

available at www.sciencedirect.comwww.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****Effects of early binocular enucleation on auditory and somatosensory coding in the superior colliculus of the rat**François Champoux^a, Benoit A. Bacon^{a,b}, Franco Lepore^a, Jean-Paul Guillemot^{a,c,*}^aCentre de Recherche en Neuropsychologie et Cognition, Université de Montréal, Montréal, Québec, Canada^bDepartment of Psychology, Bishop's University, Sherbrooke, Québec, Canada^cDépartement de Kinanthropologie, Université du Québec à Montréal, Montréal, Québec, Canada

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ABSTRACT

The present study aimed at investigating the effects of early visual deprivation (bilateral neonatal enucleation) on auditory and somatosensory coding in the polysensory deep layers of the superior colliculus of the rat. The proportion of cells responding to auditory and somatosensory stimulation and the receptive field properties of single neurons were assessed in both normal and enucleated rats. As expected, in enucleated rats there was a drastic increase in the number of unresponsive units and visual responses could no longer be evoked. Most importantly, the proportion of cells that responded to auditory stimulation was drastically reduced. However, the few cells that remained responsive to auditory stimulation were well tuned to noise stimuli presented in both azimuth and elevation, principally in the contralateral hemifield. Enucleation also increased the proportion of cells responding to somatosensory stimulation, particularly to the vibrissae. Implications in terms of neural plasticity and functionality are discussed.

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1. Introduction

The ability to localize an object in space often depends on the integration of audiovisual inputs. Moreover, similar multisensory processes can occur when visual or auditory objects come in contact with the body.

The superior colliculus (SC), a mid-brain structure known for its involvement in orienting behavior, is generally believed to be a key structure in multisensory integration (Meredith and Stein, 1983; Stein and Meredith, 1993). The superficial layers of the SC mainly contain visually responsive neurons organized

to form a retinotopic map of visual space (Dräger and Hubel, 1975). Neurons in the deep layers can also be visually driven but they also respond to auditory and/or somatosensory stimulation (Chalupa and Rhoades, 1977; King and Palmer, 1983). It has been shown that these multisensory cells can show either facilitatory or inhibitory cross-modal interactions (King and Palmer, 1985; Meredith and Stein, 1986).

Neurons in the deep layers of the SC are organized to form maps of visual space, of auditory space and of the body surface (Knudsen, 1982; Meredith and Stein, 1983) that have been shown to be topographically aligned (Dräger and Hubel, 1975;

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Abbreviations: cd/m², candela per meter square; deg., degree; imp./s, impulses per second; PSTH, post-stimulus time histogram; RF, receptive field; SC, superior colliculus; SD, standard deviation

Knudsen, 1982; King and Palmer, 1983; King and Hutchings, 1987). Therefore, a target in a given region of space can activate neurons via multiple sensory channels and consequently combine these inputs to orient eyes, ears or gaze, via motor output neurons, towards that target (Meredith and Stein, 1983; Knudsen and Brainard, 1995).

Receptive field (RF) properties of non-visual neurons in the deep layers of the SC of the normal rat are well known. Gaese and Johnen (2000) have shown that auditory RFs mainly represent the contralateral hemispace and are selective to a limited range of azimuthal positions. Despite variability in the auditory spatial representation, Gaese and Johnen (2000) show that SC neurons' best azimuthal positions change with respect to anterior–posterior recording sites, such that neurons sensitive to frontal positions are located in the anterior part of the SC and neurons sensitive to rear positions are found in its posterior pole. Moreover, in rodents, most of the SC somatosensory neurons are devoted to the body map representing the contralateral face and vibrissae (Rhoades, 1980; Kao et al., 1989; Benedetti, 1991, 1992; Garcia Del Cano et al., 2004).

