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BRAIN RESEARCH

Visual stimulation synchronizes or desynchronizes the activity of neuron pairs between the caudate nucleus and the posterior thalamus

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ABSTRACT

Recent morphological and physiological studies have suggested a strong relationship between the suprageniculate nucleus (Sg) of the posterior thalamus and the input structure of the basal ganglia, the caudate nucleus (CN) of the feline brain. Accordingly, to clarify if there is a real functional relationship between Sg and CN during visual information processing, we investigated the temporal relations of simultaneously recorded neuronal spike trains of these two structures, looking for any significant cross-correlation between the spiking of the simultaneously recorded neurons. For the purposes of statistical analysis, we used the shuffle and jittering resampling methods. Of the recorded 288 Sg-CN neuron pairs, 26 (9.2%) showed significantly correlated spontaneous activity. Nineteen pairs (6.7%) showed correlated activity during stationary visual stimulation, while 21 (7.4%) pairs during stimulus movement. There was no overlap between the neuron pairs that showed crosscorrelated spontaneous activity and the pairs that synchronized their activity during visual stimulation. Thus visual stimulation seems to have been able to synchronize, and also, by other neuron pairs, desynchronize the activity of CN and Sg. In about half of the cases, the activation of Sg preceded the activation of CN by a few milliseconds, while in the other half, CN was activated earlier. Our results provide the first piece of evidence for the existence of a functional cooperation between Sg and CN. We argue that either a monosynaptic bidirectional direct connection should exist between these structures, or a common input comprising of parallel pathways synchronizing them.

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1. Introduction

The central nervous system is composed of a cooperating network of cortical areas and subcortical structures. The linear transmission of information is a widely accepted theory in neurophysiology (Hubel and Wiesel, 1962, 1965; Lennie, 1980; Nowak and Bullier, 1997; Stone et al., 1979). However, in the recent years more and more evidence has been accumulated to suggest the existence of parallel loops in the central nervous system. This type of information processing is a characteristic feature of the basal ganglia (McHaffie et al., 2005), as the various functions of them are virtually based on such loops.

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The caudate nucleus (CN) is the main input structure of the basal ganglia loop. It is involved in adjusting visuomotor behavior and contributes to the control of visually guided oculomotor and skeletomotor functions (Barneoud et al., 2000; Hikosaka et al., 2000; Lynd-Balta and Haber, 1994; Schwarz et al., 1984). Accordingly, a number of studies have been performed to clarify the role of CN in visual information processing (Brown et al., 1995; Hikosaka et al., 1989; Kolomiets, 1993; Nagy et al., 2003; Pouderoux and Freton, 1979; Rolls et al., 1983; Strecker et al., 1985). Despite of these studies there is some degree of uncertainty concerning the pathways conveying sensory information to the basal ganglia. Earlier neuroanatomical findings in cats and rabbits stressed the predominant role of the geniculostriate pathway that conveys visual information toward CN (Hollander et al., 1979; Webster, 1965). However, recent neuroanatomical and physiological studies have seemed to support the suggestion that the extrageniculate ascending tectofugal pathways project to CN in amniotes, where the suprageniculate nucleus of the posterior thalamus (Sg) or the rotund nucleus in reptiles and birds seem to be the thalamic input structure of CN (Guirado et al., 2005; Harting et al., 2001).

Besides the proven anatomical connection, it is already known that the visual receptive field properties are similar in the two structures. The visual receptive field was found to be large, covering almost the whole visual field of the investigated eye. Furthermore, retinotopical organization was not detected in these structures. The units responded optimally to small stimuli moving at intermediate or high velocities in a particular direction of the huge receptive field. This supports the notion that the CN and Sg process dynamic visual information. Neurons within both structures responded optimally to low spatial frequencies and exhibit low spatial resolution and lowpass spatial tuning. The neurons displayed optimal responses to high temporal frequencies and narrow temporal frequency tuning (Nagy et al., 2008; Paróczy et al., 2006; Rokszin et al., 2010). The very high similarity of the visual receptive fields of the CN and the Sg points to the existence of a very intensive exchange of information between the two stages of visual processing.

In this study we sought to investigate the above mentioned extrageniculate thalamic connection of the caudate nucleus of the feline brain. Our main question was if there might be synchronization and/or temporal coupling between the activity of neurons in the Sg and CN. Another goal was to find out if visual stimulation synchronizes or desynchronizes the activity of the simultaneously recorded Sg–NC neuron pairs. Our results are the first to provide evidence on the cross-correlated neuronal activity in the posterior thalamus and the CN, suggesting a monosynaptic nonlinear, bidirectional information flow between Sg and CN.

2. Results

Altogether 138 visually active neurons were recorded with stable spontaneous activity from the Sg and 142 from the CN. From these neuron pools we could form 283 simultaneously recorded Sg–CN cell-pairs the synchronization of which has been investigated in this study.

2.1. Correlation during spontaneous activity

To get a notion about the baseline synchronization without the presence of visual stimuli, we analyzed cross-correlation during the period of black blank screen background presence in the visual field. On the whole, 26 pairs (9.19%) showed significant correlation, the residual 257 pairs (90.81%) were not significantly correlated. All the detected interactions were excitatory, indicated by a positive peak on the cross-correlogram. The most intriguing finding of the present study is that it could not be determined unambiguously whether Sg or CN is the leading structure in the information processing pathway. In 13 cases (50%) the peak on the cross-correlogram, with a mean time lag of 6.8+/-2.52 ms, indicates that Sg leads CN (Fig. 2A,B). On the other hand in 11 cases (42.31%) CN seems to be the information transmitter, and Sg is the receiver, the mean time lag being 5.7+/-2.10 ms (Fig. 2C,D). Moreover, in two cases (7.69%) the peak appeared with $0 \text{ ms time } \log_{1}^{1}$ which indicates that the two structures were simultaneously activated.

2.2. Correlation during static random dots stimulation

When we analyzed the cross-correlograms during the stationary random dot stimulation, we found significant correlation in 19 pairs (6.71%); all of them indicated excitatory interaction.

In 8 cases (42.11%) the Sg (mean time lag 5+/-2.56 ms, Fig. 2), in 7 cases (36.84%) CN (mean time lag=5.86+/-2.91 ms, Fig. 3) seemed to be the preceding structure, and we could detect simultaneous activation with a time lag of 0 ms for this type of stimuli in 4 cases (21.05%). All the pairs which showed significant cross-correlation were different from those which showed significant interaction during the spontaneous period. So it seems that there are different subpopulations among the directly connected Sg-CN neuronal pairs. Visual stimulation can either synchronize the neuronal activity between the Sg and CN (those 19 neuron pairs that showed no significant cross-correlation in the analysis of spontaneous activity but showed cross-correlation during static visual stimulation) or can also desynchronize the activity of the Sg and CN neurons (those 26 Sg-NC neuron pairs which showed cross-correlated spontaneous activity but no cross correlated activity to static visual stimulation).

2.3. Correlation during randomly moving dots stimulation

We also calculated the cross-correlation between the two structures during the time period of the randomly moving dots stimulation. In 21 cases (7.42%) we found significant excitatory interaction between the two structures, and no inhibitory interaction was indicated.

Sg seemed to be the preceding structure in 10 cases (47.62%, Fig. 4), with a mean time lag of 5.7 + / - 2.8 ms, and CN was indicated to be preceding in 8 cases (38.10%, Fig. 5), with the mean time lag of 4.25 + / - 1.8 ms. Simultaneous activa-

 $^{^{1}}$ 0 ms timebin=0+/-1 ms — because of the 1 ms bin resolution this range means synchronization.

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