European Science Foundation
Standing Committee for the European Medical Research Councils (EMRC)
Standing Committee for Life, Earth and Environmental Sciences (LESC)

ESF EMRC-LESC EXPLORATORY WORKSHOP

Understanding Mushroom Body Function – Scientific Report

La Maison du Haut Salat, Seix (St. Girons), France, 16-19 September 2004

Convened by: Martin Giurfa

1. Executive summary

The ESF meeting on Mushroom Body Function was held at the Auberge du Haut Salat in Seix, Ariège, France, from September 16th to 19th. Thirty participants from four different European countries (France, Germany, Spain, Greece) including external invitees from USA gathered there to present their latest research on insect brain and cognitive processes from different perspectives going from molecular biology to experimental psychology.

The meeting responded to a specific necessity, which was to put together the different European groups which, using different experimental approaches, study the insect brain as a model for understanding basic and intermediate levels of cognitive processing. Indeed, the insect brain is capable of extracting the logical structure of the world to an impressive extent. Learning and memory are well-established capacities of this brain and can be traced to the cellular and molecular level in an *in vivo* learning insect. This constitutes a unique advantage of insects with respect to vertebrates in the frame of studies on the mechanistic basis of learning and memory.

Within this context, the mushroom bodies, which are a central and voluminous structure of the insect brain, were at the very core of the meeting due to their recurrent association with experience-dependent plasticity phenomena. Talks on other associated brain structures such as the antennal lobes, the main olfactory neuropile in the insect brain, were also delivered by some participants (see below 'Scientific Content of the Meeting").

The meeting started with a presentation by Dr. Hui Wang, who introduced in detail the European Science Foundation and the different funding instruments that it provides for supporting different sorts of initiatives in European scientific research. This presentation was followed by the scientific talks, which were organized in six thematic blocks:

- **Anatomy: Mushroom body development, neurogenesis and organisation**
- **Neurotransmitters, channels and memory**
- **Optophysiological approaches to mushroom body function**
- **Neurogenetics of mushroom body function**
- **Associative learning and memory and the role of mushroom bodies**
- **Computational neuroscience: modelling mushroom body function**

Blocks of General Discussion were interspersed all along the meeting (particularly at the end of each thematic block; see program below) in order to prioritize scientific exchange. This was indeed on of the most valuable characteristics of the meeting: the possibility of having long, productive and intense discussions on the topics covered, a fact that is neither usual nor allowed in normal scientific conferences, and that was greatly appreciated by all participants.

At the end of the meeting, a global discussion took place, in which participants analyzed the possibility of applying for a ESF network ('A la Carte' Program). This discussion was enlightened by the technical information provided by Dr. Hui Wang. The unanimous consensus was that the groups represented at the meeting are ready to engage in such a program that will certainly allow to coordinate efforts efficiently in order to make progresses in our understanding of the insect brain and its inherent plasticity. It was underlined that the different groups represented in Seix have several specific technical achievements and expertise to study neural activity in the insect brain and that formalized cooperative links should be finally created between these groups.

To better define the scientific profile of the network a deep discussion on "*What we have vs. What we need*" was conducted, and potential additional partners identified. The general conclusion was not to focus on a single brain structure as the mushroom bodies, because this structure is a functional part of a more complex network that acts as a functional unit. In defining this aim, the number of European groups that may be included in the network increased with respect to those present in Seix. It was therefore proposed to apply for an 'A la Carte' Program based on a research program on "***Cognitive Processing and Mini Brains***".

Martin Giurfa was elected unanimously as the **Speaker and Main Applicant** for the future network.
A **Bureau** was also elected, which included **Drs. Martin Heisenberg (Germany), Alberto Ferrús (Spain), Makis Skoulakis (Greece) and Thomas Préat (France**).

2. Scientific content of the event

As mentioned above, the meeting was organized in six thematic blocks:

- **Anatomy: Mushroom body development, neurogenesis and organisation**
- **Neurotransmitters, channels and memory**
- **Optophysiological approaches to mushroom body function**
- **Neurogenetics of mushroom body function**
- **Associative learning and memory and the role of mushroom bodies**
- **Computational neuroscience: modelling mushroom body function**

These blocks regrouped the main experimental approaches represented in the meeting: development and neuroanatomy, functional molecular biology, optophysiology (imaging), genetics, experimental psychology, mathematics and modeling.

