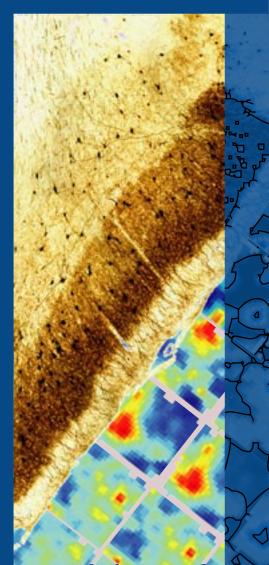
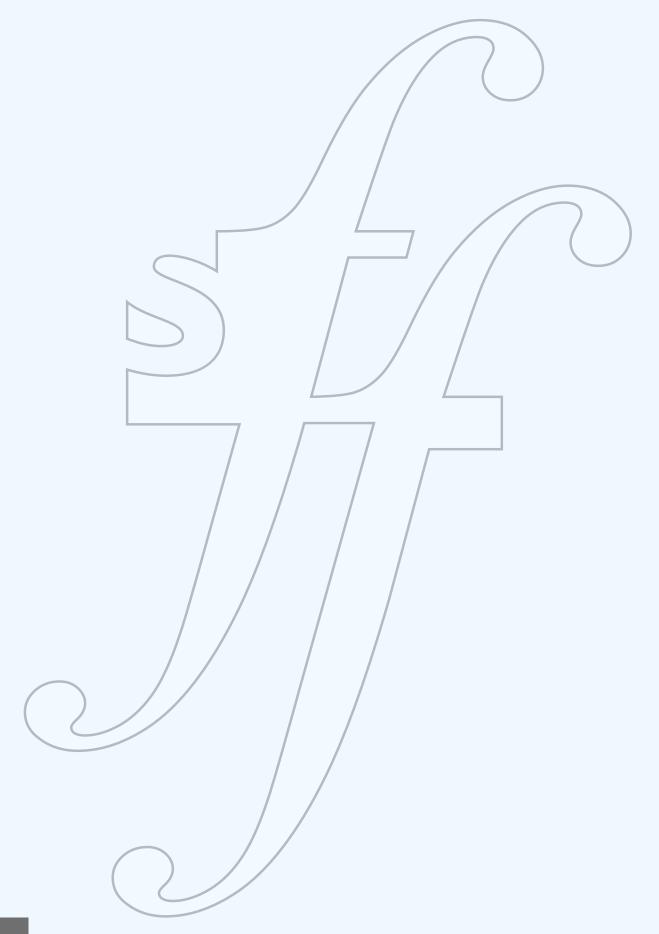




Annual Report 2004 Centre for the Biology of Memory

NTNU Norwegian University of Science and Technology





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Annual Report from the Centre for the Biology of Memory

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Searching for the memory trace



Professor May-Britt Moser and Edvard Moser outside the Medical-Technical Research Centre where CBM is located

2004 was the second year of the Centre for the Biology of Memory (CBM). Since its start-up on the 1st of December 2002, the Centre has developed into one of the world's most fertile convergence arenas for experimental and theoretical studies of memory in brain networks. Through its unique combination of neuroanatomical, neurophysiological, behavioural and mathematical concepts and methods, the Centre has established fundamentally new knowledge about the functional organization of

memory at the interface between medium-term storage sites in the hippocampus and long-term sites in the neocortex. In the eyes of many neuroscientists, the Centre has become one of the world's leading centres for studies of the biological fundament of memory.

The scientific goal of CBM is to understand the biological processes responsible for memory. This ambitious aim requires a multidisciplinary and multilevel approach which can only be accomplished by close collaboration between experts in several disciplines. To realize the integration of methods and concepts across disciplines, seven internationally leading neuroscientists work at the Centre periodically each year. These scientists, coming from the United States, the U.K., the Netherlands, Germany and Italy, share an interest in how memory forms in cell assemblies and brain circuits. During 2004, they spent a total of approximately 90 days at the Centre, in addition to active collaboration over the internet during the rest of the year. The goal is to determine, using a combination of behavioural and neurophysiological methods, how neurons in the hippocampus and neocortex collectively give rise to specific memory operations such as encoding, storage, consolidation and retrieval and how networks of neurons together encode and store information that can be recalled at a later time. Research during 2004 took important steps towards the realization of that goal.

