

Dynamical Olfaction

Workshop

Brighton

30 June - 2 July 2010



as part of the





SysBio initiative.

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Overview

Animals are able to experience complexly structured plumes of different combinations of chemicals as individual olfactory percepts. It appears that the olfactory system utilizes rich temporal dynamics to achieve this goal but exactly how is still an open challenge for modern neuroscience. In the last few years rapid progress has been made in our understanding of olfactory information processing.

In this focused workshop on Dynamical Olfaction we will share recent developments, both experimental and theoretical, between the active researchers in the field.

Programme committee

Sylvia Anton (sylvia.anton@versailles.inra.fr) Dominique Martinez (Dominique.Martinez@loria.fr) Thomas Nowotny (T.Nowotny@sussex.ac.uk) Jean-Pierre Rospars (rospars@versailles.inra.fr)

Local organiser

Christopher L. Buckley (c.l.buckley@sussex.ac.uk)

Programme

Wednesday 30 June, 2010

- 10:00 Brighton walk
- 12:15 Lunch & Poster setup
- 13:45 Opening remarks

Session 1

Session Chair. Sylvia Anton

- 14:00 Giovanni Galizia Multiple networks in the antennal lobe
- 14:45 **Thomas Nowotny** Minimal model of blend recognition in the moth pheromone system
- 15:15 Coffee break

15:30 Mark Stopfer

Temporally diverse firing patterns in olfactory receptor neurons underlie spatiotemporal neural codes for odors

16:15 Jean-Pierre Rospars

Olfactory receptor neurons: A comparative analysis of their response properties with diverse stimuli in different species

16:45 Coffee break

17:00 Maxim Bazhenov

Coincidence detection vs. temporal integration in olfactory networks

17:45 Aaditya Rangan

Network mechanisms influencing sensitivity and reliability within the fly antennal lobe

- 18:15 Closing remarks
- 20:30 Pub rendez-vous Black Lion Pub (open end).

Thursday 1 July, 2010

9:00 Welcome & Organizational remarks

Session 2

Session Chair: Jean-Pierre Rospars

9:15 Johannes Reisert

Response kinetics of vertebrate olfactory receptor neurons

10:00 Philippe Lucas

Properties of the Ca^{2+} -dependent chloride current in moth olfactory receptor neurons and role in the dynamic of their response

10:30 Coffee break

10:45 Hong Lei

Dynamic control of odor-induced responses to a wide range of odor concentrations

11:30 Christoper L Buckley

Critical Rate Dynamics Explain the Dynamic Range of the Moth Pheromone System

- 12:00 General Discussion
- 12:30 Lunch & Poster session

Session 3

Session Chair. Christopher L Buckley

13:30 Peter Kloppenburg

Specific properties of local interneuron subtypes suggest distinct tasks during odour processing in the antennal lobe

14:15 Sylvia Anton

Plasticity of central odour coding in a moth

14:45 Coffee break

15:00 Brian Smith

Associative and nonassociative mechanisms tune transient dynamics of early olfactory processing

15:45 Emilia Leszkowicz

Modulation of excitatory/inhibitory balance in the accessory olfactory bulb influences oscillatory neural activity in the accessory olfactory bulb of anaesthetised mice

- 16:15 Coffee break
- 16:30 **Massimo Vergassola** Infotaxis: searching without gradients
- 17:15 **Dominique Martinez** Stereotyped firing response patterns in moth antennal lobe neurons: experiments and models
- 17:45 General Discussion
- 18:15 Close of Thursday sessions
- 19:00 Workshop dinner: Nooris Indian restaurant
- 21:00 Pub rendez-vous Black Lion Pub

Friday 2 July, 2010

8:45 Welcome & organizational remarks

Session 4

Session Chair. Dominique Martinez

9:00 Stephen Trowell

Building a better electronic nose quantitative lessons from biology

9:45 Time Pearce

Stimulus and Network Dynamics Can Collide in a Ratiometric Model of the Antennal Lobe Macroglomerular Complex

10:15 Coffee break & Poster session

11:30 Jan Wessnitzer

Associative learning in Drosophila: experiments and models

- 12:15 Eduardo M. Moraud Scent-tracking by autonomous robots: Infotaxis and beyond
- 12:45 General Discussion & Closing Remarks

Speakers Abstracts

Multiple networks in the antennal lobe

C. Giovanni Galizia

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Bees collect nectar and pollen, and learn to associate color and odor with these rewards. This appears as an adaptive behavior that ensures efficient foraging by the hive. But how are these memories stored in the nervous system? We investigated the effect of associative learning on early sensory processing, by combining classical conditioning with in vivo calcium imaging of secondary olfactory neurons, the projection neurons in the honeybee antennal lobe. We found associative changes of odor representations 2 to 7 hours after appetitive odor conditioning. These changes affected both the global projection neuron response strength and the spatial pattern of activated neurons. Our data suggest that odor learning affects the intra-glomerular network at the level of olfactory receptor neuron-to-projection neuron synapses and inhibitory local neuron-to-receptor neuron synapses. The observed changes are consistent with the idea that odor learning optimizes odor representations and facilitates the detection and discrimination of learned odors. Which are the networks that shape odor information? Multiple populations of local neurons are present, with different properties in physiological odor responses and in biochemical complements. One approach to understand this diversity is to look at the expression of neuropeptides in the brain. Indeed, neuropeptides may be the most ancient chemical messengers between neurons. As all insects, bees have are a large number of different peptides and peptide receptors, most of which have been characterized only poorly, if at all. Neuropeptides are also a powerful tool for neuroanatomical studies, because they can be used to characterize small populations of neurons based on their neuropeptide expression patterns.

Minimal model of blend recognition in the moth pheromone system

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For some moths, especially those closely related and sympatric, recognizing the concentration ratio of components in a pheromone blend is essential. We propose, and determine the properties of, a minimalist competition-based feed-forward neuronal network model capable of recognizing a specific 1:1 concentration ratio of pheromone components. We find that in our minimalist model

(1) satisfactory ratio recognition over a wide range of concentrations can only be achieved with a sufficient convergence of olfactory receptor neurons onto local neurons (LNs),

(2) other than generally inducing competition, the details of intrinsic LN to LN connectivity is less influential than one may expect, and,

(3) recognition is better with a population rate based code than with latency based coding in single LNs.

