

TEMPORALLY ADVANCED DYNAMIC CHANGE OF RECEPTIVE FIELD OF LATERAL GENICULATE NEURONS DURING BRIEF VISUAL STIMULATION: EFFECTS OF BRAINSTEM PERIBRACHIAL STIMULATION

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Abstract—Processing of visual information in the brain seems to proceed from initial fast but coarse to subsequent detailed processing. Such coarse-to-fine changes appear also in the response of single neurons in the visual pathway. In the dorsal lateral geniculate nucleus (dLGN), there is a dynamic change in the receptive field (RF) properties of neurons during visual stimulation. During a stimulus flash centered on the RF, the width of the RF-center, presumably related to spatial resolution, changes rapidly from large to small in an initial transient response component. In a subsequent sustained component, the RF-center width is rather stable apart from an initial slight widening. Several brainstem nuclei modulate the geniculocortical transmission in a state-dependent manner. Thus, modulatory input from cholinergic neurons in the peribrachial brainstem region (PBR) enhances the geniculocortical transmission during arousal. We studied whether such input also influences the dynamic RF-changes during visual stimulation. We compared dynamic changes of RF-center width of dLGN neurons during brief stimulus presentation in a control condition, with changes during combined presentation of the visual stimulus and electrical PBR-stimulation. The major finding was that PBR-stimulation gave an advancement of the dynamic change of the RF-center width such that the different response components occurred earlier. Consistent with previous studies, we also found that PBR-stimulation increased the gain of firing rate during the sustained response component. However, this increase of gain was particularly strong in the transition from the transient to the sustained component at the time when the center width was minimal. The results suggest that increased modulatory PBR-input not only increase the gain of the geniculocortical transmission, but also contributes to

faster dynamics of transmission. We discuss implications for possible effects on visual spatial resolution. © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: visual system, dorsal lateral geniculate nucleus, receptive field dynamics, brainstem stimulation, cholinergic modulation.

INTRODUCTION

Several lines of evidence indicate that visual processing of stimuli has a fast transient response component responsible for the detection and generation of coarse impressions, and a subsequent more sustained component responsible for the generation of more detailed and stable visual impressions (e.g. Breitemeyer, 1975; Marr and Poggio, 1979; Hegdé and van Essen, 2004). Early studies of neurons at different levels of the visual pathway demonstrated the characteristic change of firing during brief visual stimulation; an initial strong transient followed by weaker sustained firing (e.g. Kuffler, 1953; Kuffler et al., 1957; Hubel and Wiesel, 1961, 1962; Baumgartner and Hakas, 1962). More recently, fast coarse-to-fine changes of response to selective stimulus features were discovered (e.g. Ringach et al., 1997; Bredfeldt and Ringach, 2002; Menz and Freeman, 2003; Frazor et al., 2004; Hegdé and Van Essen, 2004). In particular, the receptive fields (RF) of single neurons at cortical and subcortical levels changes rapidly during a brief presentation of a visual stimulus of duration similar to normal fixation intervals between saccadic eye-movements (e.g. Wörgötter et al., 1998; Suder et al., 2002; Allen and Freeman, 2006; Ruksenas et al., 2007; Einevoll et al., 2011). In the dorsal lateral geniculate nucleus (dLGN), there is a pronounced shrinkage of the RF-center of thalamocortical (TC) neurons during the initial transient firing component, indicating rapid and dynamic increase of spatial resolution. Minimum width appears about 60–80 ms after stimulus onset, followed by a slight widening to a rather steady size during the sustained firing component (Ruksenas et al., 2007; Einevoll et al., 2011). Experimental and theoretical analyses of the transition between the initial highly dynamic transient and the subsequent sustained response suggested that the two components reflect

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Abbreviations: dLGN, dorsal lateral geniculate nucleus; EEG, electroencephalography; H–C, Horsley–Clarke coordinates; OX, optic chiasm; PBR, peribrachial region of the brainstem; RF, receptive field; TC, thalamocortical.

distinct neural mechanisms that operate with partial temporal overlap (Einevoll et al., 2011).

The transmission of visual signals from retina to cortex through dLGN occurs in a state-dependent manner regulated by ascending input from brainstem and hypothalamus (reviewed in Steriade et al., 1997; Jones, 2007). The presumably most prominent modulatory input comes from cholinergic neurons in the peribrachial region (PBR) of the mesencephalic brainstem (De Lima et al., 1985; De Lima and Singer, 1987; Francesconi et al., 1988; Raczkowski and Fitzpatrick, 1989; Fitzpatrick et al., 1989; Montero, 1991; Beaulieu and Cynader, 1992), which show increased firing during arousal (reviewed in Steriade, 2003). Thus, TC neurons give increased firing to visual stimuli during arousal, with particular enhancement of the sustained response component (Coenen and Vendrik, 1972; Livingstone and Hubel, 1981; Sawai et al., 1988). Consistently, electrical stimulation of PBR, or local application of acetylcholine in dLGN, decreases response latency and increases the firing rate of TC neurons to visual stimuli (e.g. Sillito et al., 1983; Eysel et al., 1986; Francesconi et al., 1988; Hartveit and Heggelund, 1993; Hartveit et al., 1993; Uhlrich et al., 1995; Fjeld et al., 2002). Available data indicate that this effect is due to a muscarine-receptor-mediated slow and long-lasting depolarization that can shift the firing mode of TC neurons from rhythmic burst firing at hyperpolarized membrane potentials during drowsiness and slow-wave sleep, to tonic firing of single action potentials during arousal and REM sleep (reviewed in McCormick and Bal, 1997; Steriade, 2003).

