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Research Report

The suprachiasmatic nucleus and the intergeniculate leaflet in the rock cavy (*Kerodon rupestris*): Retinal projections and immunohistochemical characterization

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ABSTRACT

In this study, two circadian related centers, the suprachiasmatic nucleus (SCN) and the intergeniculate leaflet (IGL) were evaluated in respect to their cytoarchitecture, retinal afferents and chemical content of major cells and axon terminals in the rock cavy (*Kerodon rupestris*), a Brazilian rodent species. The rock cavy SCN is innervated in its ventral portion by terminals from the predominantly contralateral retina. It also contains vasopressin, vasoactive intestinal polypeptide and glutamic acid decarboxilase immunoreactive cell bodies and neuropeptide Y, serotonin and enkephalin immunopositive fibers and terminals and is marked by intense glial fibrillary acidic protein immunoreactivity. The IGL receives a predominantly contralateral retinal projection, contains neuropeptide Y and nitric oxide synthase-producing neurons and enkephalin immunopositive terminals and is characterized by dense GFAP immunoreactivity. This is the first report examining the neural circadian system in a crepuscular rodent species for which circadian properties have been described. The results are discussed comparing with what has been described for other species and in the context of the functional significance of these centers.

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1. Introduction

A wide variety of behavioral and physiological processes show circadian rhythms which are generated by a time-keeping system, also called circadian timing system. This system in mammals is built from a neural network consisting of three major functional components: (1) a central pacemaker, which generates rhythmicity even in the absence of external stimuli; (2) input pathways, including retinal afferents to allow the synchronization of the rhythms to the environmental cycles; and (3) output pathways connecting the pacemaker to the brain and body's effectors.

Since the discovery of an unequivocal retinohypothalamic projection (Hendrickson et al., 1972; Moore and Lenn, 1972), other experimental evidence have emerged to support the role of the circadian pacemaker ascribed to the suprachiasmatic nucleus (SCN) of the hypothalamus (see Klein et al., 1991; van Esseveldt et al., 2000; Reuss, 2003; Morin and Allen, 2006).

The SCN is a paired nucleus located at the anterior hypothalamus, on either side of the third ventricle immediately

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dorsal to the optic chiasm. The neurochemical characterization of the SCN, as studied by immunohistochemical techniques, has revealed both consistencies and variations among the species. For example, in the SCN of virtually all mammals studied, two major cell populations have been identified, one consisting of vasopressin (VP)- and another formed by vasoactive intestinal polypeptide (VIP)-producing neurons. As a rule, VP cells are located in a dorsomedial position and VIP cells in a ventral or ventrolateral position, as observed in coronal sections of the SCN (Card et al., 1981; Ueda et al., 1983; Card and Moore, 1984; Van den Pol and Tsujimoto, 1985; Cassone et al., 1988; Smale et al., 1991; Mai et al., 1991; Morin et al., 1992; Tessoneaud et al., 1994; Negroni et al., 1997, 2003; Goel et al., 1999; Smale and Boverhof, 1999), although there are some exceptions (Cassone et al., 1988; Martinet et al., 1995; Wang et al., 1997; Abrahamson and Moore, 2001). The VIP cell territory is the preferable site for the arborization of dense retinal afferents, neuropeptide Y (NPY)-containing terminals of the geniculohypothalamic tract (GHT) and serotonin (5-HT) terminals from the midbrain raphe (Moore et al., 2002). The differential arrangement of VP and VIP cells allied with the pattern of distribution of its afferents provided the basis for the division of the SCN into dorsomedial and ventrolateral portions in the rat (Van den Pol and Tsujimoto, 1985; Card and Moore, 1991). These terms were replaced by "shell" and "core", based on the configuration observed in the hamster (Moore et al., 2002). Although it is difficult to generalize to all species, considering the great variability, a compartmentalization of the SCN stems in the neurochemical phenotype (Van den Pol and Tsujimoto, 1985), the pattern of distribution of their afferent terminals (Moga and Moore, 1997), the organization of their outputs (Leak and Moore, 2001), and even their molecular basis (Dardente et al., 2002).

Many other substances acting as neurotransmitters, neuromodulators or related enzymes were found in both perikarya and terminals of the SCN, such as NPY, 5-HT, gamma-aminobutyric acid (GABA), glutamate (GLU), bombesin (BBS), gastrin-releasing peptide (GRP), cholecystokinin (CCK), substance P (SP), angiotensin II, enkephalin (ENK), neurotensin (NT), somatostatin (SS), thyrotrophin-releasing hormone (TRH), tyrosine hydroxylase (TH), and nitric oxide synthase (NOS), among others (see Reuss, 2003).

