification of neurons in the mammalian visual cortex developed by Orban we have found that LVE collicular cells could be classified as either velocity-low-pass (14/27; 52%) or low-velocity-tuned (13/27; 48% of the sample). In several earlier studies of single neurons in the superior colliculus of the cat (see Refs 22, 78 and 79) cells with very similar velocity—response profiles constituted the majority of cells recorded from the superficial layers.

As indicated in Fig. SB, LVE cells were characterised by: (i) low “spontaneous” activities (mean 1.3 spikes/s; range 0—6 spikes/s; see Ref. 22); and (ii) low-to-moderate peak discharge rates (mean 19.7 spikes/s; range 5—47.2 spikes/s). Furthermore, as indicated in Fig. SC, the excitatory discharge regions of cells responding poorly to fast-moving stimuli tended to be relatively small (mean area 42.9±46.2 deg² mean diameter 6.0±3.0 deg).

Finally, LVE cells constituted the majority of cells (17/25; 68%) recorded from the SGS and a large minority of cells (11/28; about 39%) recorded from the SO (Fig. 9).

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**Cells responding only at low to moderate velocities**

**Low-velocity-excitatory cells.** These cells gave their strongest excitatory responses at stimulus velocities not exceeding 40°/s. They invariably appeared to have strong suppressive regions in their receptive fields, at least partly overlapping with the excitatory discharge regions and
Fig. 2. Patterns of discharges of collicular neurons to photic stimuli moving at different velocities. In A, B and C are shown peristimulus time histograms for three neurons. In each case only the responses to stimuli presented via the dominant eye are presented. In each histogram the stimulus (a light bar) moves forwards and backwards across the receptive field. The angle of the bar and the direction of movement are indicated beneath the bottom histogram. 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 40°/s and 100°/s) or 800 ms (at velocities >100°/s), outside the receptive field before moving back in the opposite direction (right half of each histogram). The period of time necessary to complete single forward and backward sweeps plus delays is indicated on the right of each histogram. Each peristimulus histogram was compiled from responses to 30 successive stimulus sweeps. In D are shown the graphs of peak response vs velocity for three LVE cells. These cells (including the cell whose responses are illustrated in A) are low-pass or low-velocity-tuned cells (see Ref. 68). In E are shown the graphs of peak response vs velocity for three cells which respond only at moderate and high velocities but not at low velocities. These cells (including the cell whose responses are illustrated in B) are velocity high-pass (HVE) cells (see Ref. 68). In F are shown the graphs of peak response vs velocity for three cells which respond over a wide range of velocities. These cells (including the cell whose responses are illustrated in C) are velocity broad-band (LVE/HVE) cells (see Ref. 68). In D, E and F the responses have been corrected for “spontaneous” activity, the levels of which are indicated by the horizontal lines through the symbols at the bottom right of each graph. All the graphs in D, E and F are based on the responses to stimuli presented via the dominant eyes.

“Suppressed-by-contrast” cell. One of the cells in our sample had a relatively high spontaneous firing rate (22 spikes/s) which was always reduced, rather than increased, by the introduction into the receptive field of any sort of photic stimulus (stationary flashing light spots or slits, slowly or moderately but not fast-moving light or dark spots or bars). This cell was recorded from the border of the SGS and SO (Fig. 9) and responded only to photic stimuli presented via the contralateral eye.

High-velocity-excitatory cells

A small number of the cells which constituted this group (4/58; about 7% of the sample) did not respond to slowly (1-10°/s) moving photic stimuli but exhibited clear-cut excitatory responses at moderate (20-40°/s) and high velocities (100-2000°/s; Fig. 2B, E). These cells did not exhibit strong suppressive regions within and/or around the excitatory discharge regions and could be classified as velocity high-pass cells (see Ref. 68). High-velocity-excitatory (HVE) cells were recorded from the lowest part of the lower SGS or from the SO (Fig. 9).