In **the first block**, the focus was placed on comparative studies about how the mushroom bodies develop in different insect brains (*N. Strausfeld, W. Gronenberg*). Functional, evolutionary neuroanatomical approaches identified homologies between mushroom body substructures and allowed to establish phylogenetic relationships based on brain development among primitive and eusocial, advanced insects. On the basis of these comparatives studies, specific models about neuronal wiring within the mushroom bodies can be proposed. A. Ferrús and A. & C. Strambi provided a less comparative view and preferred to concentrate on the mechanistic basis of synaptic establishment in *Drosophila* (*A. Ferrús*) and on the fascinating fact that some insect mushroom bodies (in crickets, for example) present well-characterized neurogenesis (*A. & C. Strambi*). Both talks thus provided a view of different ways of changing the organization of neural networks. Functional studies on the consequences of interfering with such development- and experience-dependent neural plasticity were presented.

In the General Discussion, the neuroanatomical approach was identified as a fundamental tool for understanding brain function as it allows uncovering the wiring of the nervous system. It was furthermore recognized that high-level neuroanatomical studies with an important evolutionary frame such as those of the invitees Strausfeld and Gronenberg constitute a discipline absent in Europe that needs urgently to be promoted.

In **the second block**, the emphasis was put on the molecular characterization of neurotransmitters and ion channels that intervene in experience-dependent plasticity in the insect brain. Cellular culture of neurons from specific brain structures such as the mushroom bodies or the antennal lobes were coupled with single-channel characterization techniques such as patch-clamp electrophysiology and neuropharmacology. Using these approaches, it was possible to identify potential new neurotransmitter systems (e.g. glutamatergic) in the honeybee antennal lobe of larvae (*G. Barbara*) besides those already known (cholinergic, gabaergic, histaminergic, etc), and to clone and characterize the molecular structure of nicotinic receptors that intervene in the processing of olfactory information in the honeybee brain (*M. Gauthier*). Characterization of the different subunits integrating nicotinic receptors together with selective neuropharmacological blocking using receptor antagonists and agonists allowed to propose a cellular model of olfactory memory in the honeybee (*B. Gruenewald*).

In the General Discussion, the advantages and limitations of molecular techniques with respect to different insect models were discussed. Clearly, insects for which the sequencing of the whole genome is not yet available do not help our progressing in this particular avenue. From this point of view, the fruit fly and the honeybee constitute currently two privileged models in which this information is available and which allow the application of these reductionistic approaches *in vitro* and even *in vivo*.

In **the third block**, studies using optophysiological approaches on honeybees and fruit flies were presented. Imaging techniques applied to the insect brain are available and provide a unique advantage, that is to visualize brain activity in a living fixed insect while it processes olfactory information and, more importantly, while it learns and memorizes it. Chameleon dyes were used to target specific neurons or subsets of neurons in *Drosophila* using the GAL4 technique and measure in this way intracellular calcium release as a consequence of olfactory stimulation (*A. Fiala*). The classical fruit fly aversive learning paradigm was used in this context, namely the pairing of an odor with an electric shock. Dopaminergic neurons subserving the neural representation of the electric shock were identified in the *Drosophila* brain and more specifically in the mushroom bodies. Using a similar approach but different dyes (fura dextran), olfactory learning in different neuronal populations was studied in the honeybee brain (*R. Menzel*). In this case, appetitive olfactory learning was used in which an odor is paired with a reward of sucrose solution. Neural activity of projection neurons conveying information to the mushroom bodies was analyzed and compared to that of the Kenyon cells, the neurons that are intrinsic to the mushroom bodies. The results show that a sparsening of the olfactory code occurs at the level of the mushroom bodies and that specific activity changes can be identified in the input region of the mushroom bodies as a consequence of associative learning. Finally, a new technique for imaging nitric oxide (NO) activity (and not Ca^{2+} as done until now) was presented for the honeybee antennal lobe (*J.C. Sandoz*). This allowed to study in parallel the close relationship between NO and Ca^{2+} release and determine the contributions of these two neurotransmitter systems in the olfactory coding.