The staff

The core activity of CBM is tied to the research group of professors May-Britt Moser and Edvard Moser. At the turn of the year (2004/2005), the group consisted of 2 regular professors, 7 visiting professors, 4 post-docs, 9 graduate students, 9 master students, 1 administrative staff, 11 technical staff (5 part-time) and 5 associated staff – a total of 48. The mean age of professors (including visiting professors), postdocs, graduate students and technical staff was 34 years. The median age was 30 years. Two out of 9 professors were female. Among post-docs and graduate students, the male: female ratios were 2:2 (3:3 from May 2005) and 5:4.

Scientific highlights

The scientific highlight of the year was the publication of two papers in the same issue of Science, one as a full Research Article (Fyhn et al., 2004) and one as a regular Report (Leutgeb et al., 2004).

The interest that work at the Centre generated in the international neuroscience community was visualized by the publication of two papers in the same issue of Science, one as a full Research Article (Fyhn et al., 2004) and one as a regular Report (Leutgeb et al., 2004). The papers were accompanied by a Perspective paper which explained the link between the two papers. Both papers were rated as 'of exceptional interest' by Faculty of 1000, a peer-based evaluation system for papers in all fields of biology and medicine (see Box). The Fyhn paper is on the top 10 list for all papers in neuroscience since Faculty of 1000 started 3-4 years ago.

Both papers provide important new insights into the functions of the hippocampus and the surrounding parahippocampal areas. The hippocampus has long been recognized as a key structure in mammalian memory. The structure is thought to operate as a temporary storage site, having particular significance for encoding and consolidation of associative memory. Human subjects with lesions in the hippocampus have profound difficulties storing new memories whereas remote memory, e.g. from their own childhood, can be retrieved with no more distortion than in control subjects. The effects of damage to the hippocampus are particularly apparent when it comes to memories for place and time. Lesions in the hippocampus disrupt the ability to learn new routes to new places. The hippocampus is activated in normal human subjects as they search for a hidden goal in a defined spatial environment. On the basis of these and other observations, many scientists in the field have concluded that the hippocampus computes and stores spatial information, adopting the role as the brain's spatial or mental map.

The first paper shows that the hippocampus receives highly processed spatial information from the entorhinal cortex, the main brain area connecting the hippocampus with the neocortex. Although this area is among the first to be affected in Alzheimer's disease, its function is largely unknown. Measuring signals from individual neurons in entorhinal cortex, Marianne Fyhn and other scientists at CBM found that principal neurons in this area have strong positional correlates. Neurons in the dorsocaudal part of the medial entorhinal cortex fire in discrete spots across the spatial environment. Different neurons have different firing fields, implying that the path of the animal can be read out from the collective discharge activity of an ensemble of entorhinal neurons. Using spike information from only eight simultaneously sampled entorhinal neurons, Sturla Molden at CBM was able to reconstruct the path of the animal with an accuracy of less than a few centimeters. These analyses

showed that spatial information is computed upstream of the hippocampus, in the entorhinal cortex or one of its afferent areas. Similar spatially modulated signals were not observed in the postrhinal cortex, from which most of the visuospatial afferent input originates, suggesting that the information is computed intrinsically in the entorhinal cortex. These data point to an entirely new function for the entorhinal cortex (spatial computation) and suggest that spatial signals in the hippocampus are derived from afferent upstream areas rather than being computed in the structure itself. This discovery 'frees' the hippocampus from the spatial domain and suggests that its primary role is the encoding and storage of associative memory, regardless of whether it is spatial or non-spatial.