Low-velocity-excitatory/high-velocity-excitatory cells

Cells constituting this group (15/58; about 26% of the sample) gave clear-cut excitatory responses over a very wide range of stimulus velocities employed by us 1-2000°/s; Fig. 2C, F). Although some of these cells were tuned for
Convergence of channels in superior colliculus

Fig. 3. Characteristics of LVE cells. A and E show outlines of the excitatory discharge fields for two LVE neurons, units 104.17 and 104.16, respectively. Note that the nearest border of the excitatory discharge field of cell 104.17 (A) is located about 50° from the area centralis (AC, center indicated by 0) while the excitatory discharge field of cell 104.16 (E) encompasses the area centralis (AC, center indicated by ®). B shows peristimulus time histograms of responses of unit 104.17 to light bars of different length moving at 40°/s across the cell’s receptive field. The peak discharge rates of unit 104.17 to bars of different length moving in the preferred direction at 4°/s across the cell’s receptive field are graphed in C. Note that responses illustrated in B and C are strongest for the shortest bar (1.2° length x 1° width) and progressively weaken as the bar is lengthened until at a length of 120° (10 width) the response disappears. Note also that responses to the shorter bars (1.20 and 30) are clearly direction selective while those to longer bars are not. The responses of cell 104.16 to a short bar (3°x1°) moving at progressively increased velocities (from 4°/s to 400°/s) are illustrated in D. The responses of the cell in D to a long bar (22°x1°) moving at progressively increased velocities are illustrated in F. The amplitudes of responses of unit 104.16 to narrow bars of different length (indicated) moving at different velocities are graphed in G. Note that at all velocities the responses of unit 104.16 are substantially weaker for the longer bars, and for both the short and long bars the response diminishes with increase in stimulus velocity. In each case only the responses to stimuli presented via the dominant eye are illustrated. For other details see legend of Fig. 2.

particular velocities (Figs 2C, F, 4D, F, G) in general these cells could be classified as velocity broad-band cells (see Ref. 68). In a significant proportion of cells constituting the third group, there were also strong suppressive regions within and/or around the excitatory discharge regions (Fig. 4). Nevertheless, all LVE/HVE cells gave clear-cut excitatory responses not only to fast-moving (100-2000°/s) short-to-medium (1-6°) bars (Fig. 4D, G) but also to fast-moving long (12-28°) bars (Figs 2C, F, 4F, C).

As indicated in Fig. 9, LVE/HVE cells were recorded mainly (12/15) from the SO and the deepest part of the SGS with only an occasional cell of this kind recorded from the upper part of the lower SGS or the uppermost part of the stratum griseum intermediale (SGI). The laminar distribution of LVE/HVE cells was significantly different from that of LVE cells (P<0.05; χ²-test).

Overall, the majority (12/19) of cells which were excited at high stimulus velocities (combined HVE and LVE/HVE cells) responded optimally at velocities exceeding 100°/s (Fig. 5A). Not surprisingly, the preferred velocities of cells excited at high velocities (mean 450±693°/s) were significantly (P<0.001; Mann—Whitney U-test) higher than those of LVE cells.

As indicated in Fig. 5B, HVE and LVE/HVE cells taken together were characterized by: (i) moderate-to-high spontaneous activities (mean 12.8 spikes/s; range 0.4—35 spikes/s; see Ref. 22); and (ii) moderate-to-high peak discharge rates (mean 74.8 spikes/s; range 10.3—165.2 spikes/s). Thus, cells responding to higher stimulus velocities differed significantly in these parameters from LVE cells (in either case P<0.0001; Mann—Whitney U-test). Furthermore, despite the fact that the receptive fields of cells responding at high stimulus velocities were located at the eccentricities not significantly different from those of the receptive fields of the LVE cells (P>0.12; Mann—Whitney U-test) the excitatory discharge regions of HVE and LVE/HVE cells (mean area 185.1±248.7 deg² mean diameter 11.7±7.5 deg) were significantly (P<0.002; Mann—Whitney U-test) larger than those of LVE cells (Fig. 5C).

