The Faculty of Science, Hokkaido University presents The 2014 Hokkaido Neuroethology Workshop on:*

Insect Dorsal Ocelli (9:00am–12:30pm, Room 304, July 27th)

Organizer: †Joshua van Kleef (University of California Berkeley, USA).

Most insects possess three simple eyes, known as the dorsal ocelli, whose role in behavior has fascinated scientists for hundreds of years. Our workshop will examine the latest optical, anatomical, neurophysiological and behavioural clues to the functions of ocelli in a diverse range of insects that includes ants, bees, dragonflies, blowflies, locusts and wasps.

Timetable

8:50am – 9:00am *Welcome*

9:00am – 9:40am Coding and signals for action in the locust ocellar pathway.
Peter J Simmons

9:40am – 10:00am An eye for every occasion: as light levels dwindle locusts switch from compound eyes to ocelli as their source of visual-feedback for roll.
Joshua P van Kleef, Travis L Massey, Michel M Maharbiz

10:00am – 10:20am Ocelli based remote control of insect flight.
Travis L Massey, Joshua P van Kleef, Kaylee Mann, Michel M Maharbiz

10:20am – 10:40am *Morning Tea*

10:40am – 11:20am Ocelli in blowflies: speeding up signals in the motion vision pathway.
Holger Krapp

11:20am – 11:40am The unusual ocellar morphology of the orchid bee.
Emily Baird, Eric Warrant, Klaus Lunau and Willi Ribi

11:40am – 12:00pm Insect ocelli: why don't they like us?
Jochen Zeil, Willi A Ribi, Ajay Narendra

12:00pm – 12:30pm *General discussion*

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* A satellite event to the 2014 ICN/JSCPB
†email: vankleef@berkeley.edu

Coding and signals for action in the locust ocellar pathway.

Peter J Simmons[‡]

A locust's three ocelli are arranged in a way that enables them to infer changes in body attitude during flight by monitoring the visual horizon. I shall describe how signals are transformed as they pass through the ocellar pathway, and suggest how the locust's ocellar pathway might act to control the flight system.

Both photoreceptors and second-order L-neurons respond to light signals with graded potentials, which are converted into all-or-none spikes in third-order neurons such as DNI. In DNI, spikes are generated relatively sparsely, but the timing of each is tightly controlled (Simmons & de Ruyter van Steveninck, 2010). Both cellular and network properties contribute to this precision, including rebound in DNI and L-neurons, and mutual inhibitory synapses amongst L-neurons. In controlling behaviour, DNI may participate in an optical proprioceptor. During level flight, the head nods with each wing-beat, providing a regularly changing light signal to the frontal ocellar field so that DNI spikes at the same phase during each wing beat. However, if the locust's attitude pitches upwards or downwards, the timing of DNI's spike will be delayed or advanced, and this could cause a change in the time of activation of particular flight muscle in a way that compensates for the change in pitch.

An eye for every occasion: as light levels dwindle locusts switch from compound eyes to ocelli as their source of visual-feedback for roll.

Joshua van Kleef[§**], Travis Massey[§], Michel Maharbiz[§]

In addition to a pair of compound eyes, almost all adult insects possess three simple single-lens eyes, known as ocelli. The functional advantages of expressing two distinct eye types remain unclear. However, in flying insects it has been shown that ocellar and compound eye signals are combined before they are transmitted down the ventral nerve chord to flight motor ganglia, presumably to provide more robust sensory feedback. We present behavioural evidence that ocelli play a crucial role in flight stabilization after sunset when low light levels compromise the compound eyes. In response to dwindling light levels, locusts alter the way they integrate ocellar and compound eye information. By filming head and steering responses to visual signals, we show that when compound eyes and ocelli receive conflicting roll signals during daylight they ignore those presented to the ocelli. However, as mean light levels decrease, the head response to light flashes delivered to the ocelli increases in amplitude, suggesting locusts no longer trust their compound eyes. Thus, we speculate that the superior light gathering ability of ocelli means they play an important role in enabling locusts to stabilize their gaze and flight in dim light environments.

[‡] Institute of Neuroscience & School of Biology, Ridley Building, Newcastle University, NE1 7RU, Newcastle upon Tyne, UK. email: p.j.simmons@ncl.ac.uk

[§] Department of Electrical Engineering and Computer Science, College of Engineering, University of California Berkeley, CA, USA

[**] email: vankleef@berkeley.edu

Ocelli based remote control of insect flight.

