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Research Report

Receptive field properties and sensitivity to edges defined by motion in the postero-lateral lateral suprasylvian (PLLS) area of the cat

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ABSTRACT

The present study investigated the spatial properties of cells in the postero-lateral lateral suprasylvian (PLLS) area of the cat and assessed their sensitivity to edges defined by motion. A total of one hundred and seventeen (117) single units were isolated. First, drifting sinusoidal gratings were used to assess the spatial properties of the cells' receptive fields and to determine their spatial frequency tuning functions. Second, random-dot kinematograms were used to create illusory edges by drifting textured stimuli (i.e. a horizontal bar) against a similarly textured but static background. Almost all the cells recorded in PLLS (96.0%) were binocular, and a substantial majority of receptive fields (79.2%) were end-stopped. Most units (81.0%) had band-pass spatial frequency tuning functions and responded optimally to low spatial frequencies (mean spatial frequency: 0.08 c./degree). The remaining units (19.0%) were low-pass. All the recorded cells responded vigorously to edges defined by motion. The vast majority (96.0%) of cells responded optimally to large texture elements; approximately half the cells (57.3%) also responded to finer texture elements. Moreover, 38.5% of the cells were selective to the width of the bar (i.e., the distance between the leading and the trailing edges). Finally, some (9.0%) cells responded in a transient fashion to leading and to trailing edges. In conclusion, cells in the PLLS area are low spatial frequency analyzers that are sensitive to texture and to the distance between edges defined by motion.

1. Introduction

The visual system can quickly detect and identify objects in natural scenes, even though these scenes are usually composed of varied, complex and often degraded visual information. Perceiving an object as a distinct entity requires that the visual system segregate that object from the rest of the scene by defining its boundaries or edges. For example, an object may be segregated from its background based on differences in luminance, color, spatial disparity, texture, and direction of motion

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Abbreviations: c./degree, cycle per degree; cd/m^2, Candela per meter squared; Imp./s, impulses per second; MT, middle temporal area; PLLS, postero-lateral lateral suprasylvian; PMLS, postero-medial lateral suprasylvian; RF, receptive field; S.D., standard deviation

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(Julesz, 1971; Nothdurft, 1993). One of the most salient cues for figure–ground segregation is relative motion between an object and its background (Nothdurft, 1993). This is demonstrated by the fact that several species of prey have evolved a "freezing" strategy so as to eliminate this cue and escape the detection of predators.

In cats, the cortical areas surrounding the lateral suprasylvian sulcus are known to be involved in the processing of motion information (Lomber et al., 1996; Spear, 1991). A number of studies suggest that these areas are implicated in attention shifts (Ogasawara et al., 1984; Hardy and Stein, 1988; Payne et al., 1996), speed discrimination (Pasternak et al., 1989), the integration of complex motion (Rudolph and Pasternak, 1996), and the detection of forms that are in motion (Kiefer et al., 1989; Krüger et al., 1993). The lateral suprasylvian cortex consists of six areas, each containing an independent retinotopic map of the visual field (Palmer et al., 1978).

Research on the lateral suprasylvian cortex has largely focused on the postero-medial lateral suprasylvian area (PMLS). The receptive field properties of cells in PMLS have been extensively studied (Camarda and Rizzolatti, 1976; Hubel and Wiesel, 1969; Rauschecker et al., 1987a,b; Spear and Baumann, 1975; von Grünau et al., 1987; Zumbroïch et al., 1986), and the spatio-temporal properties of these cells have been well defined (Morrone et al., 1986; Zumbroïch and Blakemore, 1987; Zumbroïch et al., 1988; Guido et al., 1990). The role of PMLS cells with regards to motion perception has been well established (Morrone et al., 1986; Blakemore and Zumbroïch, 1987; Rauschecker et al., 1987a; von Grünau and Frost, 1983; Yin and Greenwood, 1992) and this area is usually considered homologous to area V5 (MT) of the macaque brain, the acknowledged motion center in primates (Payne, 1993).

Much less is known about the postero-lateral lateral suprasylvian cortex (PLLS). It is generally accepted that this area, like PMLS, contributes to motion analysis but the specific responses of cells in this area and the exact role they play in this process remains poorly defined.

