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COMPLEX MOTION SENSITIVITY OF NEURONS, IN THE VISUAL PART OF THE ANTERIOR ECTOSYLVIAN CORTEX IN CATS

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Abstract—In cats, it is generally believed that the visual part of the anterior ectosylvian cortex (AEV) is involved in motion integration. It receives a substantial proportion of its afferents from cortical (e.g. lateral suprasylvian cortex) and subcortical (e.g. lateral posterior–pulvinar complex) areas known to participate in complex motion analysis. It has been established that a subset of AEV neurons can code the veridical motion of a moving plaid pattern (pattern-motion selectivity). In our study, we have further investigated the possibility that AEV neurons may play a role in higher-order motion processing by studying their responses to complex stimuli which necessitate higher order spatial and temporal integration. Experiments were performed in anesthetized adult cats. Classical receptive fields were stimulated with (1) complex random-dot kinematograms (RDKs), where the individual elements of the pattern do not provide coherent motion cues; (2) optic flow fields which require global spatial integration. We report that a large proportion of AEV neurons were selective to the direction and speed of RDKs. Close to two-thirds of the cells were selective to the direction of optic flow fields with about equal proportions being selective to contraction and expansion. The complex RDK and optic flow responsive units could not be systematically characterized based on their responses to plaid patterns; they were either pattern- or component-motion selective. These findings support the proposal that AEV is involved in higher-order motion processing. Our data suggest that the AEV may be more involved in the analysis of motion of visual patterns in relation to the animal's behavior rather than the analysis of the constituents of the patterns.

Key words: receptive field, optic flow, random dot kinematogram, plaids, extrastriate cortex, direction selectivity.

Motion is ubiquitous in the environment, whether it is caused by self-motion or motion of elements in the environment. Complex motion patterns need to be analyzed and properly understood by the brain in order to ensure an adequate behavior. In the cat, several cortical areas have been associated with motion analysis and most of them lie along the suprasylvian sulcus. It has been shown that neurons in the posteromedial suprasylvian sulcus and anteromedial suprasylvian sulcus (PMLS and AMLS) as well as the posterolateral region (posterolateral suprasylvian sulcus, PLLS) can respond to complex motion signals (Li et al., 2000; Ouellette et al., 2004; Villeneuve et al., 2006). Another visual area likely to contribute to higher-motion analysis would be the anterior ectosylvian visual area (AEV). This structure lies at the bottom of the sulcus and is surrounded by auditory and somatosensory areas. It has reciprocal connections with several cortical areas (e.g. PMLS, PLLS, AMLS, ALLS) as well as thalamic structures, and in particular the lateral posterior–pulvinar complex (LP–pulvinar) and the suprageniculate nucleus (Sg) (Mucke et al., 1982; Roda and Reinoso-Suarez, 1983; Miceli et al., 1985), the latter two also being involved in motion analysis.

Very little is known about the response properties of visual neurons in the AEV. The few studies that have been conducted indicate that cells in this area have large 'classical receptive fields' (CRF), highly sensitive to the direction and velocity of objects in motion (Mucke et al., 1982; Benedek et al., 1988; Nagy et al., 2003). Cells sensitive to motion in depth were also reported, but this property was not investigated in a systematic way (Ptito et al., 1987; Rauschecker and Korte, 1993). A decade ago, Scannell et al. (1996) reported that a large proportion of AEV neurons (55%) could integrate the veridical direction of motion of plaid patterns, suggesting that the AEV participates in higher-order processing of visual information. At the behavioral level, this area was shown to be involved in spatial orientation (Wilkinson et al., 1996; Jiang et al., 2002).