Low-velocity-excitatory/high-velocity-suppressive cells

Cells constituting this group had rather unusual receptive field properties and as far as we know collicular neurons with such properties have not been described before. In particular: (i) presentation of slowly moving (2-10°/s) short-to-medium (2-6°) or long (12-28°) bars or small (2-4° in diameter) spots
revealed excitatory discharge regions in their receptive fields (Figs 6A, B, 7A, B, C); (ii) most of the cells responded poorly or not at all to photic stimuli moving across their receptive fields at moderate velocities (20–40°/s; Figs 6A, 7A, B); (iii) both long and short bars moving at high velocities (over 100°/s) evoked purely suppressive responses which tended to be non-direction selective (Figs 6A, B, C, D, 7B, C); (iv) photic stimuli moving slowly outside the excitatory discharge region did not evoke any responses (Fig. 6C and D upper histograms); (v) suppressive, but not excitatory, responses could be evoked by fast-moving stimuli which were positioned well outside the excitatory discharge regions (Fig. 6C and D, lower histograms); and (vi) while there could be some axis-of-movement preference in the excitatory responses to slowly moving stimuli (Fig. 7C, upper histograms) such preferences were not apparent in the suppressive responses to fast-moving stimuli (Fig. 7C, lower histograms).

As indicated in Figs SB, 6 and 7, LVE/high-velocity-suppressive (HVS) cells were characterized by moderate background activities (mean 11.0 spikes/s; range 7–17 spikes/s) and moderate peak discharge rates (mean 26.8 spikes/s; range 15–43.3 spikes/s).

Consistent with the fact that in all five cats we have recorded from the central part of the superior colliculi where in the superficial layers the central 20–25° of the visual field are represented (Fig. 1A, see Refs 9, 27 and 49) the excitatory discharge regions of a substantial proportion (3/10) of our LVE/HVS cells were centered or encroached on the area centralis (Fig. 8). Furthermore, the excitatory discharge regions of all our LVE/HVS cells were either centered or at least encroached on the vertical and/or horizontal meridians (Fig. 8).

The excitatory discharge regions of LVE/HVS cells were located at eccentricities not significantly different from those of the excitatory discharge regions of the LVE cells (P>0.7; Mann—Whitney U-test). Similarly, the sizes of the excitatory discharge regions of LVE/HVS cells (mean area 48.6±28.6 deg² mean diameter 6.8±2.3 deg) were not significantly different (P>0.3; Mann—Whitney U-test) from those of LVE cells (Figs 5C, 8). At the same time the suppressive regions had diameters six to eight times those of the excitatory discharge regions and invariably included a portion of the visual hemifield contralateral to the excitatory discharge regions (Figs 6, 7).

Cells constituting the LVE/HVS group (10/58; about 17% of the sample) were recorded in the deep SGS, SO or the upper part of the SGI (Fig. 9) of all five animals studied by us. However, one LVE/HVS cell was recorded above the deepest part of the SGS (Fig. 9).
Fig. 5. Properties of collicular neurons of different classes. (A) Percentage histogram of preferred velocities of LVE, HVE and LVE/HVE neurons. Note that while over 85% of LVE cells responded maximally at velocities not exceeding 100/s, only 20% of LVE/HVE cells responded maximally at such velocities. Note also that all HVE cells and over 53% of LVE/HVE cells responded optimally at velocities exceeding 1000/s. (B) Peak discharge rate to presumably optimal stimulus vs level of “spontaneous” activity. Note that cells with higher spontaneous activity tend to respond more strongly (higher peak discharge rates) to photic stimuli. Note also that LVE neurons exhibit very little or no spontaneous activity and tend to respond weakly (low peak discharge rates) to photic stimuli. (C) Excitatory receptive field areas of collicular neurons vs distance of the centre of the excitatory discharge region from the area centralis (AC). Note lack of clear correlation between the receptive field size and the distance from the AC. In each case the data are based on the responses to stimuli presented via the dominant eyes.

