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Research report

Comparison of visual receptive field properties of the superior colliculus and primary visual cortex in rats

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ABSTRACT

The rat visual system comprises cortical and subcortical pathways. The receptive field properties of cells in the visual cortex have been extensively studied; however, the fundamental roles of the two circuits in visual information processing are not well understood. To address this question, we have applied quantitative methods to compare and characterize the spatiotemporal receptive field (RF) properties of neurons in primary visual cortex (V1) cells and superficial layers of the superior colliculus (SC) in rats by means of extracellular recordings. An analysis of visual stimulus processing revealed distinct functional characteristics of the two visual circuits. RF diameters of SC neurons were significantly larger than those of V1 cells. Most cells in both regions had high orientation selectivity, but the mean orientation bandwidth of the SC was broader than that of V1 cells (101.5° vs. 60.2°). The mean optimal spatial frequency (SF) of SC cells was lower but had a broader bandwidth than that of V1 cells (0.03 vs. 0.068 cpd). The majority of SC and V1 cells (70% and 68%, respectively) had RFs with band-pass temporal frequency (TF) tuning profiles and similar optimal TFs. However, temporal band-pass profiles of the SC showed narrower mean temporal bandwidths than those of V1 cells (1.42 vs. 2.36 octaves). The majority of neurons in visual cortical and subcortical structures were activated in response to high-contrast, drifting gratings in the preferred orientation. The percentage of V1 neurons with a low-contrast threshold was larger than the proportion of SC neurons (45.6% vs. 30%), indicating that the former adapt better to contrast. The substantial overlap in latency distributions between SC and V1 areas suggests that the two visual systems process and analyze visual signals in parallel. However, the two areas use different neural encoding mechanisms based on different latency distribution trends. These results indicate that SC cells have poor spatial acuity and are better suited to detecting high-contrast, moving stimuli in larger visual fields. In contrast, V1 cells are adapted to extracting shape information and detailed features of objects.

1. Introduction

Visual and emotional stimulus processing involves cortical and subcortical visual pathways (Tamietto and de Gelder, 2010). Visual information from an image is processed hierarchically by the visual cortex. V1 is the anatomical area that receives information from the retina and lateral geniculate nucleus (LGN) and transfers information to higher cortical areas; as such, V1 is an important area in the study of mammalian vision. However, recent studies have indicated that the subcortical pathway also plays a significant role in the rapid processing of visual stimuli associated with affect (Jarvis et al., 2005; Cohen and Castro-Alamancos, 2007), although the fundamental differences between the two different pathways are not well understood.

The subcortical pathway includes the superior colliculus (SC), visual pulvinar, and amygdala in rats and birds (Tamietto and de Gelder, 2010; Garrido et al., 2012). In mammals, visual information is received by superficial layers of the SC directly from retinal ganglion cells; neurons in the deeper layers are responsible for visuomotor integration in saccadic eye movements and avoidance responses (Schiller and Malpeli, 1977; Sahibzada et al., 1986; Sparks and Hartwich-Young, 1989). It is presumed that the SC is the first post-retinal subcortical structure to receive visual information, and its activity is largely unaffected by lesions in cortical visual areas; this is especially true for coarse (i.e., low spatial frequency [SF]) visual input. In contrast, the cortical visual pathway extracts detailed information about object features that enables their recognition (Vuilleumier et al., 2003; Tamietto and de Gelder,

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2010; Tamietto et al., 2012; DiCarlo et al., 2012). This functional distinction between cortical and subcortical visual pathways has been confirmed in rodents by examining task behavior with lesions in different brain structures: 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 rat to perceive SFs up to normal levels, that is, 1.0 c/deg (Dean, 1981). Thus, it seems that SC lesion does not impair spatial acuity, the detailed visual information is probably more importantly processed in the cortical visual pathways (Cowey et al., 1982). These findings probably demonstrate that the superior colliculus, the earliest post-retinal subcortical structure, is suitable to process coarse stimuli (that is, low spatial frequency).

The majority of studies involving the SC have examined relay structures associated with visual and visuomotor behavior (Keller et al., 2000; Prusky et al., 2000). Visual receptive field (RF) properties of SC neurons have been examined by extracellular recordings in many mammals such as cats; however, rodents have been less well studied (Binns and Salt, 1997). One study that examined changes in RF properties such as size, type, and directional selectivity during maturation found that the cortico-tectal pathway is only weakly involved in establishing the directional selectivity of collicular neurons in rats (Fortin et al., 1999). In addition, SC cells in rats have poor spatial resolution and respond mainly to high-contrast, moving stimuli (Prévost et al., 2007), whereas subcortical pathways respond to coarse (i.e., low SF) emotionally charged stimuli (Cohen and Castro-Alamancos, 2007).

The primary visual cortex (V1 area) receives projections from the ventral LGN. It is not known whether there are differences in visual RF properties between SC and primary visual cortical (V1) neurons; however, these may reveal mechanisms underlying affective visual information processing by neurons. The present study compared visual RF (i.e., size, type, contrast, motion, and spatiotemporal) properties of neurons in the SC and primary visual cortex in rats to clarify the specific roles of cortical and subcortical visual pathways.