The last point is particularly interesting as it arises only in a spiking neuron model and not in an otherwise equivalent rate model.

Overall, the work sheds some light on concentration independent ratio recognition in general and highlights that the general coding debate is still open. Further directions will include ratio recognition of other than 1:1 ratios, recognition of blends with more than 2 components and applications to technical applications in artificial olfaction.

Temporally diverse firing patterns in olfactory receptor neurons underlie spatiotemporal neural codes for odors

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Odorants are represented as spatiotemporal patterns of spikes in neurons of the antennal lobe (AL; insects) and olfactory bulb (OB; vertebrates). These response patterns have been thought to arise primarily from interactions within the AL/OB, an idea supported, in part, by the assumption that olfactory receptor neurons (ORNs) respond to odorants with simple firing patterns. However, activating the AL directly with simple pulses of current evoked responses in AL neurons that were much less diverse, complex, and enduring than responses elicited by odorants. Similarly, models of the AL driven by simplistic inputs generated relatively simple output. How then are dynamic neural codes for odors generated? Consistent with recent results from several other species, our recordings from locust ORNs showed a great diversity of temporal structure. Furthermore, we found that, viewed as a population, many response features of ORNs were remarkably similar to those observed within the AL. Using a set of computational models constrained by our electrophysiological recordings, we found that the temporal heterogeneity of responses of ORNs critically underlies the generation of spatiotemporal odor codes in the AL. A test then performed in vivo confirmed that, given temporally homogeneous input, the AL cannot create diverse spatiotemporal patterns on its own; however, given temporally heterogeneous input, the AL generated realistic firing patterns. Finally, given the temporally structured input provided by ORNs, we clarified several separate, additional contributions of the AL to olfactory information processing. Thus, our results demonstrate the origin and subsequent reformatting of spatiotemporal neural codes for odors.

Olfactory receptor neurons: A comparative analysis of their response properties with diverse stimuli in different species

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Olfactory receptor neurons (ORNs) present a number of intriguing response properties with their high (or low) sensitivity and small (or wide) dynamic range. The moth pheromonal ORN is a good example for studying these properties and analysing how the spiking response reflects quantitatively the intensitive and temporal features of the olfactory stimulus. In recent years we have studied experimentally and theoretically various aspects of the stimulus-response relationships of this ORN type. First, we present the basic response properties (thresholds, dynamic ranges, latencies and firing rates) of a population of moth pheromonal ORNs in response to short square pulses of pheromone at different concentrations. Second, we compare these properties with those determined in similar conditions in a population of frog "ordinary" ORNs in order to identify the properties that might be common to all ORNs and those more specific of pheromone ORNs. Third, we consider ORN responses to natural stimulus conditions in which atmospheric turbulence breaks the pheromone plume in discrete clumps and filaments. We give quantitative arguments indicating that moth ORNs are evolutionary adapted to the statistical characteristics of the pheromone plume in natural conditions.

Coincidence detection vs. temporal integration in olfactory networks

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Ideally, a coding strategy used by a sensory system should provide an optimal representation across the full possible range of stimulation conditions. For the olfactory system, this task involves optimally encoding odors at different concentrations, an ability critical in many species for survival. How successive layers of neural circuits in the olfactory system regulate sensory input to maintain stable odor representations across broad ranges of concentration remains a mystery. Drawing on results obtained with biophysical network models of the insect olfaction, I will discuss intrinsic and circuit properties that contribute to encoding olfactory information at different levels of odor processing, and the role of the intrinsic dynamics of the olfactory system in optimizing odor representations. I will present a hypothesis how circuit properties of the olfactory system allow adopting an optimal strategy of information processing, shifting from coincidence detection to temporal integration as the odor concentration changes. The ability to shift operational modes can be achieved readily by a combination of environmental contingencies and network interactions.

Network mechanisms influencing sensitivity and reliability within the fly antennal lobe

Aaditya Rangan

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Several recent experiments indicate that there exists substantial synaptic-depression at the synapses between olfactory receptor neurons (ORNs) and projection neurons (PNs) within the drosophila antenna lobe (AL). This synaptic-depression may be partly caused by vesicle-depletion, and partly caused by presynaptic-inhibition due to the activity of inhibitory local neurons within the AL. While it has been proposed that this synaptic-depression contributes to the nonlinear relationship between ORN and PN firing-rates, the precise functional role of synaptic-depression at the ORN and PN synapses is not yet fully understood.

To investigate the relationship between synaptic-depression and the coding properties of the fly AL, we created a computational model consisting of 5 glomerular channels. By analyzing the dynamics of this computational model, we have been able to distill two hypotheses linking the information-coding properties of the fly AL with the network mechanisms responsible for ORN and PN synaptic-depression. Our first hypothesis concerns the possible variance coding of odor-concentration information once stimulation to the ORNs is sufficiently high to saturate glomerular responses, further stimulation of the ORNs increases the reliability of PN activity while maintaining PN firing-rates. The second hypothesis proposes a tradeoff between spike-time reliability and coding-capacity governed by the relative contribution of vesicle-depletion and presynaptic-inhibition to ORN and PN synaptic-depression. Synaptic-depression caused primarily by vesicle-depletion will give rise to a very reliable system, whereas an equivalent amount of synaptic-depression caused primarily by presynaptic-inhibition will give rise to a less reliable system that is more sensitive to small shifts in odor stimulation. This second hypothesis may shed some light on the functional role associated with the balance of vesicle-depletion and presynaptic-inhibition within the fly AL.

Response kinetics of vertebrate olfactory receptor neurons

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Olfactory perception in vertebrates begins with odorant delivery to the nasal cavity by the inhaled air and the binding of odorant molecules to odorant receptors located on olfactory receptor neurons (ORNs). The activation of a G protein-coupled second messenger cascade ensues, leading to an increase in cAMP, subsequent transduction channel opening and ultimately action potentials generation. To reliably relay odorous information olfactory transduction should be fast enough to follow the rhythmicity imposed by breathing or sniffing. We are investigating how ORNs code information during stimulation protocol designed to mimic low breathing or high sniffing frequencies and which cellular mechanisms control the speed of activation and termination of the olfactory response. First, the role of the cyclic nucleotide-gated (CNG) channel and its negative feedback via Ca/CaM is examined. Unlike previously thought, this feedback contributes less to adaptation but rather to rapid CNG channel closure at the end to odor exposure. Second, olfactory marker protein (OMP) has been known for over 30 years to be selectively expressed in nasal chemosensory cells, but its functional role has remained unclear. We found that OMP serves as a major accelerator of the odorant response, since ORNs which lack OMP have response kinetics in which not only the onset but also the termination phase is slowed, the latter around 10 times. These changes also alter the patterns of action potential generation, leading to delayed firing and longer spike trains with behavioral consequences regarding a mouses ability to discriminate odorants quickly.