**DISCUSSION**

*Parallel information channels in superior colliculus.*

*Low-velocity-excitatory cells.* In view of the clear preference of LVE cells (constituting almost 50% of cells in our sample) for slowly moving stimuli and their lack of responsiveness for fast-moving photic stimuli, it appears that these cells receive their principal visual input from the W-channel and do not receive a significant excitatory input from the Y-channel. There are additional lines of evidence which support this conclusion. First, about 75% of collicular neurons which receive W-type input as indicated by the conduction velocity of their retinal afferents respond poorly or not at all to fast-moving photic stimuli moving at velocities exceeding 100/s. Second, all but three cells recorded from that part of the SGS where W-but not Y-type RGCs terminate (between 200 and 600 m from the collicular surface; Fig. 9), like W-type RGCs, not only responded poorly to fast-moving photic stimuli but had low spontaneous activities, low peak discharge rates and contained strong suppressive regions in their receptive fields.

Third, the velocity low-pass cells recorded from area 19 (which receive their principal thalamic input from the W-type cells) are also characterized by low spontaneous activities, low peak discharge rates and in most cases contained strong suppressive regions in their receptive fields (hypercomplex or end-stopped cells, see Refs 23, 41 and 68). Fourth, as mentioned in the introduction, although most, if not all, neurons in the SGS which receive W-type excitatory input from the retina receive also excitatory input from the visual cortex, this input is not of the Y-type. Fifth, although cells responding poorly to fast-moving photic stimuli were also encountered in the deeper part of the SGS and the SO which receive substantial Y-type retinotectal and corticotectal inputs, the receptive field properties of those cells were indistinguishable from those of their counterparts in the upper part of the SGS. Furthermore, the majority of morphologically identified neurons encountered in the deeper part of the SGS receive W-type but not Y-type inputs. Indeed, this finding is consistent with earlier findings of Berson that not all W-driven cells in the lower SGS and SO receive Y-type input.

In view of the fact that the excitatory discharge regions of collicular neurons with W-type excitatory input are substantially larger than those of W-type retinal ganglion cells, it appears that there is a substantial excitatory convergence of W-type RGCs on single collicular neurons. Since ablation of the ipsilateral visual cortices does not affect the size of the collicular excitatory discharge fields it is unlikely that the large size of the excitatory discharge fields of collicular cells reflects the convergence of corticotectal fibers.

However, a word of caution is needed here. Thus, lack of responsiveness to fast-moving photic stimuli does not necessarily imply that LVE cells receive only W-type excitatory input. First of all, in view of the fact that area 17 which is dominated by X-input (see Refs 23 and 86) provides strong
Fig. 6. Responses of a LVE/HVS cell. The hatched oval in the centre of the diagram shows the excitatory discharge field (ellipsoid hatched area) which is embedded in the much larger suppressive field (grey), the outer boundary of which has not been accurately determined. Note however that the suppressive field involves not only a large part of the visual field ipsilateral to the excitatory discharge field but also extends into the visual field contralateral to the excitatory discharge region. AC, area centralis; © indicates the center of the area centralis. (A) The peristimulus time histograms on the left show the responses to a long bar (20° x 1.2° moving forward and backward across the entire receptive field. Note the excitation at low velocities (4°/s and 10°/s) and a clear suppression at high velocities (100°/s or more) with virtually no response at the intermediate (40°/s) velocities. (B) A short light bar (about 40°, similar to the width of the excitatory discharge field) produces strong excitation at a low velocity (10°/s) and clear suppression at a high velocity (200°/s). (C and D) When the long bar is moved outside the excitatory discharge region there is no response at low velocities (10°/s) but again a clear suppression at high velocities (200°/s). As in Figs 2, 3 and 4 all illustrated responses are responses to stimuli presented via the dominant eye. As in Figs 2 and 3 in each case only the responses to stimuli presented via the dominant eye are illustrated. Other conventions as in Figs 2, 3 and 4.

