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The Pulvinar Thalamic Nucleus of Non-Human Primates: Architectonic and Functional Subdivisions

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Chapter 11
GABA Inactivation of the Pulvinar

A direct way to access the pulvinar-cortical interaction is to pharmacologically inactivate the pulvinar and measure the impact on cortical activity. To this aim, we have focused our efforts on recording in cortical visual area V2. The main afferents to area V2 originate in the primary visual cortex (Federer et al. 2009). However, pulvinar subregions PI and PL also provide robust projections to V2 and constitute the major subcortical input to this area. Pulvinar terminal zones align with regions of increased cytochrome oxidase staining in V2, avoiding the pale stripes (Levitt et al. 1995). All V2 stripes receive input from V1. However, the strongest V1 inputs target the V2 pale stripes. This suggests that inputs from V1 and from the pulvinar target distinct V2 modules of visual processing (Sincich and Horton 2002).

We used γ-aminobutyric acid (GABA) injections to inactivate parts of the PI and PL subregions of the capuchin monkey pulvinar (Soares et al. 2001). Our inactivation device included three cannulas placed evenly around a recording electrode. We could thereby monitor pulvinar inactivation using electrophysiological recordings. We usually obtained a 60% reduction in pulvinar neuronal activity immediately after the injection. Recovery of pulvinar activity to levels observed prior to GABA injection could take up to 70 min. Therefore, the corresponding projections from the pulvinar to the cortex were presumably shut down during a significant period. During this period, we were able to record the electrophysiological activity of single neurons in area V2, whose receptive fields matched the topographic representation of the pulvinar inactivation site. Pulvinar inactivation resulted in a myriad of physiological effects in area V2, but two main effects can be here highlighted. The first effect consisted in a general baseline shift in neuronal firing for both spontaneous and stimulus driven activity, which provides further evidence that the

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pulvinar may be involved in the large-scale modulation of cortical arousal. The second effect of pulvinar GABA inactivation involved changes in the receptive field properties of V2 receptive fields, namely, their selectivity for stimulus orientation and direction of motion.

The majority (~67%) of the recorded V2 cells showed changes in baseline activity after pulvinar GABA inactivation, with slightly more V2 neurons undergoing response increment as compared to response reduction (~40% vs. 27%, respectively). GABA can act over several neuronal structures that constitute the complex synaptic glomeruli of the pulvinar. In some cases, it may reduce the postsynaptic depolarization of neurons projecting to the cortex. As a result of pulvinar inactivation, V2 would lose a direct excitatory modulation, which could explain the reduction in its neuronal activity. Alternatively, pulvinar projections could target V2 inhibitory interneurons, causing thereby an increase in general V2 activity after GABA inactivation. The fact that the majority of V2 neurons show a response increase with pulvinar inactivation suggests that inhibitory interneurons may constitute an important component of pulvinar-V2 interaction. Figure 11.1 illustrates a V2 single unit, which showed a reduction in stimulus driven activity to a moving bar after pulvinar inactivation with GABA. Note the substantial reduction in cell response, which starts to recover 83 min. after the injection. The cell activity was recorded before (0) and at different time intervals (21, 83, and 133 min) after injection of GABA. Figure 11.2 illustrates another V2 single unit that increased its baseline activity with GABA inactivation of the pulvinar. Neuronal activity was recorded before (0) and at discrete time intervals (28, 60, and 149 min) after injection. We observed an increment in neuronal activity for both spontaneous and stimulus driven responses. While the stimulus-driven activity begins to normalize at 149 min postinjection, spontaneous activity remains high for reasons which are not completely clear.

An even larger proportion of V2 neurons (~91%) showed changes in orientation or direction selectivity after pulvinar inactivation, where a decrease in selectivity was the most commonly observed effect. This indicates that the pulvinar may play an active role in the neuronal circuit responsible for shaping V2 stimulus selectivity. Note, for example, the successive changes in orientation/direction selectivity that take place during pulvinar inactivation in Fig. 11.2.

