



Selective interhemispheric circuits account for a cardinal bias in spontaneous activity within early visual areas

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ABSTRACT

Ongoing brain activity exhibits patterns resembling neural ensembles co-activated by stimulation or task performance. Such patterns have been attributed to the brain's functional architecture, e.g. selective long-range connections. Here, we directly investigate the contribution of selective connections between hemispheres to spontaneous and evoked maps in cat area 18 close to the 17/18 border. We recorded voltage-sensitive dye imaging maps and spiking activity while manipulating interhemispheric input by reversibly deactivating corresponding contralateral areas. During deactivation, spontaneous maps continued to be generated with similar frequency and quality as in the intact network but a baseline cardinal bias disappeared. Consistently, neurons preferring either horizontal (HN) or vertical (VN), as opposed to oblique contours, decreased their resting state activity. HN decreased their rates also when stimulated visually.

We conclude that structured spontaneous maps are primarily generated by thalamo- and/or intracortical connectivity. However, selective long-range connections through the corpus callosum – in perpetuation of the long-range intracortical network – contribute to a cardinal bias, possibly, because they are stronger or more frequent between neurons preferring horizontal and/or cardinal contours. As those contours are easier perceived and appear more frequently in natural environment, long-range connections might provide visual cortex with a grid for probabilistic grouping operations in a larger visual scene.

Introduction

Accumulating evidence from the last few decades has been changing the perspective of the brain as a mere input-output system. It is known that the brain does not passively react to external stimulation but rather expresses a diversity of active ongoing processes. Variations in spontaneous activity prior to stimulus presentation account for inter-trial variability in motor cortex activation and human behavior (Fox et al., 2006, 2007) as well as differences in the precision of stimulus detection (Schölvinck et al., 2012; Emadi et al., 2014), facial recognition (Hesselmann et al., 2008) and auditory perception (Sadaghiani et al., 2009). Pre-stimulus activity also allows for predictions of choice in specific tasks (Bode et al., 2012; Colas and Hsieh, 2014) as well as general patterns of behavior (Davis et al., 2013). Summarizing, it seems likely that external stimuli do not determine brain activity but instead modulate spontaneous activity finally giving rise to output such as perception or behavior (Fiser et al., 2004).

Ongoing brain activity is not random. It has spatial features resembling neural ensembles co-activated by stimulation or task performance. Spontaneous neuronal firing is strongly correlated between functionally related neurons (Tsodyks et al., 1999). Evoked spiking patterns for specific sound frequencies seem to replay from a wider set of possible spontaneous patterns (Luczak et al., 2009). Spontaneous activation of a large population of neurons is capable to generate modular maps of iso-orientation preference in the primary visual cortex (Kenet et al., 2003). Even larger networks of ongoing activity between cortical areas, resembling evoked activity have been observed (Smith et al., 2009). These networks are often referred to as intrinsic connectivity networks (ICNs) or resting-state networks (RSNs) (Sadaghiani and Kleinschmidt, 2013).

There is manifold evidence that neurons in the visual cortex responding to contours of the same orientation are preferentially linked by long-range patchy connections (Gilbert and Wiesel, 1989; Malach et al., 1993; Bosking et al., 1997; Schmidt et al., 1997a; Stettler

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et al., 2002). A close relationship between the anatomical configuration of that patch system as determined by tracer injections, and the structure of maps acquired through visual stimulation has been suggested (Muir et al., 2011). Along this line, also spontaneous maps like the ones found by Kenet et al. (2003) have been associated with the architecture of long-range intra- and corticocortical intrinsic and/or feedback connections.

The aim of the present work was to causally investigate the contribution of selective connections to intrinsically generated modular orientation maps. Interhemispheric connections between the two primary visual cortices of cats are thought to perpetuate the intrahemispheric network across the visual field's midline, are also patchy (Houzel et al., 1994) and selectively link neurons of similar orientation (Schmidt et al., 1997b; Rochefort et al., 2007) and direction preference (Peiker et al., 2013). As visual interhemispheric connections (VIC) can be easily manipulated by reversible deactivation without directly interfering with the recorded ipsilateral responses, we chose them as a model for a selective long-range connection between homotopic visual areas.

While imaging central parts of contralateral cat area 18 including the 17/18 areal border using voltage-sensitive dyes (VSD) with and without visual stimulation we confirm that modular maps resembling evoked orientation preference maps occur spontaneously. During deactivation of contralateral input these spontaneous maps continue to be generated but the commonly observed cardinal bias in their frequency of occurrence disappears. As spontaneous cortical activity of a single neuron can be predicted by the spatial pattern of spontaneous population activity in a large cortical area (Tsodyks et al., 1999) we also examine spiking activity during these conditions. In line with the VSD data spontaneous spiking activity of neurons preferring horizontal and vertical contours decreases during contralateral deactivation.

