Background and Significance

The study of birds as non-primate/non-mammalian vertebrates with an advanced visual system and cognitive capabilities promises to lead to new insights in systems neuroscience. There is increasing evidence that birds rival mammalian behavioral adaptability and cognitive performance[5–8]. This is underscored by the also increasing evidence for a homology between cortical areas in mammals and certain nuclear areas in the avian telencephalon[9]. These homologous areas possess matching connectivity patterns and molecular markers in neuronal cell types[9–14]. **The avian visual system is particularly advanced.** Due to their evolutionary history as diurnal flying vertebrates, almost all bird species use the visual system as primary sense. From a neuroethological perspective, this means that birds evolved efficient solutions to many problems in visual processing and their visual system may prove especially suited to guide, for example, flight maneuvers at high velocities. **A visual avian telencephalic area, the so called 'visual Wulst', is considered homologous to the primary visual cortex V1.** However, compared to our knowledge on the mammalian cortex, the microcircuit of the avian visual Wulst is still largely unknown. Studying this microcircuit will allow answering questions about how deep the homologies extent. In the long run, it will contribute to the understanding of how cognitive abilities emerge in two divergent classes of vertebrates. **I want to approach the clarification of the Wulst local circuitry by focusing on two populations of motion selective neurons within the zebra finch visual Wulst.**

The zebra finch is one of the most accessible bird species for behavioral and physiological experiments in the lab. It is already one of the most intensely studied birds that recently received wider attention for its vocal learning capability[15]. Accordingly, the implementation of new neuroscientific methods for the zebra finch is progressing quickly. This includes optical imaging[16,17], fMRI[18,19] and even genetic approaches[20–23]. I propose to conduct *in vivo* loose patch electrophysiology in combination with neurobitin cell fill in the zebra finch visual Wulst.

The avian 'Wulst', a large part of the dorsal telencephalon, is considered homologous to the mammalian primary visual cortex (V1) and primary somatosensory area (S1)[13]. *Visual* Wulst and V1 receive input from the retina via the thalamus; the two areas possess similar molecular composition[14], and include cell populations representing object orientation and motion direction. In the zebra finch the visual Wulst is involved in sexual imprinting[24] and in spatial discrimination during foraging[25]. Evidence from other birds demonstrated its involvement in associative learning behaviors like reversal learning in a visual discrimination task[26–30]. However, the visual Wulst appears unimportant for simpler visual discrimination tasks[31–34]. In order to approach the question how the visual Wulst is involved in higher cognitive visual tasks I want to first understand the microcircuit of two specific areas within the hyperpallium apicale, the dorsal lamina of the zebra finch visual Wulst that represent motion direction.

In the zebra finch visual Wulst, motion direction selective neurons are arranged in distinct topographic maps[16,17]. These maps were described using flavoprotein autofluorescence imaging (Mayer, Eckmeier et al. in preparation) and belong to the hyperpallium apicale (HA). HA is the most dorsal lamina of the visual Wulst and its predominant output region[35,36](figure 1 A-C). The HA appears to be homologous to layer 5 of the mammalian V1[14]. Differences in preferred motion direction between the two maps in HA could be shown by means of extracellular electrophysiology in a recent study (Mayer, Eckmeier et al. in preparation). The origin of the input to these areas was addressed by tracing of afferent projections which showed that the two topographic maps receive bilateral input from distinct sub-regions in the thalamic nuclei that were already shown to project into the Wulst[11,36,37]. However, as seems typical for birds with

lateral eyes[37,38], neurons recorded in the visual Wulst mainly responded to input from the contralateral eye[39]. Only minor responses to ipsilateral stimuli were found[39]. The new study (Mayer, Eckmeier et al. in preparation) now indicates that in the representation of the frontal part of the visual field, the ipsilateral input is inhibited.

The HA microcircuit contains several different cell types. Montagnese et al.[37] were first to describe different cell types within the visual Wulst. A more detailed, recent study on strawberry finches[41], however, classified two different types of projection neurons ('pyramidal' and 'multipolar' cells) and two types of interneurons ('stellate neurons' and 'local circuit neurons'), which matched descriptions by Montagnese et al.[39](figure 1D-G). In particular, the projection neurons appear to be further separable by their spine densities. Both studies used Golgi staining and did not determine which neurotransmitter each cell type expressed. However, the existence of GABAergic neurons in the Wulst was shown, for example, by GAD labeling[42].

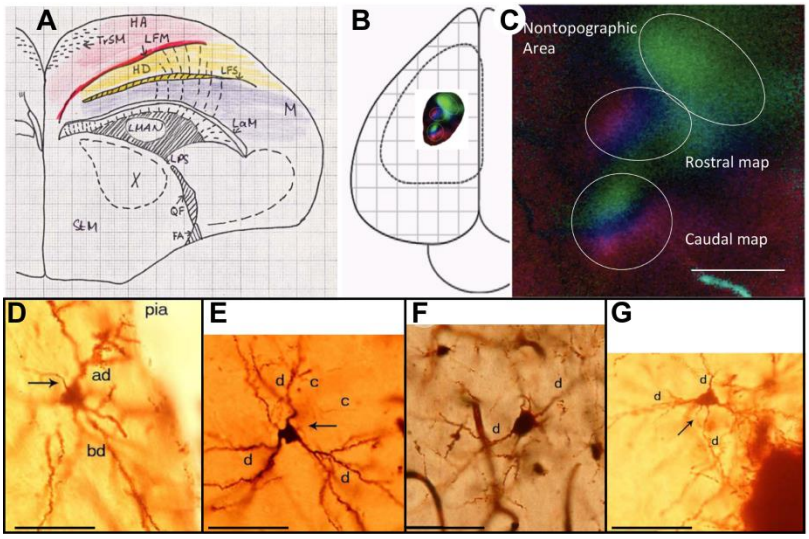

Figure 1 The zebra finch visual Wulst. A Sketched transversal brain section of one hemisphere (1mm grid; 4.41 mm anterior to Y-point). Colored areas indicate the Wulst. Red: Hyperpallium apicale (HA), yellow: hyperpallium dencocellulare (HD). **B** dorsal view on the left telencephalon, dotted line envelopes the Wulst, the positions of motion direction selective topographic maps are indicated (1mm grid). **C** details of the same maps (scale bar 1mm). **D-G** cell types of HA (from Chand et al.[41], resized to equal scale by DE). **D** pyramidal neuron **E** multipolar cell **F** local projection cell **G** stellate neuron. ad apical dendrite, bd basal dendrite, d dendrites, c axon collaterals, and arrow shows axon. Scale bar = 50 µm