What is then the hippocampus doing during memory formation? This is the topic of the second Science paper. Measuring spike activity from populations of individually distinguishable neurons in the two major hippocampal subfields - CA3 and CA1 - Stefan Leutgeb and Jill Leutgeb at CBM showed for the first time that these subfields have distinct computational functions. Up to this point, behavioural and physiological studies had not been able to point to clear differences in the operations performed by cells or cell assemblies in these areas, in spite of their very different anatomical organization. The Leutgebs showed that cell assemblies in CA3 have a much better ability than CA1 to distinguish, or orthogonalize, incoming multisensory input from the entorhinal

Exceptional F1000 Factor 10.4

New Finding

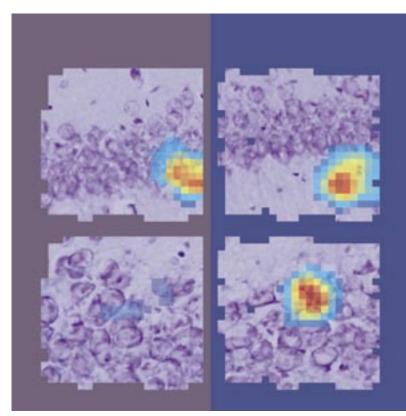
Spatial representation in the entorhinal cortex.

Fyhn M, Molden S, Witter MP, Moser EI, Moser MB Science 2004 Aug 27 **305**(5688):1258-64 [abstract on PubMed] [related articles] [order article]

Selected by | John Lisman / Randolf Menzel / Mayank Mehta / James Knierim / Wendy Suzuki First evaluation 2 Sep 2004 | Latest evaluation 18 Oct 2004

Wew evaluations

Screenshot from Faculty of 1000 Webpage



Place fields in CA3 pyramidal cells (Stefan Leutgeb and Jill Leutgeb.)

cortex. Rats were tested in boxes of similar or different shapes in a number of recording rooms, some of which differed only minimally. In CA1, there was strong overlap between the neuronal activity in the two rooms. In CA3, in contrast, different subsets of cells were active, even when the rats were tested in identical boxes in rooms that shared a number of prominent landmarks. Combined with a parallel study by Marianne Fyhn and colleagues showing only minimal distinction between the rooms in upstream ensembles in the entorhinal cortex, these results suggest that a major function of CA3 is to enhance small differences in information coming into the hippocampus, such that memories can subsequently be stored with minimal overlap. This function is presumably essential for interference-free memory storage, i.e. the ability not to mix up similar

memories, and thus points to a major general function of the hippocampus. The broader significance of this paper and two papers published almost simultaneously by other groups is explained in a commentary paper in Neuron (Guzowski, Knierim and Moser).

Collectively, the two Science papers suggest that the hippocampus has a general function in associative declarative memory, and that a key function of the hippocampus, and the CA3 subfield in particular, is to maximize differences in input during storage of overlapping content. The computation of spatial location occurs before the hippocampus, probably with the dorsocaudal medial entorhinal cortex as a key structure. The result of this computation is that spatial information enters the hippocampus to become part of almost every memory stored by the

activity of neurons in this area. The discovery of distinct memory systems in the hippocampus and entorhinal cortex will contribute importantly to the understanding of how memory is disrupted in humans with dementia and other types of memory loss.

The two Science papers represent the results of collaborative work with two of the visiting professors of the Centre: Menno Witter, who is an expert on hippocampal and parahippocampal neuroanatomy, and Alessandro Treves, whose expertise is in computational and quantitative neuroscience.