The General Discussion concentrated on the necessity of creating new dyes addressing different neurotransmitter systems and specific subsets of neuronal subpopulations. It also acknowledged the fact that optophysiological approaches to insect brain function constitute an original and strong aspect of European research and that efforts need to be coordinated between the different groups using these techniques (Berlin, Würzburg, Toulouse, Trondheim, Lund) in order to be more efficient in understanding the cellular mechanisms of learning and perception using these kind of tools.

In **the fourth block**, studies using neurogenetic interference tools based on the GAL4 technique were presented. These studies were performed in *Drosophila* as the GAL4 method remains an exclusivity of this insect. The rationale of these works is to turn off or on selected genes in the fly brain, in specific subsets of neurons and/or in a reversible manner, in order to determine their potential contribution to learning and memory processes. Starting with simpler forms of learning, a study on the role of *Drosophila* 14-3-3-ζ mutants in the protection from premature habituation (*M. Skoulakis*) allowed to discuss the role of the mushroom bodies in the context of non-associative learning. Furthermore, the role of these structures was also discussed in the context of locomotor activity on the basis of the centrophobism / thigmotactism paradigm (*J.R. Martin*) in which flies moving in a flat arena search the borders and avoid its centre. Using the more traditional paradigm of aversive olfactory learning (see above), it was shown that blocking γ axon pruning in *Drosophila* mushroom bodies impairs short-term memory, but not long-term memory (*J.M. Dura*). In a similar set of studies, the role of dopamine signaling in olfactory memory phases was presented (*T. Préat*). Such studies allowed to redefine a new view of memory dynamics in *Drosophila* olfactory learning in which memory phases can organize sequentially differently depending on acquisition and training procedure. The differential contributions of the dopaminergic and the octopaminergic systems for aversive and appetitive learning, respectively, were presented in an elegant study showing how these two different learning contexts solicit different neurotransmitter systems subserving the corresponding unconditioned stimuli, electric shock and sugar, respectively *(M. Schwaerzel*).

The General Discussion focused on memory formation and organization and on the potential role of the mushroom bodies for arresting irrelevant behaviors. The presence of different groups in different European countries using neurogenetic tools to understand learning and Memory in *Drosophila* was debated as it was immediately realized that no cross-talking exists between these groups across country frontiers. This field was identified as one for which the creation of an ESF network would have a tremendous impact as it would allow to coordinate research activities of excellent level in a more productive manner.

In **the fifth block**, behavioral approaches to study mushroom body function were in the foreground. A first study revealed that *Drosophila* larvae can be used as an experimental model for associative learning (*B. Gerber*), an interesting finding given the reduced amount of neurons available in their nervous system. A more classical study on memory formation in honeybees tackled the issue of extinction vs. reconsolidation using protein synthesis blockers injected at different phases of the acquisition / retrieval processes (*D. Eisenhardt*). An experimental psychological study addressed the importance and impact of the interval between the conditioned and the unconditioned stimulus (the odor and the electric shock, respectively) in classical conditioning in *Drosophila* (*H. Tanimoto*) and showed that, besides the classical aversive learning in forward conditioning, backward conditioning can result in a preference for the odor that is presented always *after* the shock as it may indicate 'relief' in this context. Another study analyzed the role of mushroom bodies in honeybee olfactory learning using elemental vs. non-elemental learning paradigms coupled with selective mushroom body lesion by Hydroxyurea (*M. Giurfa*). A definitive proof for the potential involvement of mushroom bodies in complex, non-elemental forms of learning is still lacking.

The General Discussion focused on the importance of controlled behavioral techniques for a functional analysis of brain function and on their strength when they are coupled with direct interference with brain structures. This field of research is certainly one in which European research is not deficitary and where a ESF network would have a tremendous impact as it would also allow to coordinate research activities of excellent level in a more productive manner.