Based on these connectivity patterns and response properties, it has been suggested that the AEV represents one of the higher-order areas along the cat's visual cortical pathways (Felleman and Van Essen, 1991; Scannell et al., 1995; Grant and Hilgetag, 2005). We postulated that the large CRFs of AEV neurons would reflect the nature of the incoming signals from hierarchically-defined lower cortical areas and from the thalamus. In this context, we investigated the sensitivity of AEV neurons to complex motion stimuli. These stimuli were proven to be effective in defining higher-order sensitivity in other structures projecting to the AEV such as the LP–pulvinar (Merabet et al., 1998; Dumbrava et al., 2001), and the LS areas (Brosseau-Lachaine et al., 2001; Ouellette et al., 2004; Villeneuve et al., 2006).

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Abbreviations: AC, area centralis; AEV, anterior ectosylvian visual area; AMLS, anteromedial suprasylvian sulcus; CRF, classical receptive field; DI, direction index; LP–pulvinar, lateral posterior–pulvinar complex; LPl, lateral part of the lateral posterior nucleus; LPm, medial part of the lateral posterior nucleus; MST, medial superior temporal area; NR, non-responsive; NS, non-direction selective; PLLS, posterolateral suprasylvian sulcus; PMLS, posteromedial suprasylvian sulcus; RDK, random dot kinematogram; SF, spatial frequency; TF, temporal frequency.

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EXPERIMENTAL PROCEDURES

Animal preparation

Normal adult cats weighing approximately 3.5 kg were used. All procedures were in accordance to the guidelines set out by the Canadian Council on Animal Care and NIH guidelines for the care and use of laboratory animals, and were approved by the ethics committee on animal research of the Université de Montréal. Efforts were made to minimize the number of animals used and their suffering. Animals were pre-anesthetized with a s.c. injection of acepromazine (1 mg/kg) and atropine (0.1 mg/kg). General anesthesia was induced using a mixture of N_2O/O_2 (50:50) and isoflurane (5–2%). A local anesthetic (lidocaine hydrochloride 2%) was s.c. injected at all surgical wounds and pressure points. A tracheotomy and a cannulation of the cephalic vein were performed before the animal was placed in a stereotaxic apparatus. The cannula allowed for the delivery of lactated Ringer solution containing gallamine triethiodide (10 mg/kg/h). The animal was then artificially ventilated with a mixture of O_2/N_2O (30:70) and halothane (0.5–1%) following the procedure described in Villeneuve and Casanova (2003). The EKG and CO_2 levels were monitored throughout the experiment, the latter being maintained between 28 and 35 mm Hg. The temperature of the animal was kept stable between 37 and 38 °C. The pupils were dilated with atropine 1% and phenylephrine hydrochloride 2.5% was used to retract the nictitating membranes. The eyes were protected with contact lenses of appropriate refractive power. Craniotomies were performed at Horsley-Clarke coordinates A-P +11 to +16 and M-L 11–16. The electrode was inserted vertically and lowered across the lateral suprasylvian sulcus through a small opening in the dura matter. The cortex was covered with warmed agar. Melted wax was added to create a sealed protective chamber.

Recordings

Varnished tungsten microelectrodes (A&M Systems, Carlsborg, WA, USA, impedance 5–10 ΩM) were used to record extracellular single unit activity in the AEV. Neuronal activity was amplified, displayed on an oscilloscope, and played through an audio monitor. A window discriminator was used to isolate single units from the overall signal. Digital signals were then fed to an acquisition software (Spike2; CED, Cambridge, UK) via an analog-digital interface (CED 1401 plus). The response to each stimulus condition was recorded as a post-stimulus time histogram (PSTH-bin width of 10 ms) and was saved for further statistical analysis. Recording for a single trial occurred over a 4 s period and mean firing frequency was calculated from all 400 bins and averaged over four presentations.

Visual stimulation

When a neuron was encountered, ocular dominance and CRF size and location were qualitatively determined. CRFs were hand plotted during the initial phase of the study. Because some CRFs were extremely difficult to define by ear, we later used computer-generated flashing white squares (20×20°) that were back projected onto a tangent screen placed 57 cm in front of the animal and covering 80×107°of visual angle. The squares were randomly presented for 4 s at 20 different locations on the screen (grid of 4×5 squares) and the response was averaged over four presentations. The area eliciting responses above 2SD of the baseline was considered as the CRF. All stimuli were generated by a MacIntosh G3 computer using VPixx 1.84 (Sentinel Medical Research, Ste-Julie, Quebec, Canada) and back projected onto the screen.