Properties of the Ca²⁺-dependent chloride current in moth olfactory receptor neurons and role in the dynamic of their response

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We are interested in insect olfaction mechanisms with special focus on transduction and modulation of odorant responses at the peripheral level. The response of insect olfactory receptor neurons (ORNs) to odorants is accompanied by an increase in intracellular Ca^{2+} concentration. The molecular target of the Ca^{2+} rise remains elusive. We therefore studied the downstream effect of Ca^{2+} in cultured ORNs of the Noctuid moth Spodoptera littoralis. Intracellular dialysis of Ca²⁺ from the patch pipette in whole-cell patch-clamp configuration activated a conductance with a $K_{1/2}$ of ca. 3 μ M. Ionic substitutions demonstrated that it is a CI- current and the anion permeability sequence of the Ca²⁺-activated Cl⁻ channel is $I \rightarrow NO_3 \rightarrow Br \rightarrow Cl \rightarrow CH_3SO_3 \rightarrow gluconate^-$. The CI⁻ current partly inactivated over time and did not depend on PKC and CaMKII activity or on calmodulin. Pharmacological studies showed that the Ca²⁺-activated current was reversibly inhibited by general CI⁻ current blockers, flufenamic acid, niflumic acid and NPPB. This CI⁻ current was cell-volume insensitive. Lowering CI⁻ concentration in the sensillar lymph bathing the ORN outer dendrites caused a significant delay in pheromone response termination in vivo. The present work identifies a new CI⁻ conductance activated by Ca²⁺ in insect ORNs likely required for ORN repolarisation. This work was supported by ANR-BBSRC Pherosys and FP7 Neurochem.

Dynamic control of odor-induced responses to a wide range of odor concentrations

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The olfactory system of any animal species must be able to cope with a wide range of odor concentrations that often fluctuate instantaneously in large magnitude in nature. Little is known on how olfactory circuits at the first synaptic center the olfactory bulb in vertebrates or antennal lobe (AL) in insects adjust their sensitivity to quickly encode the concentration fluctuations. We have conducted a series of experiments in the AL of the hawk moth, Manduca sexta, to gain insights on this gating mechanism. In moth AL a special set of enlarged glomeruli located at the beginning portion of male AL the macroglomerular complex or MGC is devoted to process the conspecific female sex pheromones. The output (projection) neurons (or PNs) of MGC can be readily identified using juxtacellular recording method in conjunction with pheromonal stimulation. Upon stimulation of a series of 5 odor pulses, PNs often produce the strongest response to the 1st odor pulse and then weaker b ut constant responses to the rest of pulses, suggesting there is a fast inhibitory feedback pathway regulating the PNs sensitivity, most likely via GABAergic local interneurons (LNs). We therefore used a known GABA-A receptor antagonist, picrotoxin, to manipulate the putative feedback pathway. After the drug was added, the cell activity changed from randomly bursting to non-spiking pattern; response to odors was also much reduced but the after-inhibition period following each response was increased. These results indicate that PNs are tonically inhibited by GABAergic LNs. As a feedback gating mechanism, the same pathway may regulate the output of PNs depending on the activity level of the same PNs, thus expanding the dynamic range of the PNs to respond to wide range of odor concentrations.

Critical Rate Dynamics Explain the Dynamic Range of the Moth Pheromone System

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Male moths can sense and locate conspecific females releasing small amounts of pheromone from more than a mile away. Integral to this behavior is the extraordinary dynamic range of Macro Glomerular Complex (MGC). While the sensitivity of the MGC to small concentrations is partially accounted for by the huge convergence in ORN pathways the origin of its dynamics range is still unclear.

Recently Kinouchi and Copelli (2006) demonstrated that the sensitivity and dynamic range of a network of excitable elements, is maximised near the critical point of a phase transition. They claim critical excitable dynamics is compatible with the role of gap junctions in vertebrate olfactory glomeruli and thus could account for these properties. Consequently it is tempting to infer a similar mechanism to explain the sensitivity of the male moth's olfactory apparatus. However, to date, gap junctions have not been reported in the olfactory glomeruli of moths and the observed dynamics of the glomeruli are not easily reconciled with a network of excitable elements.

Here we develop an alternate notion of critical dynamics that can be achieved in a broader class of neural system. Specifically we demonstrate that optimal dynamic range can be achieved in the MGC if the network of local neurons (LNs) is poised at a bifurcation in their rate dynamics. We develop a three level modeling approach to demonstrate this. First we construct a detailed conductance based model of the MGC. Then, assuming dominance of slow $GABA_B$ connections we construct a formally equivalent rate model. Lastly, we use a mean field description of the LN network to show analytically how the dynamic range of the MGC is maximised at a critical point in its dynamics.

This model also describes, how strong disinhibitory pathways can arise from networks of LNs in the absence of any explicit structure. Lastly, this framework suggests how the temporal patterning observed in the wider olfactory system could arise from transient dynamic interactions between networks of glomeruli.

Specific properties of local interneuron subtypes suggest distinct tasks during odour processing in the antennal lobe

Peter Kloppenburg

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Behavioural and physiological studies have shown that neuronal interactions among the glomerular pathways are essential for odour information processing in the insect antennal lobe (AL). These interactions are mediated by a diverse population of inhibitory and excitatory local interneurons that help to process, structure and spatially represent olfactory information in the AL. As an important step towards a better understanding of the cellular mechanisms that mediate information processing in the insect AL we analyse in detail the LNs morphological, biochemical and physiological properties. This work was supported by DFG Grants KL 762/2-2 and KL 762/4-1.