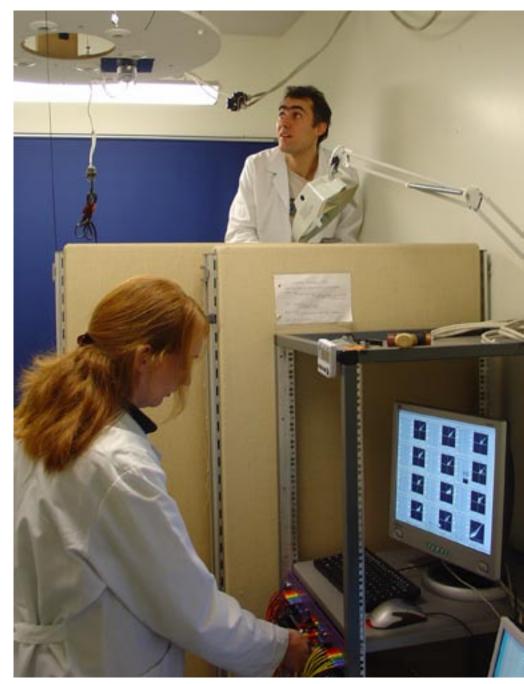
The work published in the two Science papers has been followed up by a study showing that the dorsocaudal medial entorhinal cortex plays a major role in spatial memory (Steffenach et al., 2005). This study breaks with a long series of papers during the past decade reporting that spatial memory is intact in animals with excitotoxic lesions of the entorhinal cortex. Hill-Aina Steffenach and colleagues showed that rats are severely impaired in retrieval of spatial memory if the lesions include the dorsocaudal tip of the entorhinal cortex. This area was generally not included in previous studies claiming that the entorhinal cortex was removed completely. The paper was published in Neuron at the turn of the year. This paper was also the result of collaborative work with Menno Witter.

Finally, and also at the turn of the year, scientists at the Centre showed that hippocampal place fields are not maintained by reverberatory activity within the hippocampus. This paper, which emerged from a collaboration with Bruce McNaughton and Carol Barnes, visiting professors at CBM, rules out one important hypothesis of how spatial firing is maintained in place cells in the hippocampus.

CBM on the international map

From the 1st of January 2004, Edvard Moser, the Director of CBM has served as a member of the Board of Reviewing Editors in Science. The journal has approximately 10 neuroscientists on its Board. Their task is, on a daily basis, to provide input on papers submitted to the journal and, more occasionally, to advice the Editors on matters related to the direction of neuroscience and science in general. From the 1st of January 2005, the Director of CBM was also elected as Reviewing Editor for the Journal of Neuroscience, as well as Chairman of the Programme Committee of the Federation of European Neuroscience Societies (FENS) for the Society's next biannual meeting to be held in Vienna in 2006. All three elections may be regarded as recognition of the quality of the work performed at the Centre.

Another important event for CBM was the election of one its visiting professors, Carol Barnes, as President for the Society of Neuroscience (SfN). SfN is the American equivalent of FENS. It has 34.000 members from around the world. More recently (2005), Richard Morris, also a visiting professor, was elected President-elect of FENS. Both elections enhance the visibility of CBM among neuroscientists in general.



Stefan Leutgeb and Jill Leutgeb working in the lab

The next generation

The post-docs represent an important international anchor of CBM: Stefan Leutgeb is from Austria, Jill Leutgeb from the United States, Francesca Sargolini from Italy and Paul Ganter from Germany. Contracts were signed during 2004 with two additional post-docs (Laura Colgin, USA; Karel Jezek, Czech Republic – both arriving in May 2005). The post-docs were recruited through personal contact or advertisement and international competition. The Directors spend considerable effort on the selection of post-docs. Their collective conceptual and methodological expertise is a major reason for the Centre's ability to compete internationally.

Along with the international team of post-docs, CBM has a clever team of graduate students, several of whom have submitted their thesis. Graduate students working at the Centre during 2004 include Sturla Molden, Frode Tuvnes, Marianne Fyhn, Vegard Brun, Kirsten Kjelstrup, Paulo Girao, Mona Kolstø Otnæss and Hill-Aina

About the programme

The physical foundations of psychological phenomena, such as thoughts, sensations, perceptions, memories and problem solving, have engaged philosophers for thousands of years. However, it is only during the course of the last couple of decades that we have developed the methods and technology required for direct study of the material that forms the basis of mental activity. In modern neuroscience it is possible to link microscopic activity in individual cells and cell populations directly to mental processing and mental disease. The Master programme in neuroscience is the first time that students can take a comprehensive, coherent graduate education in neuroscience in Norway. This is an interdisciplinary programme that combines basic and far-reaching knowledge in fundamental biology, psychology, physics and mathematics. The lectures are organized by neuroscientists from four faculties at the Norwegian University of Science and Technology (NTNU) departments and the Centre for the Biology of Memory. Lectures are also given by specialists from other universities in Norway and abroad.

