Cholinergic and GABAergic pathways in fly motion vision

ABSTRACT

The interaction of excitatory and inhibitory pathways is essential for the computation of visual motion responses and discussed in the context of the Reichardt model for motion detection.

INTRODUCTION

Background The fly visual system is characterized by its repetitive, retinotopic organization of four layered structures: the lamina, the medulla, the lobula and the lobula plate. Every layer is composed of thousands of columns each of which contains the same number and types of neurons. In contrast to our detailed knowledge about the anatomy of these columnar elements, not much is known about their visual response properties except for the large lamina monopolar cells. Due to the small diameter of the fibers, intracellular recordings are hard to accomplish in most cases. Thus, most data on columnar neurons arise from 2-deoxy-glucose activity staining which, however, cannot easily be assigned to individual cell types. Nevertheless, there exists anatomical evidence for at least three major parallel processing streams in the fly optic lobes: the first two pathways arise from receptor cells R1-6, which are connected through lamina cells L1 and L2 and transmedulla neurons to the lobula plate. These two pathways are thought to be involved in motion processing. The third pathway receives input from retinula cells R7 and R8, and, by way of lamina cells L3, projects mainly to the lobula. This pathway is supposed to be involved in the processing of form and color. Amongst the best-studied cells of the fly visual system are the large lobula plate tangential cells (LPTCs), which, due to their large diameter axons (about 8-10 microns) are relatively easy to record from intracellularly. LPTCs also possess a large dendritic arbor on which they receive input from numerous columnar elements arising presumably from the medulla and the lobula (for review see: Many of these LPTCs do not produce regular action potentials but rather respond to excitatory or inhibitory stimuli by a graded shift of membrane potential. Typically, LPTCs respond to visual motion in a directionally selective way: They depolarize when stimulated by preferred direction motion, and become inhibited by motion along the opposite or null direction. According to our current view, their direction selectivity is produced by the antagonistic action of local elements tuned to opposite directions of motion. These input elements are thought to be only weakly selective for the direction of motion. The direction selectivity of the LPTCs is enhanced to such a high degree as it is observed in the electrical responses solely through the subtractive inhibition taking place on the dendrites of the LPTCs. Evidence for this type of input arrangement comes from pharmacological experiments where the inhibitory input is blocked by PTX. Under these conditions the preferred direction response is enlarged and the response to null direction is inverted resulting in an excitation. However, all conclusions pertaining to the response properties of the input elements to the tangential cells are based on indirect evidence only, since, for the reasons outlined above, only few intracellular recordings exist from them. Another line along which to identify these input elements could be their transmitter system. Here, the tangential cells have been shown physiologically to possess at least two different transmitter receptors on their dendrite: a cholinergic receptor with a typical nicotinic pharmacological profile, and a γ-aminobutyric acid (GABA) receptor. Antibodies against the ARD subunit of nicotinic acetylcholine receptors (nAChRs) and the RDL subunit of the GABA receptor in Drosophila

allowed us to investigate the distribution of these receptors in the fly visual system. In the following we will present immunocytochemical data of antibody staining against nAChRs, GABA receptors and the inhibitory neurotransmitter GABA itself. The distribution of immunoreactivity in the fly visual system for these receptors and GABA is analyzed and the putative pharmacology and cell types of the motion pathway are discussed.

CONCLUSION

Conclusions Putative cellular constituents of the fly motion pathway In earlier studies two main candidates were proposed to constitute the elementary motion detector of the fly visual system: the T4- and the T5 cells, both types also called the 'bushy T-cells'. The reason why these cells are so suggestive candidates is that i) both of these cells come in 4 different subtypes, each of which ramifies in a different layer of the lobula plate, ii) 3H-deoxyglucose measurements using 4 cardinal directions of motion (up, down, left, right) revealed a specific staining pattern of exactly these 4 layers in the lobula plate. Furthermore, LPTCs occupy with their large dendrites preferentially those layers in the lobula plate, which correspond to these different directions of motion. In one case, a direct synaptic contact has been demonstrated at the EM level between a T4-cell and the dendrite of an HS-cell. Taken the available immunocytochemical evidence presented in this paper together with what is known about the anatomy of columnar elements and the physiology of LPTCs, the following picture about the cellular implementation of motion detection in the fly visual system can be drawn in the most parsimonious way: The first major step of motion detection, i.e. the non-linear interaction between input channels, is realized on the dendrites of T4-cells and the input elements of T5 cells in the proximal layer of the medulla by a combined cholinergic-GABAergic mechanism. This results in weakly directional signals for each of the four cardinal directions of motion split into a cholinergic pathway, providing direct excitatory input onto the LPTC dendrites through T4-cells, and an indirect GABAergic pathway, relayed through the posterior layer of the lobula via T5-cells, providing inhibitory input to LPTC dendrites. Thus, the second step in the computation of direction selectivity, i.e. the subtraction, is mediated by the opponent interaction between T4- and T5 cell input on the dendrites of each LPTC. Finally, these signals become integrated by the LPTC dendrite. At present, this proposal, is highly speculative, but may proof useful to be challenged in the future by electrophysiological or optical recordings from several of the putative constituents of the motion detection circuit.