Plasticity of central odour coding in a moth

Sylvia Anton, Romina Barrozo, Antoine Chaffiol, Nina Deisig, Christophe Gadenne, Cesar Gemeno, David Jarriault, Jan Kropf, Philippe Lucas, Jean Pierre Rospars, Simon Vitecek

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Male moths use sex pheromones to find a mating partner and plant odours to find food sources. Mixtures of both have often a synergistic effect on attraction behaviour, optimizing the chances of the males to find a potent female. However, behaviour towards any of these odours can change with mating status: newly-mated males cease to be attracted to pheromone but still respond to plant odours. In the migratory moth, Agrotis ipsilon, we studied the responses within the antennal lobe, the primary olfactory centre, to a behaviourally active plant compound (heptanal), the sex pheromone and their mixture as a function of the mating status with electrophysiological and optical imaging techniques. In virgin males responses to heptanal were found in sexually isoform ordinary glomeruli (OG) and responses to the sex pheromone within the male-specific macroglomerular complex (MGC). Mixtures of sex pheromone and heptanal elicited enhanced responses in neurons in OG and reduced responses in the MGC. In mated males, responses to heptanal were largely unchanged or in some cases stronger than in virgin males, whereas responses of antennal lobe neurons to the sex pheromone decreased strongly in sensitivity after mating. Antennal lobe processing of mixtures remained unchanged within the MGC, but differed from responses in virgin males within OG, now displaying a reduced response to the mixture as compared to the synergistic response observed in virgin males. We discuss neural processing of the different odours in the context of the observed behaviour in male moths.

Associative and nonassociative mechanisms tune transient dynamics of early olfactory processing

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Early olfactory processing is fundamentally similar in animals as different as mammals and insects. Because of this similarity there have been very significant advances in understanding of sensory encoding by primary sensory cells the olfactory epitheliums of these animals. Yet a similar understanding of how sensory information is transformed at the first synapses in the brain remains elusive. The primary objectives of this research are to understand how early processing in the brain transforms sensory input, and how this transformation is modified by associative and nonassociative plasticity. The honey bee Antennal Lobe (AL) is the analog of the mammalian Olfactory Bulb (OB). The networks in the AL and OB both transform sensory inputs into spatiotemporal patterns that encode odors by a sequence of activity states, or transients, and information about the identity of the odor is in the specific sequence of states in the transient. Moreover, these networks are sensitive to modulation by feedback from other areas in the brain that represent reinforcement (e.g. food). When odors are associated, or explicitly not associated, with food these modulatory systems change the way that odors are represented by the AL and OB networks. We have shown in the honey bee, using bioimaging and electrophysiological data, that the paths that the transients take are pushed farther apart by association of odors with food reward in Pavlovian conditioning paradigms. Furthermore, nonassociative plasticity induced via repetitive unreinforced exposure to odors modifies competitive interactions between neural representations. We have also shown that disruption of this modulation by RNA interference disrupts behavioral conditioning of odors. We are integrating this information into computational models of the antennal lobes. Furthermore, this information about modulation can have far reaching impacts for understanding disease states that affect early sensory processing and for development of artificial systems for pattern recognition.

Modulation of excitatory/inhibitory balance in the accessory olfactory bulb influences oscillatory neural activity in the accessory olfactory bulb of anaesthetised mice

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In mice, mate recognition is proposed to involve a learning-induced increase in feedback inhibition, which is dependent on noradrenaline, and selectively gates the transmission of the learned signal at the level of the accessory olfactory bulb (AOB) (1). Coupling between excitatory projection neurons and inhibitory interneurons, at reciprocal synapses in the AOB, generates oscillatory neural activity evident in the local field potential (LFP) recorded in the bulb. In the present study, we have investigated how manipulating the balance of excitatory and inhibitory neurotransmission influences the oscillatory dynamics of AOB activity, with the potential to affect functional coupling with other brain areas (2). Mice were anaesthetised by intraperitoneal injection of urethane and a bipolar recording electrode with an integral drug delivery cannula was inserted in the mitral/tufted cell layer of the AOB. LFP total power and spectral centroid (weighted mean frequency) in different frequency bands were analysed pre-injection and following a 1(snip) I infusion of either drug or artificial cerebrospinal fluid (CSF) at intervals up to 1 hour post-injection. Infusions of 100pmol of the type II metabotropic glutamatergic receptor agonist DCG-IV, 1nmol of the GABAA receptor agonist isoguvacine and 1mM of noradrenaline each led to significant and lasting decreases of around 50 % in total power in frequency bands between 4 and 90Hz, compared to CSF. Infusions of DCG-IV and isoguvacine resulted in small, but significant, reductions in spectral centroid in the 12.1-30Hz band compared to CSF. In contrast, despite having a similar effect on oscillatory power, noradrenaline infusion resulted in a slowly developing increase in spectral centroid in the 30.1-60Hz band compared to pre-injection level. The results suggest that both power and frequency of oscillatory neural activity depend on the balance between excitatory and inhibitory neurotransmission in the AOB. However, it is doubtful whether such small effects on frequency of network oscillation would be sufficient to decouple neural oscillators in the AOB from neural oscillators in central brain areas, as has previously been hypothesised as a mechanism for memory recall (2).

[1] Brennan and Zufall (2006) [2] Taylor and Keverne (1991)

Infotaxis: searching without gradients

Massimo Vergassola

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I shall discuss challenges faced by macroscopic organisms trying to locate and move towards sources of nutrients, odors, pheromones, etc.. Microorganisms, such as bacteria performing chemotaxis, can rely on local concentration cues to use gradientclimbing strategies. Macro- organisms, such as insects and birds, lack local cues because chaotic mixing breaks up regions of high concentration into random and disconnected patches, carried by winds and currents. The animal must then devise a strategy of movement based upon sporadic cues and partial information. A search algorithm, infotaxis, designed to work under such conditions will be presented. The idea is that the rate of acquisition of information on the source location, can play the same role as local concentration in bacterial chemotaxis. Infotaxis maximizes the expected local rate of information gain and the resulting trajectories feature zigzagging and casting paths similar to those observed in flights of moths and birds. Infotaxis is relevant to the biomimetic design of olfactory robots with applications to the detection of chemical leaks and explosives.