Travis L Massey[††‡‡], Joshua P. van Kleef[††], Kaylee Mann[††], Michel Maharbiz[††]

Although significant progress has been made in designing and fabricating micro air vehicles (MAVs), flying insects still significantly outperform the most sophisticated flying robots in efficiency, stability, and maneuverability. The restrictions that such a small spatial scale places on the energy that can be stored on-board and the lack of artificial actuators that compare in efficiency with insect flight muscles means this gap is expected to persist for years to come. Several laboratories are therefore pursuing a novel MAV design that utilizes an actual flying insect, capitalizing on their remarkable natural flying abilities. Thus far, these systems have attempted to bias flight with electrical stimulation of the insects' muscles. Although muscle stimulation initially induces a movement, this movement is detected by the insect, interpreted as an unintended motion and subsequently counteracted. Furthermore, the insect itself can fire action potentials to flight muscles resulting in a competition between the controller and the controlee. We attempted to overcome these problems using sensory stimulation to trick the insect's sensorimotor system into responding to fictitious self-movements. We demonstrate that preprogrammed insect backpacks capable of providing optical stimulation to the ocelli can bias flight, but that stimuli are ignored during volitional turns.

Ocelli in blowflies: speeding up signals in the motion vision pathway.

Holger G. Krapp[§§]

Blowflies, like many other flying insects, employ several sensory systems to support gaze and flight stabilization. The secondary visual system in blowflies, the ocelli, consists of three small under-focussed lens eyes that sample light intensity changes within large overlapping areas of the animals' dorsal visual field upon attitude changes. Fast 2nd order ocellar interneurons connect the system with the lateral protocerebrum where they convey light intensity changes to multisensory descending neurons which integrate the signals from several sensory streams, including the motion vision pathway. Studies of lobula plate tangential cells (LPTCs), thought to be involved in processing self-motion-induced optic flow, suggest that ocellar signals may indeed be combined with motion vision information early in the viso-motor pathway. Parsons et al. (2006) reported ocellar stimulation mimicking rotations around horizontal body axes of the fly to modulate the activity in LPTCs of the so-called vertical system. These results had been interpreted as a strategy to speed up the response to attitude changes in the notoriously slow motion vision pathway. More recent behavioural studies on compensatory head movements suggest that signals from the ocelli and the motion vision pathway are combined in a non-linear way which seems to contradict earlier evidence for a linear multisensory signal integration within the gaze stabilization system (Hengstenberg 1993, Schwyn et al 2011). I will present an interpretation of the results based on a simple model that includes a static non-linearity at the level of the descending neurons.

[††] Department of Electrical Engineering and Computer Science, College of Engineering, University of California Berkeley, CA, USA

[‡‡] email: tlmassey@berkeley.edu

[§§] Department of Bioengineering, Imperial College London, South Kensington Campus, London SW7 2AZ email: h.g.krapp@imperial.ac.uk

The unusual ocellar morphology of the orchid bee

Emily Baird[***,†††], Eric Warrant[***], Klaus Lunau[‡‡‡] and Willi Ribi[§§§,††††]

Orchid bees are fast flying highly aerobatic hymenopterans that are capable of navigating over tens of kilometers through the dense rainforests of Central America. This habitat is densely cluttered and dim due to the thick canopy that often occludes much of the sky. Does the visual system of orchid bees have specialisations that allow them to cope with the challenges imposed by navigating over large distances through this environment? To begin to answer this question, we performed morphological analyses of their large ocellar system and found several unusual features. The most surprising feature of the orchid bee ocellar morphology is the organisation of the rhabdoms. In the median ocellus, the rhabdoms are oriented about the horizon (0°), in the left lateral ocellus they are oriented ~40° upwards and in the right lateral ocellus, ~40° downwards. This organisation hints at the possibility that the three ocelli function together as a polarized light analyser. We also find that, unlike in many insects, the ocellar retinae are separated from the thick, rounded lens by a large clear zone. Hanging drop measurements suggest that this arrangement results in a relatively focussed image being formed within the retina in the median and lateral ocelli. The curious features of the orchid bee ocelli suggest that these bees have indeed a visual system that is adapted for the peculiarities of the dense rainforest environment.

Insect ocelli: why don't they like us?

Jochen Zeil[§§§,****], Willi A Ribi[§§§,††††], Ajay Narendra[§§§]

We conducted a comparative study of the functional anatomy of ocelli in different insect groups, with particular emphasis on dorso-ventral specializations of the ocellar retina and the organization of ocellar photoreceptors. We briefly summarise the behavioural evidence for the role of ocelli in orientation and navigation, including some lesser known or less accessible older work, and then review our state of knowledge of the polarisation sensitivity and the arrangement of photoreceptors in ocelli. We note in particular how little we know about the electrophysiological properties of ocellar photoreceptors and the role of ocelli in polarisation vision. We suggest that the contributions of ocelli-mediated attitude and bearing control may be state-, time- and ambient light-dependent, which may be one of the reasons why it is so difficult to identify the behavioural function of ocelli.

[***] Department of Biology, Lund University
[†††] email: emily.baird@biol.lu.se
[‡‡‡] Institute for Sensory Ecology, Heinrich Heine Universität Düsseldorf
[§§§] Research School of Biology, Bldg 46, Biology Place, The Australian National University, Canberra ACT 0200, Australia.
[****] email: jochen.zeil@anu.edu.au
[††††] The Private University of Liechtenstein, Dorfstrasse 24, Triesen FL-9495, Liechtenstein