Finally, in the **sixth block**, mathematical modeling of mushroom body function was presented. Small-world algorithms that allow to establish efficient and plastic connections between reinforced units were used to establish a general model of insect olfaction (*R. Huerta*). Similar approaches that included self-organization algorithms were used to propose how such a generic system can perform olfactory discrimination and generalization (*T. Nowotny*). At the end, a general model of the *Drosophila* mushroom bodies was introduced on the basis of a long and complete series of experiments addressing visual and olfactory learning in the fruit fly (*M. Heisenberg*).

The General Discussion acknowledged the importance of the modeling approach, since the ultimate goal of all research disciplines studying mushroom body function is to converge on a generic model of this and other brain structures. It was also acknowledged that European research is deficitary with respect to this kind of studies as applied to the insect brain and that interactions with physics, mathematics, informatics and engineering have to be reinforced to promote research on mathematical modeling of insect brain function.

3. Assessment of the results, contribution to the future direction of the field, outcome

Most of what corresponds to the assessment of the results was presented above in the paragraphs that presented the General Discussion following each specific thematic block. All the participants underlined the uniqueness of the ESF meeting with respect to more traditional meetings as it allowed long, deep and rich discussions on specific as well as on global scientific topics.

The participants decided therefore unanimously to build a European network based on the groups present at Seix and to apply for an ESF "A la Carte Program". From this perspective, the main strategic advantage of the ESF meeting was to identify the fields and approaches to the functional study of the insect brain in which European research is particularly strong and those in which it is still deficitary. The final Discussion focused precisely on this distinction of "*what we have vs. what we need*". Clearly, the strong areas are behavior, neurogenetics, optophysiology, pharmacology and molecular biology; the areas that have to be developed are neuroanatomy, intracellular electrophysiology, modeling and evolutionary and ecological perspectives. The incorporation to a potential ESF network of external groups as those leaded by some of the external invitees in USA and Japan would allow training young researchers in these fields and to incorporate these approaches and tools to European research.

A fundamental outcome of the meeting was the necessity of focusing on the insect brain as a whole, in order to understand basic and intermediate levels of cognitive processing, and not only on a particular structure such as the mushroom bodies. It was acknowledged that mushroom bodies can only bee understood in the context of an integrative study of the different networks that they build with other brain structures such as the antennal lobes, the lateral protocerebrum and the different visual neuropiles, among others. A future ESF network should therefore focus on the potentiality of the insect brain to visualize *in vivo* and with high spatial and temporal resolution in the complete animal how cognitive processes related to learning and memory occur. This is certainly a unique advantage of invertebrate systems that can be hardly equated by vertebrate preparations. The future ESF network will therefore be called "***Cognitive Processing and Mini Brains***".

Having decided the general profile of the network, other European groups were identified that could participate in such a potential ESF network. These groups were not originally invited to Seix because they do not perform research on mushroom body function although they do it on other structures of the insect brain.

4. Final program

Thursday 16 September 2004

Arrival in Toulouse throughout the day - Bus leaving Toulouse (University Paul Sabatier) at 17h00
Arrival at the Maison du haut Salat, Seix, at 18h30-19h00 - Dinner at the Maison du Haut Salat

Friday 17 September 2004

09:00 – 09:05: **Martin GIURFA** (Toulouse)
Welcome

09:05 – 09:15: **Hui WANG** (ESF Standing Committee for the Life, Earth and Environmental Sciences)
Aims and scope of ESF Exploratory Workshops: defining the frame of the meeting

Anatomy: Mushroom body development, neurogenesis and organisation

09:15 – 10:15: **Nick STRAUSFELD** (Tucson)
Mushroom body evolution: shared and divergent organization.

10:15 – 10:45: **Alberto FERRUS** (Madrid)
Synapse dynamics in development and learning.

Coffee Break

11:00 – 11:30: **Alain STRAMBI** and **Colette STRAMBI** (Marseille)
Synergic actions of environment and juvenile hormone on adult neurogenesis in the house cricket.

11:30 – 12:30: **Wulfila GRONENBERG** (Tucson)
Mushroom bodies in Hymenoptera – a comparative view.