2. Materials and methods

2.1. Animals

Adult male Long–Evans rats (8 weeks old, weight: 250–300 g; $n = 26$) were used in this study. A microelectrode array was implanted in the superficial layers of the SC of 12 rats and in the primary visual cortex of 14 rats to record neuronal activity. Rats were maintained on a 12:12 h light/dark cycle with free access to food and water in the Animal Center of Henan Province. Experiments were carried out according to the guidelines proposed by the Chinese Council on Animal Care and the National Institutes of Health, and protocols were approved by the Animal Care and Use Committee of Zhengzhou University.

2.2. Surgery and electrophysiological recordings

Rats were deprived of food one day prior to the experiments. On the day of recording, animals received an intramuscular injection of atropine sulfate (0.05 mg/ml/kg) to reduce bronchial secretions and induce mydriasis and were anesthetized with an intraperitoneal (i.p.) injection of 3% (30 mg/ml) sodium pentobarbital (2.2 ml/kg). The rats' heads were fixed in a stereotaxic apparatus (Kopf Instruments, Tujunga, CA, USA) and body temperature was maintained at 37–38 °C with a thermostatically controlled heating pad with continuous heart rate monitoring (Kent Scientific, Torrington, CT, USA). Local anesthetic (2% lidocaine hydrochloride) was regularly applied to cranial muscles and incisions. A small trepanation was made over the contralateral SC (anterior–posterior, A–P: −5.0 to −8.0 mm; medial–lateral, M–L: 0.0–2.0 mm; dorsal–ventral, D–V: −3.0 to −3.4 mm) and V1 area (A–P: −5.0 to −8.0 mm; M–L: 3.0 to 5.0 mm; D–V: −0.6 to −1.2 mm). The dura was removed under a high-magnification dissecting microscope. We designed a stair-stepping microwire electrode array suitable for implantation in deep brain according to SC curvature, in order to implant at the correct location in the SC. The 16-channel 4′4 channel microwire electrode array was custom-made by Wayne State University. The grids were implanted on the cerebral cortex of the SC. Then a platinum–iridium microwire electrode array was dipped in a 3% solution of 1,1′-dioctadecyl-3,3,3′,3′-tetramethylindocarbocyanine perchlorate (DiI; Invitrogen, Carlsbad, CA, USA) in dimethylformamide to label the electrode insertion track (Zhang and Zhang, 2010). Histological examination of the DiI deposit was necessary to validate the data collected.

Data were acquired with the microelectrode array (interelectrode spacing for V1 area, 250 μm and for SC, 150 μm) with the impedance maintained at 0.50–1.5 M Ω at 1 kHz. The electrode was inserted to 600–800 μm below the brain surface to record from the V1 area and to 3000–3400 μm for the SC. Recordings were limited to the superficial layers of the SC and layer IV in the primary visual cortex. The exposed brain was covered with warm agar (3–4% in saline) to prevent drying.

After the surgery, anesthesia was maintained with 0.5% isoflurane for the duration of the recording session. Extracellular neuronal activity recorded by the electrodes was pre-amplified, band-pass-filtered (0.3–5 kHz) with a digital two-pole Butterworth filter and sampled at 30 kHz using a Cerebus 128-channel acquisition system (Blackrock Microsystems, Salt Lake City, UT, USA). The implantation procedure and recording conditions are described elsewhere (Shi et al., 2013).

Threshold amplitude crossing was used to detect spikes; the threshold was defined as $4\delta_n$, $\delta_n = \text{median}\{\frac{|x|}{0.6745}\}$, where x is the band-pass-filtered signal and δ_n is an estimate of the standard deviation of background noise. Each spike was represented using 1.6 ms (48 sampled points). Spikes were sorted with the WaveClus approach (Quiroga et al., 2004)—an unsupervised spike-sorting algorithm that combines wavelet transform and super paramagnetic clustering—and were analyzed with Matlab (MathWorks, Natick, MA, USA).

2.3. Visual stimulus presentation

Visual stimuli were generated with Matlab and displayed on a 10 inch light-emitting diode monitor (mean luminance, 32 cd/m^2; resolution, 1280 × 960 pixels) located 25 cm in front of the animal's eyes. Stimulus onset was monitored with a photodiode and saved as an analog channel that was synchronized to the Cerebus Neural Signal Processing system (Blackrock Microsystems, Salt Lake City, UT, USA).

The RF size and spatiotemporal properties were calculated from sparse noise stimuli encompassing a 15 × 15 binary chessboard, where the length of one chess square spanned a visual angle of 3.8°. We measured orientation, SF, temporal frequency (TF), contrast tuning, and properties of neural responses using multiple repetitions of a drifting sinusoidal grating. The latter comprised four parameters, i.e., direction, contrast, SF, and TF. The drifting grating had eight possible directions: 0, 45, 90, 135, 180, 225, 270, and 315°. As a convention, a vertically oriented grating drifting to the right was 0°, a horizontally oriented grating drifting downward was 90°, etc. The drifting grating and a gray blank were alternately presented for 1 s each with stimulus conditions randomly interleaved; the gray blank condition (mean luminance) was presented between all stimulus sets to estimate the spontaneous firing rate.