Career opportunities

The study is suitable for students motivated for education and research in neuroscience in particular and the natural sciences in general. Graduates with this Master degree will be able to apply for positions at universities, university colleges, upper secondary schools and a broad range of research institutes, as the introduction of experimental and analytical methods has also become very relevant for other fields of study. The methodological skills acquired will also enhance career opportunities within the administrations of universities and research institutes.

Admission requirements

The first rounds of admission in the autumns of 2003 and 2004 were limited to 10 students each. The admission requirement is a bachelor's degree in biology, physics or psychology with possible specialization in neuroscience areas. It is also possible to gain admission on basis of other kinds of disciplinary background (such as medicine, informatics, philosophy) following individual assessment. The admission to the master's programme takes place every autumn (the three-year Bachelor degree ends in the spring). Steffenach. Molden defended his thesis in February 2005, and Tuvnes, Steffenach, Fyhn and Brun have submitted their theses. Expecting some turnover among the graduate students, CBM has recruited two new graduate students (Trygve Solstad and Hanne Lehn) and, depending on availability of lab and office space, it may recruit more during the next year.

A major platform for recruitment to CBM and to neuroscience in Norway more generally is the newly established Master degree in Neuroscience at NTNU (see Box). Each year, 10 students are admitted. Approximately one-third of the applicants were admitted in 2004. Students are highly motivated for a future in neuroscience and follow an advanced curriculum with extensive theoretical and practical training. Visiting professors at CBM participate in the teaching. The Master studies are in their second year with the first students submitting their master theses before Christmas 2004.



Timm stain of mossy fibres

The local and national neuroscience communities

While the research aim of CBM is strongly focused, the Centre tries to develop a limited number of links to other strong research groups. The Centre has active collaborations with Robert Biegler at the Department of Psychology (on path integration and spatial memory) and with Hanna Mustaparta at the Department of Biology (through Randolf Menzel, a visiting professor at the Centre). In addition, during 2004, a new collaboration was initiated with the Magnetic Resonance Centre at NTNU. Building upon new knowledge about the organization of memory at the systems level established at CBM, the collaboration aims to use fMRI to determine

whether similar operational principles underlie human memory. One of the new graduate students (Hanne Lehn) is working on this collaborative project, with professor Olav Haraldseth as her main advisor.

The Director of CBM is Chairman of the Programme Committee for Neuroscience at NTNU, whose main task is to stimulate recruitment and collaboration in neuroscience at NTNU.

At the national level, CBM has established new collaborations with neuroscientists at the Universities of Oslo and Bergen. CBM participates in a large-scale Research Council funded project on the function of direct entorhinal inputs to the hippocampus ("Storforsk"), coordinated by professor Johan Storm at the Centre for Molecular Biology and Neuroscience, the twin Centre of Excellence in Oslo (Storforsk awarded February 2005). A smaller functional-genomics project (FUGE) was initiated between the same partners at the beginning of 2004.

May-Britt Moser, co-director of CBM, was elected as the leader for the FRIBOFYS physiology and anatomy group of the Norwegian Research Council. One of her ambitions has been to improve the funding situation for basic research in biomedicine.



Representative sample of people at the Centre

Organization of the Centre



The Board of the Centre for the Biology of Memory (from left: Julie Feilberg, Arnstein Finset, Gunnar Bovim og Jan Morten Dyrstad)

Like its two twin Centres of Excellence at NTNU, CBM is placed directly under the University Director. Financial and other administrative matters are taken care of by the central administration of NTNU, in collaboration with office manager Ingunn Bakken, who is responsible for all administrative work at the Centre. Yet the Centre also has links to the Faculties of Medicine and Social Science (Department of Psychology). The Centre has graduate students from both faculties. The Master's degree programme in neuroscience is administered by the Faculty of Medicine. Technical and administrative staff is appointed by the Faculty of Social Science. This organizational structure has essentially remained unchanged since the Centre was established in December 2002. The direct placement under the University Director, with direct access to the central management and administration of NTNU, greatly facilitates administrative work at the Centre.