12:30 – 13:00: GENERAL DISCUSSION

Lunch

Neurotransmitters, channels and memory

14:30 – 15:00: **Guillaume BARBARA** (Toulouse)
Ionotropic receptors of cultured pupal honeybee antennal lobe neurons

15:00 – 15:30: **Bernd GRÜNEWALD** (Berlin)
From ion channels towards a cellular model of memory formation in the honeybee brain

15:30 – 16:00: **Monique GAUTHIER** (Toulouse)
Brain nicotinic receptors and the formation of memory in the honeybee

16:00 – 16:30: GENERAL DISCUSSION

Coffee Break

Optophysiological approaches to mushroom body function

16:45 – 17:15: **André FIALA** (Würzburg)

Optical imaging of neuronal activity in higher brain centers of Drosophila.

17:15 – 17:45: **Jean-Christophe SANDOZ** (Toulouse)
Optical imaging of calcium and NO activity in the honeybee brain

17:45 – 18:45: **Randolf MENZEL**, **Paul SZYSZKA** and **Giovanni C. GALIZIA** (Berlin & Riverside)
Mushroom bodies imaged: a new understanding of olfactory coding and learning in the mushroom bodies.

18:45 -20:00: GENERAL DISCUSSION

Dinner

Saturday 18 September 2004

Neurogenetics of mushroom body function

9:00 – 9:30: **Efthimios SKOULAKIS** (Athens)
Protection from premature habituation requires the mushroom bodies and is defined by Drosophila 14-3-3-ζ mutants.

9:30 – 10:00: **Jean-René MARTIN** (Orsay)
Implication of the mushroom bodies in centrophobism / thigmotaxis in Drosophila.

10:00 – 10:30: **Jean-Maurice DURA** (Montpellier)
Blocking γ axon pruning in Drosophila mushroom bodies impairs short-term memory, but not long-term memory.

Coffee Break

10:45 – 11:15: **Thomas PREAT** (Gif-sur-Yvette)
Role of dopamine signalling in olfactory memory in Drosophila.

11:15 – 11:45: **Martin SCHWAERZEL** (Columbia & Saarbrücken)
Extinction of olfactory memories in Drosophila.

11:45 – 12:30: GENERAL DISCUSSION

Lunch

Associative learning and memory and the role of mushroom bodies

14:00 – 14:30: **Hiromu TANIMOTO** (Würzburg)
Bidirectional plasticity in associative learning in Drosophila.

14:30 – 15:00: **Bertram GERBER** (Würzburg)
Simple brains – simple learning ? The Drosophila larva as a study case.

15:00 – 15:30: **Dorothea EINSENHARDT** (Berlin)
Memory consolidation in the honeybee.

15:30 – 16:00: **Martin GIURFA**, **Bernhard KOMISCHKE**, **Dagmar MALUN** and **Jean-Christophe SANDOZ** (Toulouse & Berlin)
The role of mushroom bodies in non-elemental forms of olfactory learning.

16:00 – 16:45: GENERAL DISCUSSION

Coffee Break

Computational neuroscience: modelling mushroom body function

17:00 – 17:30: **Ramón HUERTA** (La Jolla)
Design of the olfactory system for efficient odor recognition: theoretical analysis.

17:30 – 18:30: **Thomas NOWOTNY** (La Jolla)
Self-organization in the olfactory system? Rapid odor recognition in insects.

18:30 – 19:30: **Martin HEISENBERG** (Würzburg)
The Drosophila mushroom body model of olfactory memory – facts and fantasies.

19:30 -20:15: GENERAL DISCUSSION

Dinner

Sunday 19 September 2004

9:00 – 10:00: GENERAL DISCUSSION:
An European Network for the Study of the Insect brain?

10:00 – 10:30: Departure

5. Final list of participants (including full title, address, tel, fax, email)

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6. Statistical information on participants (age bracket, countries of origin, etc.)

Disciplines represented:
Molecular Biology
Pharmacology
Neuroanatomy
Neurobiology
Neurogenetics
Electrophysiology
Optophysiology
Experimental Psychology
Computational Neurosciences
Mathematics and Modeling

Countries represented
France, Germany, Spain, Greece
External invitees from USA (which were British, German and Spanish)

Age bracket

20 – 30	30 – 40	40 – 50	50 – 60	60 – 70
1	12	11	5	1

Martin Giurfa

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