Other neurons we studied completely lost their selectivity to orientation or direction but still showed this late rebound effect in the spontaneous activity as seen in Fig. 11.2 and, to a smaller degree, in Fig. 11.1. The physiological mechanisms behind the late rebound effect could be partially explained by the existence of indirect circuits involving other cortical visual areas that receive pulvinar projections and that also project to V2, such as V4 (Zeki and Shipp 1989), MT (Rockland and Pandya 1979), and the inferotemporal cortex (Felleman and Van Essen 1991).

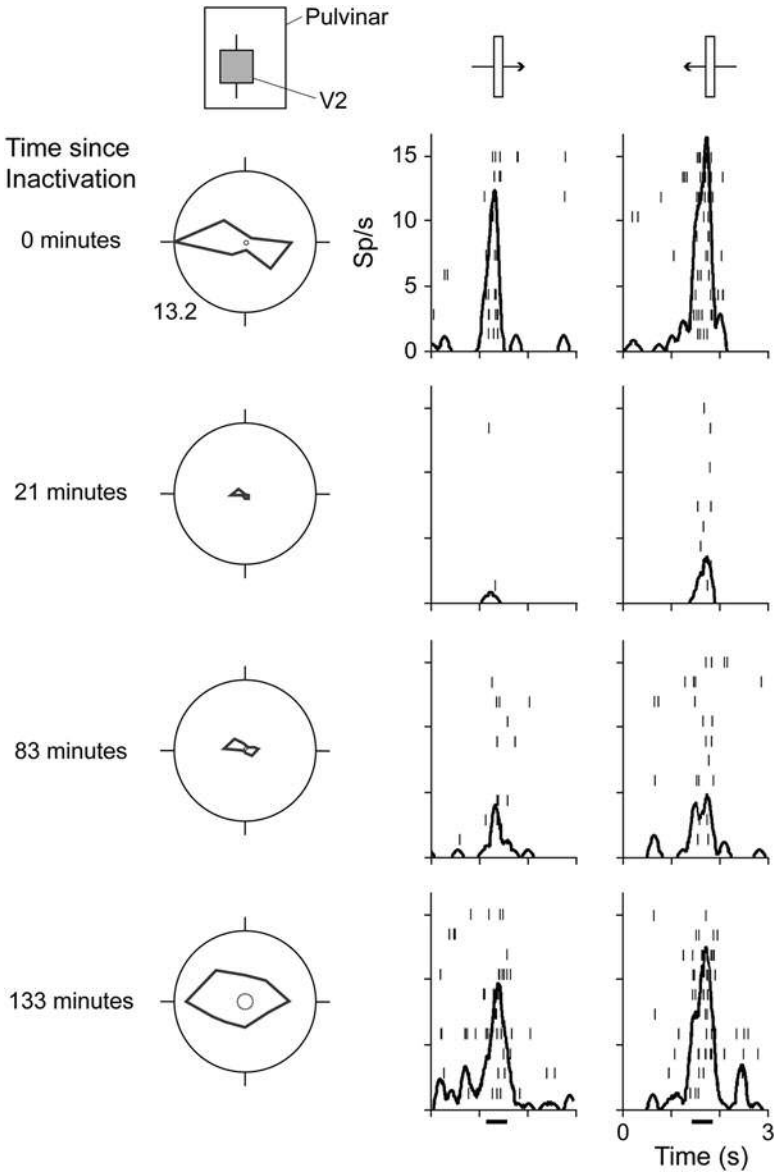

Fig. 11.1 Overall activity decrease of a single V2 unit after GABA inactivation of the pulvinar. Neuronal activity in area V2 was recorded before (0) and at discrete time intervals (21, 83, and 133 min) after GABA injection in the pulvinar. Note the substantial decrease in neuronal activity with GABA, which starts to recover 83 min after the injection. Right: PSTHs of the responses to the preferred stimuli. Left: Polar diagrams displaying the mean response rates for the full set of stimulus directions (45° steps). Dotted-line circles at the center of polar diagrams correspond to the mean spontaneous activity of the cell. The radii of the external circles indicate the maximum recorded response (13.2 spikes/s). Black bars below the PSTHs indicate the time interval during which the stimulus was moving inside the V2 RF. (Modified from Soares et al. 2004)