non-Y corticotectal input to the superficial collicular layers it is very likely that LVE cells also receive some excitatory input from the X-channel. Second, lack of responsiveness to fast-moving photic stimuli does not necessarily imply that LVE cells do not receive any excitatory input from the Y-channel. Indeed, 20—25% of cells in the primary visual cortices of the cat (areas 17 and 18) which receive excitatory Y-type input as indicated by the conduction velocity of their retinogeniculate afferents respond poorly to photic stimuli moving at velocities exceeding 100°/s. Similarly, about 10% of collicular neurons which receive excitatory Y-type input via the ipsilateral visual cortex respond poorly to photic stimuli moving at velocities exceeding 100°/s. Furthermore, in 40% of layer V cells recorded from area 17 of the cat, blockade (with lignocaine) of visuotopically corresponding parts of layer V of area 18 revealed responses to high-velocity photic stimuli which were ineffective before the blockade.2

The suppressed-by-contrast cell recorded by us is strongly reminiscent of the W-type “suppressed-by-contrast” or “uniformity detectors” ganglion cells described in the cat’s retina. A few collicular cells with such properties have been reported previously (see Refs 22, 35, 36 and 38).

Taking into account the laminar distribution of collicular cells projecting to the cat’s dorsal and/or ventral lateral geniculate nuclei (LGNd and LGNv) and/or the retinorecipient zone of the pulvinar and the fact that geniculate cells in those regions which receive collicular input as well as cells in the retinorecipient zone of the pulvinar (RRZ) exhibit W-like properties (see for reviews Refs 30 and 86) it is likely that collicular neurons receiving W- but not Y-input project to the LGNd, LGNv and the RRZ.

High-velocity-excitatory cells. HVE cells which constituted about 7% of the sample appeared to receive Y-type but not W-type inputs. Unlike cells receiving only W-input these cells were characterized by: strong excitatory responses to fast-moving photic stimuli; poor, if any, responses to slowly moving photic stimuli; moderate-to-high spontaneous activity; moderate-to-high peak discharge rates; and absence of strong suppressive regions in their receptive fields. All these cells were located in the deep SGS or SO where there is a strong Y-type input coming directly from the retina and/or indirectly via the visual cortices. Indeed, it has been reported by Hoffmann that virtually all collicular neurons which receive Y-type input directly from the retina respond vigorously at stimulus velocities exceeding 200°/s. Again, a word of caution is needed here. Thus, despite the lack of responses to the slowly moving photic stimuli a subthreshold W-input to HVE cells is a distinct possibility.
Convergence of different information channels

Low-velocity-excitatory/high-velocity-excitatory cells. Over a third (12/34) of the cells recorded from the lower part of the lower SGS and SO as well as one cell recorded from the SGI and two cells recorded in the upper half of the lower SGS were LVE/HVE cells characterized by good excitatory responses over a wide range of stimulus velocities (Fig. 9). Those cells appear to have received their excitatory visual inputs from both W- and Y-channels. Further support for this conclusion comes from the fact that up to 25% of collicular neurons which receive direct excitatory input from W-type retinal ganglion cells responded not only to photic stimuli moving at slow-to-moderate velocities but also quite clearly to stimuli moving at velocities exceeding 100°/s.38,79 Like other cells receiving excitatory Y-input (see above) cells responding well over a wide range of stimulus velocities were characterized by moderate-to-high spontaneous activities; moderate-to-high peak discharge rates and usually weak suppressive regions in their receptive fields. Furthermore, their excitatory receptive fields tend to be larger than those of the LVE neurons (see above). The laminar distribution of these cells suggests that their Y-type input originates directly from the retina and/or is relayed via the visual cortex. Note that a substantial degree of excitatory convergence of different information channels is apparent in all visual cortical areas of the cat so far studied (see for review Ref. 16).