Stereotyped firing response patterns in moth antennal lobe neurons: experiments and models

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Pheromonal communication in moths constitutes an exceptionally favorable model system for studying neural circuits and odor-guided behavior. In this study, we report experimental analysis and computational modelling on the activity of pheromone-sensitive neurons in the antennal lobe of the moth Agrotis ipsilon. Dual extracellular recording experiments were conducted using unique odor puffs and pulsed stimulations with the complete pheromonal blend. The large majority of the recorded neurons (43 out of 60) exhibited a multiphasic response consisting in an excitatory phase (E1) followed by an inhibitory phase (I) and a long tonic excitation (E2). The second group of neurons (14 out of 60) exhibited a pure tonic excitatory response. For multiphasic neurons, the duration of E1, but not of I, depends on stimulus concentration and duration. These neurons were able to follow pheromone pulses up to several Hertz. Moreover, their responses (E1 phases) were very precise (spik e timing jitter < 4 ms) and reliable (probability of missing spikes < 0.1) over repeated trials, which was not the case for monophasic neurons. These results indicate that only multiphasic neurons are adapted to detect the fine structure of odor plumes. We then developed a biophysical neuron model capable of reproducing and explaining the stereotyped E1/I/E2 response. The model predicts that a small conductance calcium dependant potassium (SK) current could be involved in the generation of the inhibitory phase. The E2 phase likely results from a long-lasting excitation of receptor neurons, in addition to a possible elevation of the extracellular potassium concentration within the glomerulus. Finally, we discuss functional implications of the different phases of the neuron responses in the stereotyped surge-and-cast behaviors of male moths.

Building a better electronic nose quantitative lessons from biology

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Biological noses outperform arrays of engineered chemical sensors, aka electronic noses (e-noses), in many ways. Therefore humans still use their own noses in the quality control of food processing. Also, humans continue to use dogs noses to detect explosives or illicit substances in a variety of settings. E-noses will need to become more sensitive, more discriminating and much faster than they are now before they could be adopted widely.

We will describe lessons learned from the responses of Drosophila olfactory receptors and how we are using this information to improve the performance of electronic noses. Specifically we will show how the selectivity, independence and sensitivity of e-nose sensors differ from those of Drosophila ORs. Cybernose is our name for an e-nose that has invertebrate ORs for its sensors. We will also describe preliminary work to model the performance of Cybernose using in vivo results obtained from Drosophila.

Stimulus and Network Dynamics Can Collide in a Ratiometric Model of the Antennal Lobe Macroglomerular Complex

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We present a model of the macroglomerular complex of the insect antennal lobe that is able to encode ratios between the concentrations of two odorants in a blend. The dynamical behaviour of the model is evaluated for two different operating regimes termed winnerless competition and winner takes all, that arise as a consequence of the connectivity pattern between inhibitory local interneurons. Our results show how the model generates ratio-specific trajectories in its projection neuron output population in both operating regimes. We compare the efficacies of the different population codes for reporting ratio-specific blend information to higher centres of the insect brain. Our key finding is that the complex spatiotemporal code observed during winerless competition may be more efficient in transmitting blend information, but that in this case the dynamics of the stimulus can collide with those generated by the antennal lobe network itself, potentially degrading ratio speci fic information.

Specific properties of local interneuron subtypes suggest distinct tasks during odour processing in the antennal lobe

Jan Wessnitzer

University of Edinburgh, UK

Establishing structure-function relationships is a fundamental issue in neuroethology. Modelling approaches allow for systematic exploration of these relationships (in simulation or in more realistic environments using robots). Here, we model network interactions in the neural circuitry of the insect antennal lobe and mushroom body, to investigate their role in olfactory learning. Using single compartment neuron models, we systematically investigate the ability of this distinct neuro-architecture for decorrelating responses to odours, and how this might support learning of complex discriminations involving compound stimuli (including binary and overlapping mixtures, negative and positive patterning, biconditional discrimination, blocking, sensory preconditioning). We compare these results with experimental data from odour-shock conditioning in flies, and the predictions from several well-known theoretical models.

Scent-tracking by autonomous robots: Infotaxis and beyond

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Autonomous scent tracking and source localisation is a major challenge in robotics, especially when confronted to open environments where odor dispersal is dominated by turbulence. The fine-scale structure of the odor plume exhibits a patchy and chaoticallyevolving structure. Under such conditions, robot navigation cannot rely on instantaneous measurements, as the local concentration gradient does not point toward the source. Instead, Vergassola et al. (2007) proposed Infotaxis, a novel decision-making strategy based on information maximization leading to higher degrees of efficiency than simpler approaches based on maximum likelihood or mere exploitation. Interestingly, infotactic trajectories share many of the behavioral characteristics observed in nature, e.g. in the flight of moths attracted by a sexual pheromone. Although animal patterns are not explicitly pre-programmed, they do emerge naturally from underlying mathematical expressions. Yet, infotaxis requires heavy co mputation which is problematic when considering robotic or biological implementations.

Here, we push further the study of Infotaxis, and assess its performance by combining robotic experiments and simulations. Our results indicate that infotaxis is both effective (seven detections on average were sufficient to reach the source) and robust (the source is found in presence of inaccurate modeling by the searcher). We also deepen the study of the biomimetic characteristics by confronting the model to pulsed sources such as those faced by animals in nature. In addition, an alternative approach to Infotactic decision-making is introduced. It also conveys the balance between exploration and exploitation, but without quantifying the knowledge of the agent (as abstractly defined in terms of global uncertainty). Instead, the decision-making is now driven by the probability of learning, under the premise that learning may be simply defined in terms of interactions with either the source or chemical particles. Resulting trajectories are shown to preserve most charact eristics encountered in Infotaxis. Yet the simplifications introduced in both the computational requirements and in the actual foundations behind the decision-making, make this approach more biologically plausible and easier to implement on a real robot for fast navigation.

Poster Abstracts

Modeling Antennal Lobe Information Processing With Linear Transformations

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In the insect antennal lobe odors are represented as spatiotemporal patterns of activity. We use a computational model to investigate the role played by lateral interactions between glomeruli in the Drosophila antennal lobe during odor processing.

We model different functional networks by employing linear algebraic matrix multiplications. This approach has the advantage of being on a similar level of resolution as the calcium imaging that gives rise to most of the physiological data about network interactions. Furthermore it is fast and relatively simple to analyse and interpret. The input vectors are derived from the public DoOR database (Galizia et al., 2010) and reflect the statistical relationships between the activation of 36 glomeruli in response to 251 different odorants.