The Board of the Centre consists of an external representative (Chairman), the Faculty Directors of Medicine and Social Science, and either University Director, Rector or Prorector. Professor Arnstein Finset has been Chairman since the start of the Centre. Present Deans of Medicine and Social Science are Gunnar Bovim and Jan Morten Dyrstad. Both have served as Board members from the beginning. Prorektor Julie Feilberg replaced University Director Vigdis Moe Skarstein when Skarstein left NTNU before 2004. In addition, the Centre has an external Advisory Board consisting of 4 internationally leading neuroscientists, professors Larry Squire (University of California San Diego; chairman), Terry Sejnowski (Salk Institute, San Diego), Erin Schuman (Caltech, Los Angeles) and Earl Miller (Picower Centre, MIT, Boston). The Advisory Board meets with the Centre members in Trondheim every 3 years, reviews their scientific progress and gives advice on future directions. The first meeting is in June 2005.

Space constraints

The main challenge confronting the Directors of the Centre and the Board has been, and is, lack of space. The Centre has the same space available as the research group had before the Centre award, although the activity has more than doubled. The available space includes 300 m2 of lab area, split among the basement and 3rd floor of the Medical Technical Research Centre, and 10 offices on the 3rd floor (10 m2 each). This space is shared among approximately 37 research fellows, graduate students, professors, and technical staff, giving an average of 3.7 persons per office. In addition, 7 students currently work on master theses at the Centre. They share a separate room. Finally, the Mustaparta group, which is associated with the Centre, has about 250 m2, and Biegler's group, also associated with the Centre, is located at Dragvoll due to the space constraints. Space has been the primary concern of the Board since the start-up of the Centre in 2002. The Directors and the Board have discussed numerous possible solutions of the problem. The Director of the Faculty of Medicine has been and is actively exploring alternatives for expansion within the Medical-Technical Centre. A solution may be within reach.



The five residents of office no. 1313 at CBM

والمراكبة الإلسارية التقال المالية والمراكبة والمراجع

Scientific publications in 2004

1. Scientific journals: Work performed at the Centre

Fyhn, M., Molden, S., Witter, M.P., Moser, E.I. and Moser, M.-B. (2004). Spatial representation in the entorhinal cortex. *Science* **305**, 1258-1264.

Leutgeb, S., Leutgeb, J.K., Treves, A., Moser, M.-B. and Moser, E.I. (2004). Distinct ensemble codes in hippocampal areas CA3 and CA1. *Science* **305**, 1295-1298.

Moser, E.I. (2004). Place cells demand attention. *Neuron* 42, 183-185.

Guzowski, J.F., Knierim, J.J, and Moser, E.I. (2004). Ensemble dynamics in hippocampal areas CA3 and CA1. *Neuron* **44**, 581-584.

2. Conference abstracts: Work performed at the Centre

Fyhn, M.H., Hafting, T., Treves, A., Moser, M.-B., and Moser, E.I. (2004). Pattern separation in hippocampus but not layers II and III of entorhinal cortex. *Society for Neuroscience Abstracts* **30**, 330.5.

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Associated groups

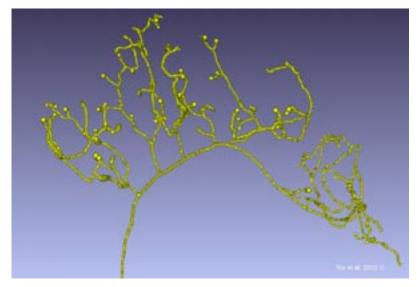
Robert Biegler

The two main areas of research in the Biegler group during 2004 were the binding of information, as needed for episodic memory, and the representation of uncertainty. The first replication of an experiment investigating how food-storing and non-storing birds bind together featural and spatial information is expected to take another six months (it involves reaching asymptotic performance in a total of 30 training conditions). It is not clear yet whether a second replication will be needed. A related experiment with rats in the radial maze is finished, and the unitrecording data are being analysed. Biegler and colleagues have finished theoretical work on how uncertainty determines when a search should be abandoned. They presented the data at two conferences, but are waiting with final publication until additional experimental data is collected. A pilot study looked perfect, but the main study failed to produce useful data, so they need to test new procedures. An experiment on path integration in bees in collaboration with Dr. Menzel's group is also finished. A book chapter on animal navigation is in press.