A secondary component of the circadian timing system is the intergeniculate leaflet (IGL), a thin retinorecipient cell layer which, in rodents, is intercalated between the dorsal (DLG) and ventral (VLG) lateral geniculate nuclei, over the entire rostrocaudal length of the thalamic lateral geniculate complex (Hickey and Spear, 1976; Moore and Card, 1994). The geniculohypothalamic tract (GHT) derives mainly from NPY-producing cells which project from the IGL ending in the SCN (Harrington et al., 1985, 1987; Card and Moore, 1989; Morin et al., 1992). As long as NPY cells are present in the lateral geniculate complex, they have been used as a marker of the IGL. In the rodent IGL, the NPY colocalizes with GABA in most of the cells (Moore and Speh, 1993; Moore and Card, 1994) and with unidentified neurotransmitter cells to compose the geniculohypothalamic projection (Card and Moore, 1989). Many interspecific variations are found in the organization of the IGL/GHT. For example, the GHT also originates from enkephalin (ENK) cells in the IGL of hamsters (Morin et al., 1992; Morin and Blanchard, 1995, 2001), but not of rats (Card and Moore, 1989).

Although the IGL is not essential to photic synchronization (Klein and Moore, 1979), it has been shown to be involved in the modulation of photic and non-photic synchronization of the circadian rhythms (Harrington and Rusak, 1986; Mrosovsky, 1995; Muscat and Morin, 2006).

The rock cavy (*Kerodon rupestris*) is a rodent which according to the traditional taxonomy is classified in the superfamily Cavioidea, family Caviidae, subfamily Caviinae, genus *Kerodon*, together with *Cavia*, *Galea* and *Microcavia* (Cabrera, 1961; Lacher, 1981). However, after a molecular phylogeny of the superfamily Cavioidea using two nuclear sequences and one mitochondrial gene, *Kerodon* is placed sister to the family Hydrochaeridae, to which belongs also the capybara (*Hydrochaeris*) and closely aligned with the subfamily Dolichotinae (Rowe and Honeycutt, 2002). Rock cavies are found in the Brazilian Northeast region where they inhabit rocky areas, in which they usually shelter in its fissures or cracks. Based in reports of local hunters, this species is seen during the day and the night, although is more exposed and easily captured at dusk (Cabrera, 1961; Lacher, 1981). These observations were confirmed in captivity, since in a laboratory controlled condition study it was registered that the rock cavy is active along all 24-hours per day, although its activity is intensified around sunset and dawn phases, suggesting a predominantly crepuscular behavior (Sousa and Menezes, 2006).

Having as a goal to establish a regional model to circadian research, the aim of this study was to identify and characterize the circadian system of the rock cavy using immunohistochemical techniques. The SCN and the IGL were evaluated as to their cytoarchitecture, retinal afferents, and the presence of neuroactive substances and neuronal or glial markers. The content in calcium binding proteins of these centers in this species has already been described in a study of our laboratory (Cavalcante et al., 2008). Likewise, retinal projections to the thalamic paraventricular nucleus, a putative circadian center was also described (Nascimento et al., 2008).

2. Results

2.1. *Suprachiasmatic nucleus*

In Nissl-stained coronal sections, the rock cavy SCN was seen as paired cluster cells located in the anterior hypothalamus, dorsal to the optic chiasm, on each side of the third ventricle. At rostral levels (Figs. 1 and 2A), the SCN appeared as a triangular shaped nucleus and at mid (Figs. 1 and 2B) and caudal (Figs. 1 and 2C) levels, the nucleus assumed a pear-shaped contour, with its larger axis directed dorsoventrally, having medial and ventral boundaries more precise than dorsal and lateral ones. In the entire extent, the nuclei were seen to be separated each other partially by the third ventricle, being contacted by only its most dorsal portions. Apparently, there was an agglomerate of compact and darkly stained cells in the central region, surrounded by an area of sparser and less stained cells. Within this cell cluster, mostly in the caudal sections, it was also possible to visualize a set of cells closely compacted forming a ventral portion, and another one of loosely collected cells, constituting a dorsal portion (Figs. 2B and C). Each SCN was around 600 μm along its rostrocaudal

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