We show that model networks implementing stochastic inhibitory connections between a defined proportion of glomeruli can increase separation between odor response vectors. In these networks, glomerular activation becomes sparser allowing for a more reliable identification of odors at the price of the total number of odors that can be distinguished upstream of the network. This effect can be modulated dynamically by changing the efficacy and/or the number of inhibitory connections. Such a mechanism might be useful for insects to quickly adapt to different odorant environments and to modulate input statistics adopting plastic changes in the brain.

Multiple Time-Scales in Olfactory Receptor Neurons: An Experimental and Mathematical Approach

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We illustrate a "bottom-up" approach to computational modeling of multiple time scales of electrophysiological data obtained from olfactory receptor neurons (ORNs). Our computational model predicts both the odorant-induced slow (transduction) and fast (action potential) currents obtained from single ORNs. In particular, we are using recordings obtained from a mouse line which lack olfactory marker protein (OMP), a protein of unknown function, which is ubiquitous and selectively expressed in vertebrate olfactory receptor neurons (ORNs). OMP-/- ORNs display a 10-fold slowed olfactory response making them particularly interesting for our modeling approach. A Bayesian model-fitting algorithm called Wedge is used to integrate a posterior distribution given recordings obtained across multiple ORNs of both wildtype and OMP-/mouse lines. This fully Bayesian approach is novel in that it provides a mechanistic approach to the action potential interval distribution (when is spike fir ing is most likely to occur) and the conditional spiking distribution (distribution of spikes within a putative spike interval). Subsequent statistical analyses of the posterior distribution of model parameters provides meaningful insights into the role of OMP within ORNs and can suggest most probable modes for diversity among the ORN studied.

Interglomerular interactions in the antennal lobe of the honeybee.

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Animals use odours to guide their behaviour (e.g. to mate, feed, communicate). In insects odours are detected by olfactory receptor neurons (ORNs) located in the antenna. The axons of ORNs form the antennal nerve and project to the central nervous system in the antennal lobe (AL) which is homologous to the vertebrate olfactory bulb. Two main types of cells exist in the AL; local neurons (LNs) whose axons do not leave the AL and projection neurons (PNs) that carry the output of the AL. PNs project to higher brain areas such as, for example, the mushroom body. The axon terminals of the ORNs, and the processes of PNs and LNs form neuropil structures called glomeruli. Each glomerulus receives sensory inputs from a specific receptor type and thus responds to particular odour stimuli. This leads to stereotyped combinatorial activation patterns in the AL that are relatively well conserved between individuals of one species. However, in honeybees, the number of LNs (4000) by far exce eds that of PNs (800). This suggests an extraordinary computational potential in the neural network of the antennal lobe. LNs projecting to several glomeruli represent good candidates for shaping the response of the AL. To learn more about interglomerular communication we have performed calcium imaging experiments in bees using Fura to selectively stain PNs while injecting neurotransmitters in a single glomerulus with a pipette. First, we show that gamma-aminobutyric acid (GABA) and acetylcholine (ACh) can be used to turn glomeruli OFF and ON, respectively. We analysed the effect of injections alone and injections combined with odour presentation. GABA suppressed the odour response in the injected glomerulus. Switching OFF a glomerulus with GABA during an odour presentation could influence the activity pattern in other glomeruli far away from the injected glomerulus. Furthermore injections of ACh in a glomerulus triggered inhibition in its neighbours, but in a distance indep endent manner. This suggests that the inhibition between glomeruli is glomerulus specific. The injection of ACh combined with an odour stimulus produced complex glomerulus specific responses. These results show that the functional connections between glomeruli can greatly influence odour processing in the antennal lobe.

Mechanisms and purpose of dual-pathway odor coding in the honeybee

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In the olfactory system of the honeybee Apis mellifera, uniglomerular projection neurons relay sensory information from olfactory sensory neurons to higher brain regions via two distinct pathways, the lateral and the medial antenno-cerebral tract (I- and m-ACT). Neurons within these two tracts exhibit complementary coding strategies regarding concentration dependence, breadth of odor tuning and mixture representation. We used a rate-code network model to describe how these distinct coding properties can be brought about by varying the strength of lateral inhibition and gain control. We were able to reproduce I-ACT specific odor representations using strong lateral inhibition and gain control, while m-ACT specific coding properties were reproduced using weak lateral inhibition and no gain control. Our results suggest that the neuronal networks which these pathways are part of have different network parameters and are at least partly segregated. In addition, our findings indicate that the development of two parallel systems with complementary coding strategies may reflect an evolutionary adaptation to cope with the search/approach task that honeybees face during foraging in their natural environment.

Frequency matching as a mechanism for sex and species recognition in mosquitoes

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In this exciting work we address the role of acoustic cues in mediating sex and species recognition in flying mosquitoes. We also address the physiological basis of such auditory interactions through the study of the antennal auditory receptor; the Johnstons organ (JO). Our previous studies, based on the nectar feeding mosquito, have shown that mating pairs of mosquitoes, which fly at similar wing beat frequencies, match the frequency of their wing beats, whereas same sex pairs actively avoid frequency matching. Surprisingly frequency matching mediates mate recognition in blood-feeding mosquitoes, where the male and females fly at different frequencies. In the malaria mosquito, Anopheles gambiae, frequency mating acts as reproductive barrier in sympatric species in the early stages of speciation. For blood-feeding vector-carrying mosquitoes frequency matching occurs above the high frequency limit at which the JO can electrically encode movements of the sound receiver. How do mosquitoes detect each others wing beat frequencies and mediate frequency matching? The basis of frequency matching lies in the nonlinear nature of the antennae which generates large F2-F1 distortion products where F1 and F2 denote the matching flight tone frequency of a pair of mosquitoes. Although both F1 and F2 are too high in frequency to be encoded by the JO the F2-F1, which has a low frequency is encoded by the JO. Through minimising the F2-F1 component mosquitoes can mediate frequency matching without detecting either F1 or F2. Frequency matching and large F2-F1 components have been found in 3 separate genera of haemophilic mosquitoes. We suggest that frequency matching is a common feature in the acoustical interactions of mosquitoes which acts as a necessary prerequisite before mating.