Taking into account: (i) the laminar distribution of collicular cells projecting to the suprageniculate nucleus (Sg) and/or lateral posterior nucleus of the cat (LP); (ii) a clear preference for high-velocity motion of Sg cells4 and many LP neurons,1 it is likely that collicular neurons receiving excitatory Y-input project to the Sg and/or the tectorecipient part of the LP complex.

The receptive field sizes versus velocity response profiles of low-velocity-excitatory cells, high-velocity-excitatory cells and low-velocity-excitatory/high-velocity-excitatory cells

At any given eccentricity the excitatory discharge regions of collicular cells presumably receiving Y-input (HVE and

Fig. 7. A further example of receptive field organization of LVE/HVS cells. (A) Shows graphs of the change in discharge rate vs velocity of bar movement for three cells which show excitation at low velocities and suppression at high velocities (0, no change in cells' ongoing discharge rates; positive values, increase in discharge rates; negative values, decrease in discharge rates). B and C show responses of a cell when stimulated via the contralateral eye (B) or via the ipsilateral eye (C; excitatory discharge field and surround from stimulation of this eye). C illustrates the fact that the excitatory discharge region is axis-of-movement-selective (low velocities), while the suppressive region is not (high velocities). Further explanations in text. Other conventions as in Figs 2, 3, 4 and 6.

Fig. 8. Plots of the excitatory receptive fields of LVE/HVS cells. Although only the receptive fields plotted through the dominant eye are illustrated, all 10 cells could be activated through either eye. Note that the excitatory receptive fields of three LVE/HVS cells encroach onto the area centralis and that the receptive fields of all cells encroach on the horizontal and/or vertical meridian. Note also that the excitatory receptive fields of four cells encroach on the ipsilateral visual field. X indicate the positions of the centres of two excitatory receptive fields which were not completely outlined.
Fig. 9. Depth and laminar distribution of the present sample of collicular neurons. The anatomical subdivisions shown at right are: SAI, stratum album intermediale; SGI, stratum griseum intermediale; SGP, stratum griseum profundum; SGS1, stratum griseum superficiale lower; SGSu, stratum griseum superficiale upper; SO, stratum opticum; SZ, stratum zonale. The laminar distributions of the W- and Y-tertiaries from the retina are shown under “retinotectal input”, while the laminar distribution of the corticotectal terminals (Y and non-Y) originating from a number of the ipsilateral visual cortices is shown under “corticotectal input” to the right (after Refs 10, 11, 14a, 28, 38, 45, 55, 57, 67 and 84).

LVE/HVE cells) are substantially larger than those of cells presumably receiving only W-input (LVE cells). Similar positive correlations between the size of the excitatory receptive fields of collicular neurons and their responsiveness to the fast moving photic stimuli were observed in earlier reports. Thus, one might argue that in order to excite the cell the stimulus has to spend some minimal time in the cell’s receptive field. To a certain extent it might be so. However, the differences in the sizes of the excitatory receptive fields of the HVE and LVE/HVE cells vs those of LVE cells are probably not sufficient to account for the good responses of HVE and LVE/HVE cells to stimuli moving at velocities exceeding 100°/s. There are several other lines of argument, indicating that the positive correlation between the size of the excitatory discharge field and the responsiveness to fast-moving stimuli is not generally applicable to the visual system at least in the cat. Thus, although at a given eccentricity receptive fields of W-type retinal ganglion cells are at least as large as those of the Y-type RGCs (see for review Ref. 86), the W-type ganglion cells, unlike Y-type cells, respond poorly or not at all to fast-moving photic stimuli. Second, although the excitatory receptive fields of neurons in cat’s visual cortical area 2la are at any eccentricity substantially larger than those of area 18 neurons, hardly any area 2la neurons respond to fast-moving (over 100°/s) photic stimuli while a very high proportion of area 18 neurons does so.

