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Research Report

Spatio-temporal receptive field properties of cells in the rat superior colliculus

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ABSTRACT

Although the rat is widely used in neurobehavioural research, the spatio-temporal receptive field properties of neurons in superficial layers of the superior colliculus are relatively unknown. Extracellular recordings were carried out in anesthetized Long Evans rats. Neurons in these layers had simple-like and complex-like receptive fields (RFs). Most cells (67%) had RFs showing band-pass and low-pass spatial frequency (SF) tuning profiles. Spatial band-pass profiles showed low optimal SF (mean=0.03 c/deg), low spatial resolution (mean=0.18 c/deg) and large spatial bandwidths (mean=2.3 octaves). More than two-thirds of the RFs (71%) were selective to orientation and only 11% were clearly direction selective. Nearly two-thirds of cells (68%) had band-pass temporal frequency (TF) tuning profiles with narrow bandwidths (mean=1.7 oct.) whereas the others showed low-pass TF tuning profiles. Temporal band-pass profiles had low optimal TFs (mean=3.5 c/s). Although some cells showed relatively low contrast thresholds (6%), most cells only responded to high contrast values (mean=38.2%). These results show that the spatial resolution of collicular cells is poor and that they respond mainly to highly contrasted moving stimuli.

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1. Introduction

The rat is commonly used in visual neuroscience research, despite the fact that its pattern vision is relatively underdeveloped (Hale et al., 1979). Although this predominantly nocturnal rodent relies more on tactile, olfactory and auditory signals to acquire food and insure its survival (Hughes, 1977), vision does play a role in its overall negotiation of the environment. Surprisingly, little is known about visual RF properties of single neurons of the rat's superior

colliculus (SC), a major analysis and relay structure for visual and visuo-motor behaviour. There are, moreover, extensive differences in the spatio-temporal properties of its constituent neurons in different rat sub-populations. Thus, spatial acuity of the Long Evans hooded rat is around 1.0 c/deg (Keller et al., 2000; Prusky et al., 2002), while that of the albino rat is lower (0.5 c/deg). Also, the latter shows a contrast response threshold of 16% (Birch and Jacobs, 1979), whereas its hooded cousin can detect stimuli having contrasts as low as 1.25% (Keller et al., 2000). This argues in favour of the hooded rat as

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Abbreviations: c/deg, cycle/degree; c/s, cycle/second; dLGN, dorsal lateral geniculate nucleus; PSTH, peri-stimulus time histogram; RF, receptive field; SAI, stratum griseum intermedium; SC, superior colliculus; SF, spatial frequency; SGP, stratum griseum profundum; SGS, stratum griseum superficiale; SO, stratum opticum; TF, temporal frequency

a more appropriate model for studies of visual system function.

It is agreed that the magnocellular pathway of the mammalian visual system processes stimuli in movement with poor detail resolution, whereas the parvocellular pathway extracts features that allow for object recognition (Schneider, 1969). This distinction between the visual pathways has been confirmed in rodents (Dean, 1981) by examining the selective effects of tectal and geniculate ablations. Hooded rats with a lesion of the dorsal lateral geniculate nucleus (dLGN) cannot detect SFs higher than 0.7 c/deg, while a lesion in the SC allows the animal to perceive SFs up to normal levels, that is, 1.0 c/deg. Thus, it seems that a tectal lesion does not impair spatial acuity, that is, parvocellular function, which is probably more importantly processed in the dLGN system in the hooded rat (Cowey et al., 1982).

More than 90% (Linden and Perry, 1983) of the retinotectal fibres of this animal project to discrete neuron clusters in the most superficial layer of the contralateral SC (Langer and Lund, 1974). As observed in other mammals (Kruger, 1970), these retinal projections are topographically organized (Cowey and Perry, 1979; Diao et al., 1983; Hayhow et al., 1962; Lashley, 1934; Lund, 1965; Siminoff et al., 1966) and transmit visual inputs with a magnification factor of 45 deg/mm along the anteroposterior axis and 24 deg/mm along the mediolateral axis (Siminoff et al., 1966), suggesting that one retinal fibre may directly influence a collicular area corresponding to about one quarter of the visual field (Grantyn, 1988; Siminoff et al., 1966). The projections from the contralateral eye terminate in the stratum griseum superficiale (SGS), and the ipsilateral afferents, which represent less than 10% of retinotectal fibres (Cowey and Perry, 1979; Linden and Perry, 1982), project in patches (Hayhow et al., 1962; Land and Lund, 1979; Lund, 1965; Lund et al., 1980) at the border of SGS and stratum opticum (SO). Hence, binocular cells in superficial layers (SGS and SO) represent less than 5% of the total (Cowey and Perry, 1979; Linden and Perry, 1982).