Thereafter, a first series of tests was conducted using a sinusoidal drifting grating (60–80% contrast) to determine the preferred direction of motion and the optimal spatial (SF) and temporal frequencies (TF). As shown by Nagy et al. (2003), AEV cells were optimally driven by low spatial frequency gratings (the mean preferred SF and TF were 0.08±0.1 c/° [ranged from 0.025–0.5] and 4.69±2.4 Hz [1.5–8.5], respectively). Direction selectivity was then quantitatively determined by varying the direction over a range of 360° with 15 or 30° steps.

Simple and complex random dot kinematograms (RDKs), composed of white dots (1° diameter, 100% contrast) on a black background were used to characterize responses to global motion. Both simple and complex RDKs were presented in a full screen manner i.e. 80×107°. Thus the stimulated area included both the area centralis (AC) and the CRF. The simple RDK was essentially a rigidly translating random dot field with no noise. Each dot followed a straight path in one common direction. This stimulus required minimal simultaneous spatial and temporal integration across an area of the visual field since each separate dot provided enough information to determine the direction of motion. In its complex form, each dot had a lifetime of two frames, as they moved only once before being randomly repositioned. Each dot had an equal probability of beginning at the first or second frame of their motion sequence. At any given time, half the dots were displaced in the motion direction while the remaining half was randomly repositioned. Over a temporal sequence of a given set of displacements, 100% of the dots contributed to the global motion sequence. In the complex RDK, there was never more than a single coherent motion before repositioning. Consequently, there must be a spatial and temporal integration of the displacement of many dots over an extended area of the visual field in order to signal the direction of motion. These stimuli have been used to successfully characterize complex motion integration in other visual structures (Dumbrava et al., 2001; Ouellette et al., 2004; Villeneuve et al., 2006).

Optic flow was also used to assess cells' responsiveness to complex motion. This stimulus consisted of white dots (1° diameter, 100% contrast) of constant size, moving along radial trajectories away (expansion) or toward (contraction) the point of origin. Responding to either direction required spatial integration but little temporal integration as there were no limitations on the lifetime of the dots. This stimulus was designed to mimic the experience of a cat walking down a straight tunnel at a speed varying between 1 and 30 m/s. The origin of motion represented the aperture at the end of the tunnel which was approximately 2° in diameter. The dots had a projection profile, in which their speed doubled with the square of the distance from the point of origin. The dot velocity can be computed from the formula:

$$s=[((\sin(d))^2/r)\times s']\times\frac{180}{\pi}$$

where d is the distance of the element from the origin (°), r the tunnel radius (°) and s' the physical speed of the cat ($^{\circ -1}$). For example, for a cat speed of 4 ms^{-1}, dots located at 5, 20 and 50° eccentricity would have a velocity of 6, 90 and 450$^{\circ -1}$.

Velocity, direction preferences, dot density and size as well as number of rays were tested and optimized. All the optimized parameters were used to quantify the velocity and direction preferences. In order to evaluate the impact of the size gradient to the optic flow response, trapezoids (100% contrast) of increasing size were also presented for a subset of cells. The elements followed the same speed pattern and doubled their size with the square of the distance. These elements subtended 0.2×0.2° at the origin and reached 1.3×4.4° and 3.8×22.4° at 20 and 50° of eccentricity, respectively. The effect of the speed gradient was also investigated by using an optic flow pattern with constant speed. The effect of varying the spatial extent of the stimulus was investigated by comparing full field pattern responses to those when the stimulus was confined to the CRF. In order to determine if the cells were selective to the position of the origin, we tested the latter at two locations: the AC and the center of the CRF. Additional details about optic flow stimuli can be found in Brosseau-Lachaine et al. (2001) and Ouellette et al. (2004).