A biophysical model reproduces the multiphasic firing patterns observed in moth antennal lobe neurons

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In the antennal lobe of the noctuid moth Agrotis ipsilon, pheromone-sensitive projection neurons (PNs) exhibit a multiphasic firing pattern when the antenna is stimulated with the pheromonal blend. At low concentrations, the PN response is biphasic and consists of an excitatory phase (E1) followed by an inhibitory phase (I). The duration of E1, but not of I, depends on stimulus concentration and duration. At higher concentrations, the response becomes triphasic with a long tonic excitatory phase (E2) coming out after the inhibition. To understand the cellular and synaptic mechanisms underlying these specific discharge patterns E1/I and E1/I/E2, we developed a biophysical model of a PN receiving inputs from olfactory receptor neurons (ORNs). The model is based on patch-clamp recordings from PNs, intra- and extra-cellular recordings from ORNs and PNs, as well as other experimental results on the synapses from ORN to PN and LN (local neuron) to ORN and PN. The PN input is modele d as a population of ORNs firing according to Poisson processes with the same firing rate under pheromone stimulation at various concentrations and durations. The PN model is based on the Hodgkin-Huxley formalism with realistic ionic currents whose parameters were fitted to whole cell patch-clamp data. Simulations revealed that the A current (transient potassium current) strongly delays the onset of the spike and the firing frequency. Simulations showed also that the SK current (calcium gated small conductance potassium current) strongly affects the firing frequency and, more importantly, the hyperpolarization of the inhibitory phase I following the E1 phase. The E2 phase likely results from the longlasting excitation of ORNs observed at high concentrations.

A model of the moth macroglomerular complex: interplay between interglomerular inhibition and neuronal intrinsic properties

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In the moth Manduca sexta, pheromone-sensitive projection neurons (PNs) exhibit a spatio-temporal pattern of spikes that consists of excitatory (E) and inhibitory (I2) phases preceded by a brief inhibition (I1). The E phases of several PNs branching in one glomerulus are synchronized and the level of synchrony is modulated by lateral inhibition from other glomeruli (Lei et al, 2002). Although experiments have highlighted the role of interglomerular inhibition in PN synchrony, little is known about the interplay with neuronal intrinsic properties. Here we investigated theoretically how intrinsic properties affect PN synchrony and temporal patterning. We developed a computational model of the moth macroglomerular complex by coupling excitatory PNs with inhibitory local neurons (LNs). Single cells are modelled as conductance-based neurons with similar intrinsic currents (Na $^+$, K $^+$, Ca $^{2+}$, A, SK) and leak but different parameter values for PNs and LNs. We examined whether a small co nductance calcium-dependent potassium (SK) current could be involved in producing the I2 phase. Blocking the SK channel in the PN model disrupts I2, as found experimentally with local injection of Bicuculline. We also studied whether the latency of the PN response could be due to the A current: when it is blocked in the model (experimentally this is done by 4-aminopyridine for example), the PN fires immediately after excitation as expected. As LNs respond significantly faster than PNs, the onset of I1 in the model coincides with inhibition from LNs. Lateral inhibition then plays the role of a reset by eliminating the influence of initial conditions, thereby synchronizing PNs receiving common glomerular inputs. Taken together, these observations suggest that synchronized PN responses result from a complex interplay between interglomerular inhibition and neuronal intrinsic properties.

Functional modules of chemical features and odor quality in the rodents olfactory bulb

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In this work, we present a framework to derive functional module maps of rat olfactory bulb uptake images (URL) that show complex compound specific activity patterns. Activity on this first relay station of the mammal olfactory system is expected to be triggered purely by input and thus is likely to link to receptor specific characteristics.

Fusing the information of several activity states for a variety of compounds, their chemical properties and psychophysical descriptions of odor quality, we use machine learning approaches and multivariate data analysis techniques to project functional modules onto a map of the olfactory bulb.

These modules might have an twofold impact, first they might help to systematically localize target regions for specific binding receptor genes and secondly they give insights into the potential coding strategies of the olfactory system into the pyriform cortex. Given the nature of this project, the data is static and without any temporal dynamics, but still a complete picture of the coding paradigms especially for post-bulbar input will contribute to the further understanding and interpretation of dynamical processes on the next level.

Due to the difficult experimental conditions it cannot be expected to get dynamic activity patterns of the mammals bulb in the near future. Techniques in other animals like e.g. honey bees these days already allow to visualize temporal patterns of odorant activity. We plan to incorporate insights of activity signature and hope to relate them to combinatorial static spatial pattern in mammals.

Stimulus and Network Dynamics Can Collide in a Ratiometric Model of the Antennal Lobe Macroglomerular Complex

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We present a model of the macroglomerular complex of the insect antennal lobe that is able to encode ratios between the concentrations of two odorants in a blend. The dynamical behaviour of the model is evaluated for two different operating regimes termed winnerless competition and winner takes all, that arise as a consequence of the connectivity pattern between inhibitory local interneurons. Our results show how the model generates ratio-specific trajectories in its projection neuron output population in both operating regimes. We compare the efficacies of the different population codes for reporting ratio-specific blend information to higher centres of the insect brain. Our key finding is that the complex spatiotemporal code observed during winerless competition may be more efficient in transmitting blend information, but that in this case the dynamics of the stimulus can collide with those generated by the antennal lobe network itself, potentially degrading ratio speci fic information.