Low-velocity-excitatory/high-velocity-suppressive cells. In a distinct group of collicular cells (about 17% of the sample) there appears to be a special type of convergence of the W- and Y-channels. Activation of the W-channel (by slowly moving photic stimuli) resulted in excitation (increase in firing rate) while activation of the Y-channel (by fast-moving photic stimuli) resulted in inhibition (reduction in firing rate). Poor responsiveness of these cells to stimuli moving at moderate velocities suggests that the two inputs act in an antagonistic manner. Furthermore, the suppressive fields revealed by the activation of the Y-input were much larger than those revealed by the activation of the W-input and in addition to the large visual field ipsilateral to the excitatory discharge field the suppressive field usually included a region of the visual field contralateral to the excitatory discharge field of the cell.

In view of the fact that the region of LVE/HVS receptive field which appears to receive the Y-input is very large and invariably extends into the ipsilateral visual hemifield, it is likely that morphological counterparts of our LVE/HVS cells located in the lower SO and upper SGI (6/10 cells in our sample of LVE/HVS cells) are “medium-sized trapezoid radiating”, or “T type” efferent cells present in these layers of cat’s superior colliculus. Indeed, the dendritic trees of the T cells located in the lower SO or upper SGI are: (i) very large in the dorsoventral axis (600—1 600 p.m) with dendrites extending into the SGS, and (ii) extend to over a 1000 p.m mediolaterally and rostrocaudally. The W-type input to these cells is likely to be relayed via the dendrites in the SGS, while the Y-input might be relayed not only via their dendrites in the SOS and SO but also more directly.
via the Y-type retinal and cortical terminals in the 561 (see Fig. 9). Furthermore, Y-input to LVE/HVS cells is presumably relayed via inhibitory interneurons and indeed, GABAergic neurons are plentiful in both the superficial and deep layers of cat's SC (see for review Ref. 59).

Another possibility, especially in relation to the LVE/HVS cells located in the upper SO and the 565 is that the suppressive Y-input to these cells is relayed via a pretectocollricular projection. Indeed, the pretectal complex, especially the nucleus of the optic tract, is characterized by a large proportion of non-direction-selective cells with large receptive fields and responding well (or exclusively) to fast-moving photic stimuli (see Refs 39 and 79). Furthermore, the pretectal complex projects to both the superficial and, to a lesser extent, the intermediate collicular layers (see Ref. 42). Many of the pretectal neurons which project to the superior colliculi are GABAergic.7 Finally, cells with receptive field properties very similar to these LVE/HVS collicular cells are present in the pretectal nucleus of optic tract of cats,47 macaque monkeys48 and diprotodont marsupials-tammar wallabies.49

Cells with excitatory input activated by the W-channel and inhibitory input activated by the Y-channel might be more common than our data would suggest. In particular, the inhibitory input would be revealed by our procedures only when the cell had a substantial spontaneous activity in the absence of specific photic stimuli. However, most of the cells responding preferentially at low stimulus velocities but not increasing their firing rates when fast-moving stimuli were presented had very low, if any, background activity. Further support for the idea that collicular cells with very extensive suppressive fields comes from the study of Rizzolatti and his colleagues42,43 in which they reported that in the great majority of neurons recorded from the retinorecipient layers of the superior colliculus of the cat the magnitude of responses to a photic stimulus moving across the cell's excitatory discharge field was significantly (but only transiently for 2—3 s) decreased by a second stimulus moving at 30—100°/s in a region 300 to 1200 from the border of the excitatory discharge region.42,43 When the second stimulus was introduced into the field ipsilateral to the cell's excitatory receptive field the decrease of the response was stronger and apparent in 95% of cells, while introduction of the second stimulus into the field contra-lateral to the excitatory receptive field produced a statistically significant decrease of the response in only 77% of the cells tested.