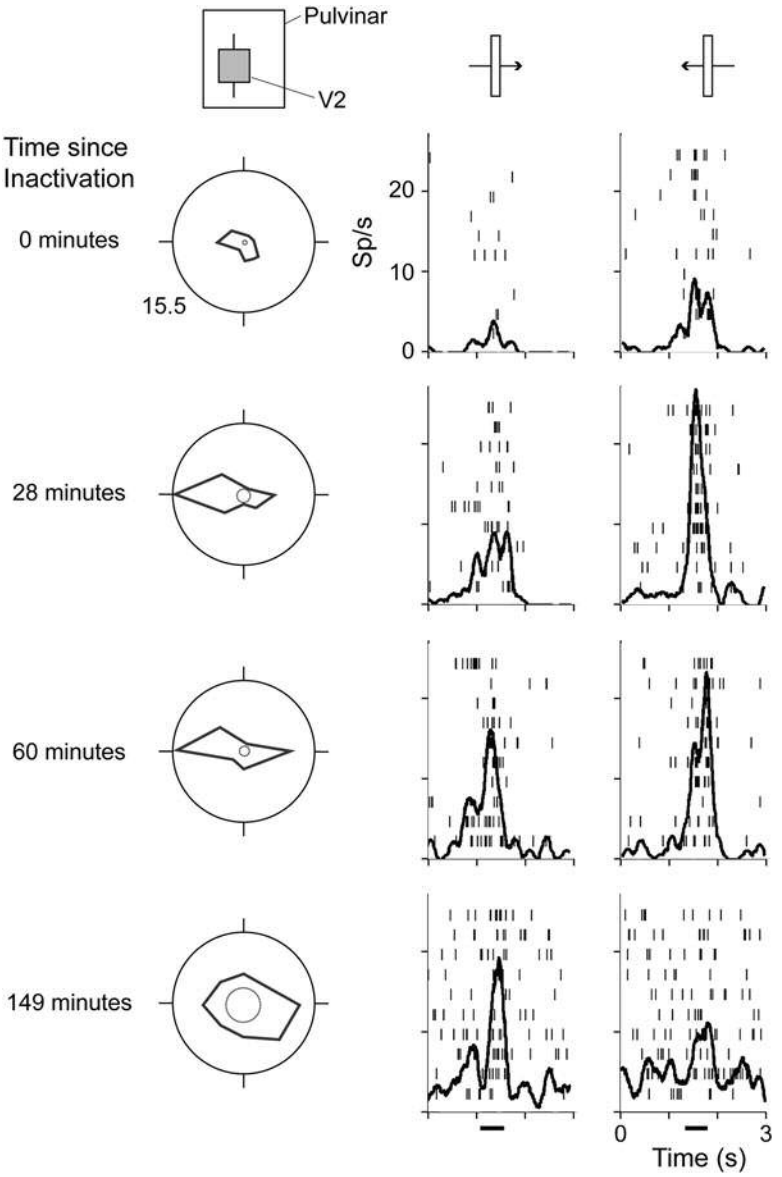

Fig. 11.2 Overall activity increase of a single V2 unit after GABA inactivation of the pulvinar. Neuronal activity in area V2 was recorded before (0) and at discrete time intervals (0, 28, 60, and 149 min) after GABA injection in the pulvinar. Right: PSTHs of the preferred stimuli. Left: polar diagrams corresponding to the tuning curve for direction of stimulus motion (conventions as in Fig. 11.1). Note that the neuron acquired an enhanced selectivity to stimulus direction after GABA injection. Directional index or DI (0 min) = 0.03; DI (14 min) = 0.83. (Modified from Soares et al. 2004)

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