Hanna Mustaparta

A major goal is to make a map of the functional neuronal network in an averaged standard moth brain in order to explain how olfactory and taste information is encoded and how the olfactory information is learned (collaboration with professor Randolf Menzel).

In searching for the neuronal network involved in olfactory learning in insects, the Mustaparta group combines behavioural, electrophysiological and anatomical studies. Studying classical conditioning of the proboscis extension reflex, they have shown that moths can learn associations between an odour stimulus (conditioned stimulus) and sucrose stimulation (unconditioned stimulus). Learning depended on concentration as well as on identity of the odorant. Moths discriminated more easily odorants detected by different sensory neurons than by the same neurones. The odorants used in these studies were previously identified as biologically relevant for the species. In heliothine moths, olfactory receptor neurons were shown to project to 60-64 glomeruli in the antennal lobe, the



Reconstructed projection of an antennal lobe neuron (Rø et al.)

primary olfactory center of the brain. Each odorant could be mapped to one, two or three specific glomeruli, as shown by optical recordings. The functional organisation of the olfactory pathways in the moth brain was further studied by intracellular recordings combined with confocal imaging and reconstruction of individual neurons and brain structures. Different morphological types of antennal lobe projection neurons were identified, i.e. neurons receiving input in a single glomerulus or in several glomeruli and projecting via one of three tracts to higher centers in the brain (the calvces of the mushroom bodies that are important for learning and memory, and the premotoric area of the lateral protocerebrum). The neurons and the innervated brain structures have been reconstructed 3-dimensionally (Figure), to elucidate the functional organisation of the tracts and neuronal projections. A digital atlas of the moth brain is being prepared in collaboration with Randolf Menzel. The atlas will allow identified neurons to be placed into an averaged brain in order to show their relative position and connectivity. Staining of the taste receptor neurons on the antennae and proboscis, combined with confocal imaging, has revealed the pathway of information from the unconditioned stimulus. Reconstructions show the taste projection area in the central nervous system (the suboesophageal ganglion and the antenno-mechanosensory and motor centre). One particular neuron has been identified that may mediate the connection between olfactory (conditioned) and taste (unconditioned) pathways. Efforts are made to identify and reconstruct more neurons in order to obtain an overall picture of the functional organisation of the neuronal network involved in appetitive learning in heliothine moths.

Operating accounts 2004 (Årsregnskap)

Income (Inntekter)	Accounts (Regnskap)	Budget (Budsjett)
Grants (Bevilgninger)		
Norwegian Centre for Excellence (SFF)		9 000 000
Other External projects (Andre eksterne prosjekt) Note 1		2 750 000
The Portugese Ministry of Science and Technology		500 000
Contribution from the Norwegian University of Science and Technology ((Bevilgning fra NTNU)	

S/O funding (S/O-midler)	1 766 203
Operational grants (Driftsbevilgning)	1 666 666
Salaries (Lønnsmidler)	1 645 541
Other benefits (Naturalytelse) Note 2	2 982 234
Total Income (Sum inntekter)	20 310 644

Expenses (Utgifter)

Net personnel costs (including social benefits)	11 181 746
(Netto faste lønnsmidler inkl sosiale kostnader)	
Scientific equipment (Vitenskapelig utstyr)	713 998
Laboratory consumables (Drift av laboratoriet)	2 309 368
Travel expenses (Reise- og oppholdskostnader)	527 430
Other expenses (Naturalytelse)	2 982 234
Transferred to 2005 for expansion of lab (Resultat overført til 2005)	2 595 868
Total expenses (Sum utgifter)	20 310 644

Note 1 - Other external projects

Grants from:

+ Fifth framework programme of the European Community (2000 - 2003)

- From the Research Council of Norway:
- Medicine and Health Programme Grant (2000 2005)

Note 2 - Other benefits

Server operations and backup, rooms and general operation, compensation for the use of administrative services. *Drift og backup av server, areal og drift, bruk av sentrale tjenester.*

Who is who?