Material and methods

Surgical procedures

All procedures were performed in accordance with the guidelines of the Society for Neuroscience and the university ethics committee for the use of animals (CEUA-UFRN). Eight adult cats, five males and three females, received a craniotomy on both hemispheres covering a portion of both areas 17 and 18 as well as the 17/18 border region. For surgery, animals were initially anesthetized with an intramuscular injection of ketamine (10 mg/kg) and xylazine (1 mg/kg) supplemented with atropine (0.1 mg/kg). Anesthesia was maintained after tracheotomy by artificial ventilation with a mixture of 0.6/1.1% halothane (for recording/surgery, respectively) and N₂O/O₂ (70/30%). After surgery each animal was paralyzed by a bolus injection of 1 mg pancuronium bromide followed by continuous intravenous infusion (0.15 mg/kg/h).

Over the left craniotomy, a recording chamber was implanted, fixed with dental cement and, after removal of the dura mater, filled with silicon oil for intrinsic signal and voltage-sensitive dye (VSD) imaging. We refer to this left to be recorded hemisphere as the ipsilateral one in the following. In case of VSD imaging, the cortex was first stained with a commercially available blue dye (RH 1838, Optical Imaging Inc) and then covered with silicon oil. Over the right hemisphere, a surface cryoloop (Lomber et al., 1999) was placed and covered with clear agar (Fig. 1A). We refer to this right to be deactivated hemisphere as the contralateral one in the following. The cooling probes were made of hypodermic stainless steel tubing shaped to fit the marginal gyrus centered on the 17/18 border (Horsley Clarke coordinates AP 0, L -3.5) including the adjacent central parts of area 17 and area 18. The dimensions of the loop used in the present experiments were 7×3.4 mm. The stainless steel tubing was connected to Teflon tubing, through which chilled methanol was pumped. The methanol was chilled by dry ice to -65 °C. The temperature of the cooled cortical

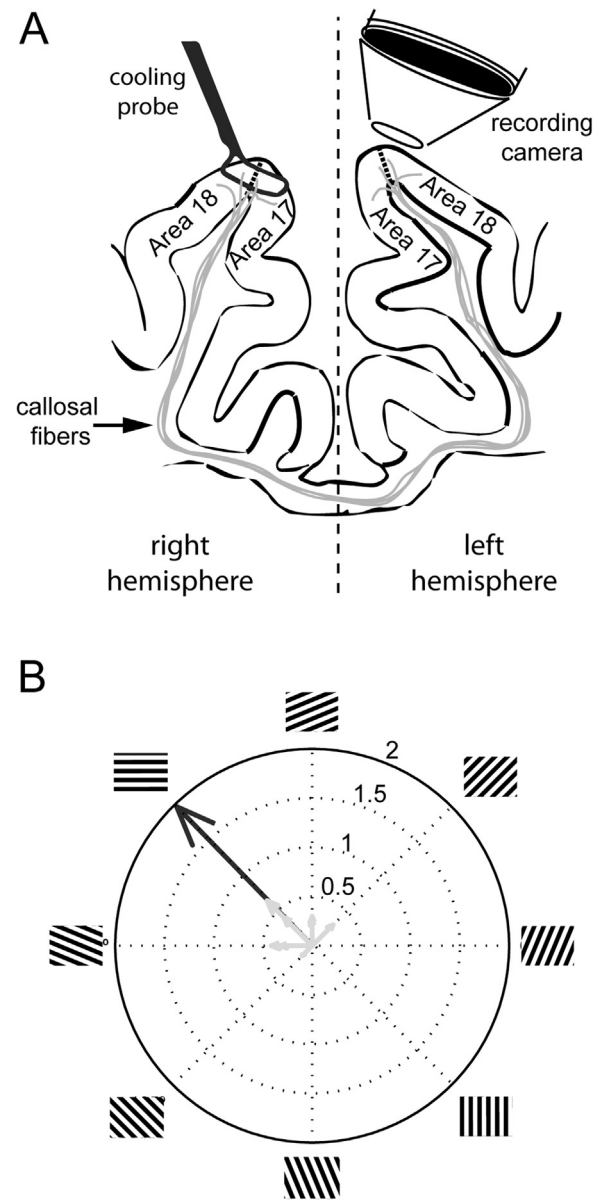


Fig. 1. A: Experimental setup with cooling loop on the right (R) and recording chamber on the left (L) hemisphere. B: Vector sum of eight correlation coefficients between one evoked single frame and eight average reference maps. Light gray arrows, correlation coefficient vectors; black arrow, resultant vector.

surface was regulated by the speed of the pump. A thermometer connected to a sub-miniature connector, attached to a copper wire soldered to the union of the loop was used for temperature monitoring. Considering the cooling spread on brain tissue, the critical temperature to cease activity and the cryoloop dimensions, we set the cryoloop temperature to around 2 °C in order to get a deactivated area of about 10×5 mm².

Visual stimulation

Visual stimuli were presented randomly on a 21" monitor placed 57 cm in front of the cats' eyes. We used intrinsic signal imaging in order to identify the 17/18 border. To this end, gratings of four different orientations in 45° steps and a spatial frequency of 0.5 cyc/° (for area 17) or 0.1 cyc/° (for area 18) and a velocity of 4°/s (for area 17) or 16°/s (for area 18). Gratings were moved back and forth for 3000 ms changing direction every 500 ms. For VSD imaging, the stimulus set consisted of 12 conditions; two conditions presented a

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