In many neurons in the intermediate and deep layers of superior colliculi of cats and macaque monkeys there is a substantial cross-modality excitation (see for recent review Ref. 91) and, to a lesser degree, cross-modality suppression (see for recent review Ref. 46). It is possible that LVE/HVS neurons recorded by us in the intermediate layers also receive a convergent auditory and/or somatosensory inputs. If so, the nature of interactions between the visual and other sensory modalities (excitatory vs suppressive) might depend on the velocity of the photic stimuli applied.

Functional role of low-velocity-excitatory/high-velocity-suppressive cells

Cells with excitatory input activated by the W-channel and inhibitory input activated by the Y-channel might play a unique functional role. One possibility is that these cells innervate, with presumable involvement of some interneurons, two types of premotor (usually tectoreticular and tecto-reticulo-spinal) cells described in the intermediate and deep collicular layers of alert cats and macaque monkeys: (i) cells which discharge tonically when the visual axis is approximately stationary reduce their discharge before the onset of the saccade which breaks the fixation and pause for most of the saccade; and (ii) “saccade” neurons which discharge before and during saccades to a specific region in the visual field and pause during visual fixation.3,31,61,66,68 The premotor cells which discharge tonically when the visual axis is stationary have been subdivided into two subclasses: (i) “fixation” neurons which have visual receptive fields that include the area centralis and discharge maximally when the animal fixates attentively the target of interest; and (ii) “orientation” neurons whose receptive fields do not include the area centralis.49 We would argue that slowly moving photic stimuli which evoke the excitatory responses of the LVE/HVS cells would in the case of the LVE/HVS cells with excitatory receptive fields involving the area centralis evoke excitatory responses in “fixation” neurons. In the case of the LVE/HVS cells with excitatory receptive fields not encroaching onto the area centralis slowly moving stimuli would evoke excitatory responses in “orientation” neurons. At the same time the LVE/HVS cells excited by slowly moving stimuli would inhibit, presumably via interneurons, the “saccade” neurons. By contrast, fast-moving photic stimuli by suppressing the ongoing activity of the LVE/HVS cells would in turn reduce the ongoing activity of inhibitory interneurons innervating saccade neurons. There is emerging evidence that at least in macaque and ferret the reciprocal inhibition between fixation and saccade-related neurons is mediated by interneurons located in the intermediate and deep collicular layers43,57 and indeed some of the LVE/HVS neurons in our sample were located in the SHL. However, most of the LVE/HVS cells in our sample were located in the superficial layers, contrary to some previous assertions, small groups of cells in the superficial collicular layers project to the intermediate and deep layers (see Ref. 6). Furthermore, a recent study of Lee and co-workers42 indicates that, at least in the tree shrew, cells in the superficial collicular layers directly excite cells in the underlying intermediate layers. It has been postulated that some of the so-called retinal-slip neurons in the nucleus of optic tract, which have receptive field properties very similar to those of LVE/HVS collicular neurons (excitatory responses to slowly moving photic stimuli and suppressive nondirectional responses to fast-moving stimuli) and are believed to drive the ocular following components of optokinetic nystagmus, function as blockers of “ocular following in response to the visual disturbances caused by saccades”.43

CONCLUSIONS

In the majority (57%) of collicular neurons in our sample of cells recorded from the retinorecipient layers there was no indication of convergence of W- and Y-channels. However, in about 43% of the cells there was clear evidence of convergence of W- and Y-channels. Furthermore, over 15% of collicular neurons (about 40% of these which receive convergent input from both W- and Y-channels) appear to receive excitatory input from the W-channel and inhibitory input from the Y-channel (LVE/HVS cells). We postulate that the LVE/HVS cells (which constitute a new class of collicular neurons) play
an important role in activating “fixation/orientation” and “saccade” premotor neurons recorded by others in the intermediate and deep collicular layers. Acknowledgements—

REFERENCES


Mellown J. T. and LuKis R. B. (1976) Distribution of direct Y-cell inputs to the cat’s superior colliculus: are there spatial gradients? Brain Res. 103, 133—138.


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