The Board



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May-Britt Moser, Professor and co-director

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Bruce McNaughton, Professor University of Arizona, USA

Randolf Menzel,

Professor





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Francesca Sargolini





Frode A. Tuvnes, Cand. scient



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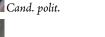


Vegard Heimly Brun, Stud. med.



Marianne Fyhn, Cand. scient.









Paulo Girão



Stig Hollup, Cand. polit.

Project students



Tora Bonnevie

Master students



Wenche Langfjord







Kamilla Medås



Trygve Solstad



Espen Joakim Henriksen









Beathe Christin Haatveit



Ingrid Funderud



Retsina Michele Meyer

Technical team



Ingvild Hammer, Bioengineer



Kyrre Haugen, Histology technician



Klaus Jenssen, Electronics engineer



Raymond Skjerpeng, Programmer



Haagen Waade, Computer engineer



Ingunn E. Bakken, Senior executive officer



Knut S. Grøn Animal technician (part-time)



Ingolf Hanssen, Veterinary (part-time)



Espen Sjulstad, Histology and electrode wiring (part-time)



Bjørn Håvard Solem, Electronics technician (parttime)



Ann Mari Amundsgård Histology and animal care



Torkel Hafting Fyhn, Ph.D. student

Associated members



Robert Biegler, Associate professor NTNU, Norway (DSCN 3038)



Hanna Mustaparta, Professor NTNU, Norway



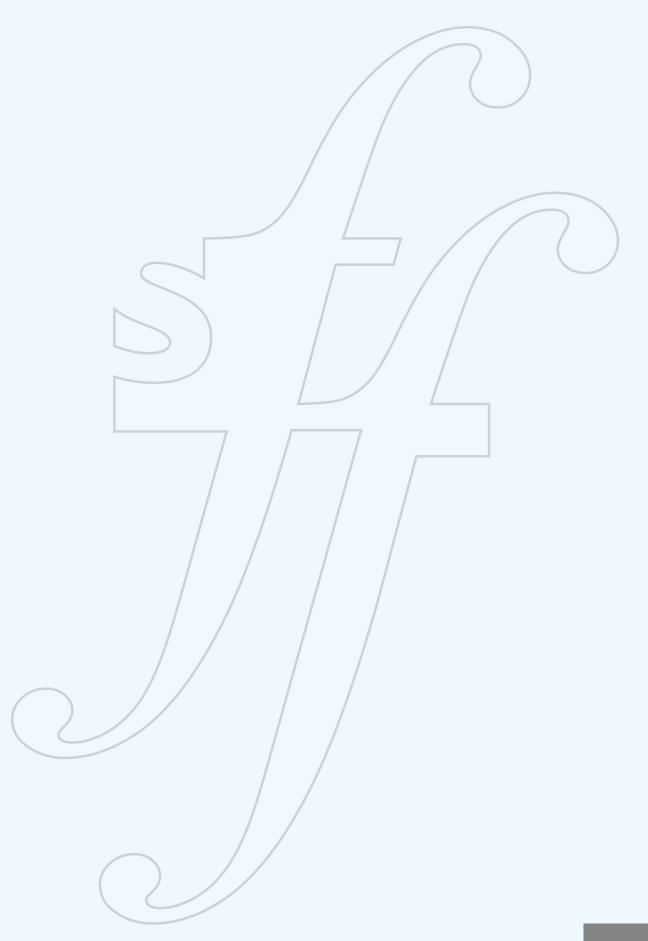
Boleslaw Srebro, Associate professor, Master Study in Neuroscience



Hanne Lehn Ph.D. student



Gerit Pfuhl, Master student







NTNU Norwegian University of Science and Technology Annual Report 2004 Centre for the Biology of Memory

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