At the neurophysiological level, several studies have shown that the construction of the auditory spatial map in the SC can be altered if visual experience is modified. Hence, the representation of auditory space in the deep layers of the SC can be shifted if small displacements of visual topography are created by surgically induced squints or by the application of prisms on the eyes, as shown in the ferret (King et al., 1988) and in the barn owl (Brainard and Knudsen, 1998). In fact, it appears that the auditory map is realigned so as to remain in register with the visual map. Early monocular enucleation, a somewhat more drastic intervention, has been shown to disrupt normal auditory maps of space in the SC of guinea-pigs (Withington et al., 1994a) but, strangely, not in the SC of golden hamsters (Rhoades, 1980).

Given the ubiquity of multimodal interactions in the SC, a complete removal of the dominant visual input from an early age would be expected to modify neural responsiveness to auditory and somatosensory stimulation. At birth, sensory inputs from different modalities are in a state of competition. In the absence of normal stimulation in one of the channels, the other modalities may come to influence a larger proportion of neurons or improve their tuning properties, as shown by Vidyasagar (1978), Wallace et al. (2004) and Rauschecker and Harris (1983). Conversely, other studies report that visual deprivation, via lid sutures or dark-rearing, cause disruptions rather than fine-tuning of the auditory map in the SC. For example, auditory RFs showed poor definition in visually deprived guinea pig (Withington-Wray et al., 1990; Withington et al., 1994b,c), barn owl (Knudsen, 1991) and ferret (King and Carlile, 1993). It has been suggested that the blurred visual image created by lid suture lead to a poorly tuned auditory map of space (King and Carlile, 1993). However, because some visual function remains, lid sutured animals may not be as severely affected as dark-reared ones (Withington, 1992).

The relationship between physiological perturbations and functional consequences is even more evident following lesion of peripheral structures. Hence, early temporal retinal lesions in the rat induced extensive and rapid reorganization in the rostral tectum (Serfaty et al., 2005). Furthermore, complete bilateral enucleation produce ultra-structural alterations in

the superficial layers of the SC (Batista et al., 2003). Compared to dark-rearing and lid sutures, enucleation also leads to substantial changes in the functional properties of neurons. Therefore, their firing patterns and excitability in the superficial and consequently in the deep layers of the SC are significantly perturbed (Turner et al., 2005). The effect of bilateral enucleation on somatosensory responsiveness has been described previously in the rat SC and has been shown to produce an important increase of somatosensory responsive units, although their topographic arrangement remained unchanged (Benedetti, 1992).

The current investigation addresses two related questions. (1) What is the contribution of peripheral receptors (the eyes) and of the spontaneous and patterned activity they generate to the establishment of non-visual representations in the deep layers of the SC? To answer this question, we shall assess how early binocular enucleation affects the relative proportion of cells that respond to the various sensory modalities represented in the deep layers of the SC of the rat. (2) Can early binocular enucleation, by modifying the nature of inter-modal competition, affect the RF properties of auditory and somatosensory cells in these layers? To our knowledge, a single study (Gaese and Johnen, 2000) has investigated auditory RFs in the deep layers of the SC of the rat and the question remains as to the importance of visual input for the elaboration of their properties. To answer these questions, we shall examine the RF properties of responsive neurons in both normal and bilaterally enucleated rats to determine whether visual deprivation leads to compensatory improvement or rather to losses in tuning properties. This will be achieved by recording the activity of single-neurons to noise burst stimuli presented in azimuth and elevation positions and to cutaneous stimulation applied to different body parts.

2. Results

2.1. Effects of early visual deprivation on polysensory coding in the SC of the rat

In a first series of experiments, a total of 330 neurons were isolated in the deep layers of the SC of 11 normal adult rats

Table 1 – Number and proportion of cells responding to the various sensory modalities in the deep layers of the superior colliculus of the rat

Modalities	Normal rat		Enucleated rat	
	n	%	n	%
Visual	75	39.1	0	0
Somatosensory	50	26	99	71.7
Auditory	10	5.2	0	0
Visual/auditory	11	5.7	0	0
Visual/somatosensory	19	9.9	0	0
Somatosensory/auditory	19	9.9	8	5.8
Visual/somatosensory/auditory	5	2.6	0	0
Undrivable	3	1.6	31	22.5
Total	192		138	

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