Effects of cholinergic modulation on the spatial RF-properties of TC neurons are less well understood. No clear change of RF-center width seems to occur by transition from sleep to awake states (Coenen and Vendrik, 1972; Livingstone and Hubel, 1981), or after iontophoretic application of acetylcholine (Sillito et al., 1983; Eysel et al., 1986). However, a slight widening combined with a small decrease of center-surround antagonism appeared by electrical PBR-stimulation (Hartveit et al., 1993; Fjeld et al., 2002). These data were mainly based on average response during the presentation of the visual stimulus, thereby mainly reflecting effects on the sustained response component. Thus, we lack information about possible specific effects of acetylcholine or increased PBR input on other response components, and in particular on the dynamic changes of the spatial RF-properties during presentation of a visual stimulus.

Here we used a time-slicing technique (Ruksenas et al., 2007) to study the width of the RF-center at different times after the onset of a spot stimulus centered on the RF, and compared the changes of center width during PBR-stimulation with changes in the control condition without PBR-stimulation. We found a similar magnitude of changes of center width in the two conditions, but the dynamic changes of RF-center width occurred earlier during PBR-stimulation.

EXPERIMENTAL PROCEDURES

Surgical procedures

The experimental procedures were approved by the Norwegian Animal Research Authority according to the Norwegian Animal Welfare Act and the European Communities Council Directive 86/609/EEC.

The experimental methods have been described in detail elsewhere (Ruksenas et al., 2007). Briefly, adult cats (2.0–3.5 kg) were prepared acutely (arterial and venous cannulation, tracheotomy and craniotomies) under anesthesia induced by xylazine (1.5 mg/kg i.m.) and ketamine hydrochloride (10 mg/kg i.m.), and maintained during surgery by halothane or isoflurane (0.9–1.5%, after induction with 2.5%) in N₂O/O₂ (70/30). Local anesthetics (Xylocain; Astra) were applied on pressure points and wound margins. After completion of surgery, the animals were immobilized (gallamine triethiodide, initial dose 40 mg, maintenance dose 10 mg/kg/h), and anesthesia was maintained throughout the experiment by halothane or isoflurane (0.4–1.2%) in N₂O/O₂ (70/30). Electroencephalography (EEG) was continuously made from a pair of silver-wires in the left visual cortex (Horsley–Clarke coordinates (H–C): posterior 3.5 mm, lateral 2.0 and 10.0 mm). Arterial blood pressure, heart rate, end tidal CO₂ (kept at 4%), and rectal temperature (kept at 38 °C by a temperature-controlled heating blanket) were also continuously monitored throughout the experiment. Level of anesthesia was adjusted to maintain stable blood pressure, heart rate, and an EEG-pattern with dominant frequencies below 4 Hz. To increase eye stability, we made bilateral cervical sympathectomy (Rodieck et al., 1967). We dilated the pupils with atropine, and retracted the nictitating membranes with phenylephrine. The eyes were focused on a video monitor 0.86 or 1.14 m in front of the cat's eyes by means of proper contact lenses.

PBR-stimulation

A bipolar stimulation electrode (0.2 mm stainless steel or tungsten), varnish insulated except for the tips (exposure 0.3–0.75 mm), was implanted stereotaxically into the optic chiasm (OX) at H–C coordinates anterior 14.0 mm with each wire located 1.75 mm from the midline. The electrode was advanced until the threshold for cortical-evoked potential to electrical OX-stimulation (single 50- μ s square-wave pulses) was minimal (Francesconi et al., 1988; Hartveit and Heggelund, 1993). For PBR-stimulation, we implanted another bipolar electrode (lateral tip separation 2 mm) at the midbrain–pontine junction (H–C AP0, 2.0–4.0 mm from the midline, horizontal about +8 mm; Ahlsén et al., 1984; Francesconi et al., 1988; Hu et al., 1989; Hartveit and Heggelund, 1993) ipsilateral to recording electrodes in dLGN (cf. Fig. 1 in Hartveit and Heggelund, 1993). For optimal positioning of the PBR-electrode, we gave OX-stimulation with and without an electrical pulse train through the PBR-electrode (five 50- μ s square-wave

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