Spiking Programmable Logic Implementation of the Insect Macroglomeru-Iar Complex for Chemical Blend Processing

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In this work we present a programmable logic (FPGA) implementation of a spiking neural network model of the insect antennal lobe Macroglomerular Complex (MGC), which encodes ratios between the concentrations of two odorants in a blend. The FPGA parallel architecture provides the capability of real-time processing of chemosensory data faster than the software counterpart. This has enabled the study of the MGC model dynamics when driven by real world Quartz Crystal Microbalance (QCM) sensor data. By associating the hardware model with the QCM chemosensor array, we are able to classify complex odours which are difficult to identify from the chemical sensor data alone. Our results show that the model can identify and retrieve ratiometric data from chemical compositions using QCM sensor inputs. Together, the combined real-time FPGA based MGC neural model and chemosensor array shows ratio-specific dynamical trajectories in its output projection neuron population, making it suitable for blend processing in real-world applications, for instance as part of an infochemical communication system (which is the focus of project iChem*)

Neuromorphic Olfaction Using VLSI Chips

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Olfactory stimuli are represented in a high-dimensional space by neural networks of the olfactory system. A great deal of research in olfaction has focused on this representation

within the first processing stage, the olfactory bulb (vertebrates) or antennal lobe (insects) glomeruli. In particular the mapping of chemical stimuli onto olfactory glomeruli and the relation of this mapping to perceptual qualities have been investigated (Galizia and Menzel 2001; Linster et al. 2001; Xu et al. 2000). While a number of studies have illustrated the importance of inhibitory networks within the olfactory bulb or the antennal lobe for the shaping and processing of olfactory information (Stopfer et al. 1997; Urban 2002; Yokoi et al. 1995), it is not clear how exactly these inhibitory networks are organized to provide filtering and contrast enhancement capabilities. Several theoretical, computational and experimental studies suggest in fact that networks encode sensory information using a small number of active neurons at any given point in time (sparse coding). This allows for increased storage capacity and low energy consumption in associative memories, makes a structure in natural signals explicit and represents complex data in a way that is easier to read out at subsequent levels of processing (Olshausen and Field 1997).

In this work, a neural network of spiking neurons is implemented on neuromorphic VLSI chips, composed by arrays of silicon I and F neurons and dynamic synapse circuits, interfaced via an asynchronous event-based communication protocol. This hardware setup is used to explore the role of each stage of processing in the antennal lobe in real-time, with particular focus on lateral inhibition and response properties of cells rather than spatial dependence. Our long term goal is to understand if sparse-coded representation of odors observed in nature (Linster et al. 2005), can be derived from the topology of connections in the model. The hardware model is based on the study of Silbering and Galizia and on measured data from olfactory receptive neurons of insects, especially Drosophila (Galizia et al., 2010).

Signal transformation from olfactory receptor neurons to central neurons

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In the male moth, sex pheromone in the plume emitted by the female is detected by a population of specialized olfactory receptor neurons (ORNs) housed in antennal sensilla. A large number of these ORNs converge onto a few glomeruli where they connect synaptically to a smaller number of projection neurons (PNs). To study the transformation of the message from ORNs to PNs, we recorded responses to different doses of sex pheromone from single ORNs and PNs in the moth Agrotis ipsilon. Responses of these neurons were characterized by their latency and firing rate. Mathematical functions (decreasing exponential for latency and Hill function for frequency) were fitted to the dose-response curves. To describe single cell variability, probability density functions were estimated for the fitting parameters and the distributions obtained from ORNs and PNs were compared. The results suggest that the ORNs with the lowest thresholds and shortest latencies in the population trigger the PN r esponse, which may explain the higher sensitivity of the PN to small amounts of sex pheromone. They also show that the relatively variable ORN responses to a given pheromone stimulation are converted into less variable responses across PNs.

Event-timing in associative learning: Bridging between molecular and behavioral levels

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A fundamental determinant of associative learning is event-timing: Fruit flies, for example, once trained with an odor that precedes electric shock, subsequently avoid this odor; training with opposite sequence of events on the other hand establishes the odor as a predictor for the shock-offset, resulting in conditioned approach. During training, an odor-induced Ca⁺⁺ signal and a shock-induced dopaminergic modulatory signal likely converge on a doubly regulated adenylate cyclase, triggering the molecular cascade, leading to the neuronal plasticity underlying the conditioned behavior. In Aplysia, a corresponding adenylate cyclase is bi-directionally regulated by modulatory transmitter and Ca⁺⁺, depending on the relative timing of the two kinds of input. We take a computational approach to bring these Aplysia molecular data together with the fruit fly behavioral data, and show that the dynamical features of the adenylate cyclase can largely account for the effects of event-timing on associative learning at the behavioral level.

Blend interactions in single neurons responses of the antennal lobe

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In this work, we aim to understand the dynamical mechanisms of blend coding in the insect antennal lobe. To this end, we compared blend interactions among responses from single neurons recordedintracellularly in the antennal lobe of the mothManducasexta with similar data generated using a computational model constructed with a morphologically-based connectivity pattern of projection neurons and local interneurons. At the peripheral level the receptor neurons of the model have a broad band tuning to the different components within a blend. For both the recordings and the simulations, we found that most interactions between odorants were non-linear, and within the non-linear interactionshypoadditivity (blend response = single components) and suppression (blend response; single components) were more common than synergism (blend response ¿ single components at blend concentrations). The good agreement between the proportions of blend interaction types found in the simulations and the recordings arises as a purely network phenomenon, since we did not include any special intrinsic properties in the neurons of our model. These results suggest the existence of a combinatorial process for odour blend coding in the antennal lobe of the moth that arises from network dynamics.

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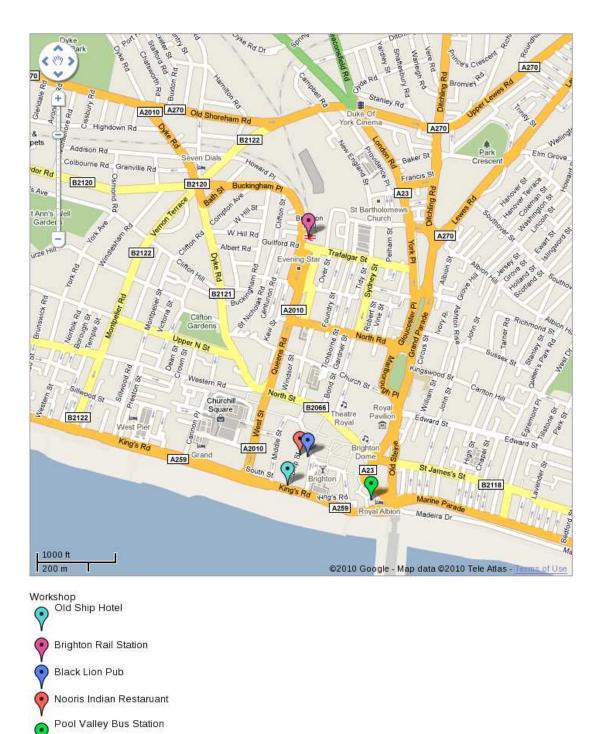


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