Descending corticotectal projections from area 17 terminate topographically in ipsilateral superficial layers, namely, in the upper SO and lower SGS (Harvey and Worthington, 1990), whereas those from area 18 terminate along two horizontal tiers: one in middle stratum griseum intermedium (SGI) and the other at the border between stratum griseum intermedium (SAI) and stratum griseum profundum (SGP). Projections from area 18a also terminate along two horizontal tiers, one at the border between lower SO and upper SGI and the other at the border between SGI and SAI.

Visually responsive neurons in the Royal College of Surgeons (RCS) rat's SC have large RFs (3° to 15°) and there is a progressive expansion of their size at increasing distance from the representation of the visual streak and at increasing depth in SO and in upper SGI (Sauvé et al., 2002). In the albino rat, RFs of cells in superficial layers have a uniform or concentric spatial organization of the ON, OFF or ON/OFF types (Fukuda and Iwama, 1978; Gonzalez et al., 1991). Only 13.8% show clear direction selectivity to light spots moving at high velocities (40 to 90 deg/s). Whereas highly contrasted stimuli are required to elicit reliable responses in the albino rat SC (Gonzalez et al., 1991), Sauvé et al. (2002) show that RFs of cells in the RCS rat's SC are sensitive to low contrast (7%). In

area V1 (Girman et al., 1999), cells of the Lister rat also respond to low contrast (6%) and, using drifting sinusoidal gratings, they are sensitive to SFs as high as 1.2 c/deg, although responding optimally to low SFs (0.1 c/deg). Wells et al. (2001) demonstrate that RFs in area V1 of the Long Evans rat are sensitive to light spots flickering up to 21.5 Hz. It is clear therefore that the hooded Long Evans rat is the most appropriate model to study visual function. The SC is a critical structure in visual analysis because it receives massive retinofugal inputs, as well as corticofugal fibres from V1 and V2 and projections from the ventral LGN (Hayashi and Nagata, 1981). However, and quite surprisingly, a systematic study of the RFs' sensitivity has still not been carried out in the superficial layers of its SC. The objective of the present study therefore is to examine precisely this problem by systematically examining the RF properties of cells in this structure in Long Evans hooded rats.

2. Results

A total of 122 neurons in the superficial layers of the rat's SC were successfully isolated from background activity. All RFs were submitted to the spatio-temporal protocol, but only those for which a complete response profile was obtained with respect to either SF tuning ($n=90$), TF tuning ($n=90$), directional sensitivity ($n=78$) and contrast response ($n=64$) were included in the data analysis.

2.1. Classification of receptive fields

All cells were robustly driven by highly contrasted drifting sinusoidal gratings. RFs were either composed of elongated flanked excitatory or inhibitory regions or overlapping excitatory and inhibitory regions. The spatial organization of 90 RFs was classified according to the criteria of Skottun et al. (1991). As a rule, response patterns of simple-like RFs (59%) and end-stopped simple-like RFs (25%) showed modulation of their responses at the optimal SF. On the other hand, response patterns of complex-like RFs (14%) and end-stopped complex-like RFs (2%) did not show modulation of their response at the optimal SF, but rather manifested an overall increase of their discharge rate.

2.2. Spatial frequency tuning

The response of 90 cells to SFs was assessed using sinusoidal gratings having a contrast between 60% and 80% and drifting (2 to 4 c/s) in the cell's preferred direction. Cells showed two types of SF tuning profiles. Fig. 1A shows a simple-like RF stimulated with sinusoidal gratings drifting (2 c/s) in the direction of 90°. This cell gave its maximal response rate at the lowest SF tested (0.005 c/deg) and a progressive attenuation of its response rate at higher SFs. Only 7 % of the cells gave their maximal response rate at the lowest SF tested and were classified as having a low-pass SF tuning profile. Otherwise, Fig. 1B illustrates a simple-like RF that, when stimulated in the direction of 0° and at a TF of 2 c/s, showed a small attenuation of its response rate at the lowest SFs tested (0.005 c/deg) in addition to a drastic attenuation at higher SFs. More than one

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