Zumbroïch et al. (1986) highlighted an important difference between PLLS and PMLS. In the PLLS area, the upper visual field is over-represented and a large proportion of neurons extend their receptive fields into the ipsilateral visual field (up to 28 degrees from the vertical meridian). Furthermore, Rauschecker et al. (1987a) reported a centrifugal–centripetal organization of the receptive fields' optimal direction in PLLS; they link this type of organization with the analysis of expanding stimuli.

At the neuroanatomical level, the PLLS area receives both direct and indirect Y inputs from the dorsal lateral geniculate nucleus (Rauschecker et al., 1987b; Raczkowski and Rosenquist, 1983). This Y pathway is associated with the detection of motion (Stone et al., 1979; Khayat et al., 2000) and the coarse analysis of form (Stone, 1983). PLLS neurons also share strong reciprocal connections with the anterior ectosylvian area (Scannell et al., 1995), a higher-order cortical region that contributes to the analysis of motion (Benedek et al., 1988; Scannell et al., 1996). Furthermore, PLLS cells send outputs to neurons in the superficial, the intermediate and the deep layers of the superior colliculus (Kawamura and Hashikawa, 1978; Niida et al., 1997; Brecht et al., 1998), a structure associated with ocular movements, fixation, and orienting behavior (Roucoux and Crommelinck, 1976; Stein, 1978). Moreover, PLLS cells discharge after voluntary ocular movements (Komatsu et al., 1983), and electrical stimulation of these cells provokes convergent ocular movements (Toda et al., 2001).

One study systematically investigated the spatial and temporal properties of cells in area PLLS (Zumbroïch and Blakemore, 1987). Based on a very small sample (13 cells), they concluded that PLLS cells are spatially similar to those of PMLS, but that they tend to prefer higher temporal frequencies.

Recently, Li et al. (2000) have shown that the vast majority (90.0%) of PLLS cells responded to optic flow patterns, although only 20–25% of the cells were selective to certain types of optic flow stimuli (i.e., translation, rotation, or expansion–contraction). This is consistent with the report that the majority of cells in the lateral suprasylvian cortex respond preferentially to optic flow movies rather than to equivalent texture movies (Kim et al., 1997). Moreover, Sherk et al. (1997) have shown that cells in the PLLS area respond preferentially to objects moving against an optic flow movie rather than to a bar moving against a uniform background. Together, these findings suggest that the PLLS area constitutes an intermediate stage of processing for optic flow fields. There is also indirect evidence suggesting that the PLLS cortex is involved in figure–ground segmentation. The PLLS/PMLS border receives dense heterotopic callosal connections from the 17/18 border (Innocenti et al., 1995; Bressoud and Innocenti, 1999), and according to Innocenti et al. (1995), these callosal connections play a role in figure–ground segregation.

The contribution of motion-cues to figure–ground segregation has mainly been investigated with two types of texture-based stimuli. The first, a static form, is defined solely by the motion of a subset of elements (visual noise or textons) within fixed spatial coordinates (Frost, 1985; Gulyas et al., 1987, 1990). The second, similar to the stimuli used in the present study, consists of a subset of elements that move coherently within a background of static elements. In this case, if the elements become static, the form disappears and a completely uniform field of dots is perceived. This type of motion-defined form can be detected by neurons in the cat's dorsal lateral geniculate nucleus (Mason, 1976) and area 17 (Hammond and MacKay, 1977), as well as in the monkey primary visual cortex (Bourne et al., 2002) and MT area (Olavarria et al., 1992; Marcar et al., 1995). A recent study from our laboratory demonstrated that almost all cells in area 19 of the cat respond to a motion-defined bar or to its edges (Khayat et al., 2000). Our results also showed that texture density has an influence on figure–ground segmentation: cell responses increased as dot density decreased.

The first objective of the present study was to assess the spatial properties of the receptive fields of a large sample of cells in area PLLS and to determine their spatial frequency tuning functions. The second and main objective was to investigate the role of PLLS cortex in figure–ground analysis based on motion cues. Random-dot kinematograms were used to create drifting edges consisting of a textured form (i.e., a horizontal bar) against a similarly textured but static background. The response rates of PLLS neurons to moving bars of different widths were measured as a function of dot size.

2. Results

One hundred and seventeen cells were isolated in area PLLS of the cat. Cells presenting unstable or erratic responses were