

# INTELLIGENCE IN ANIMALS AND MACHINES

Autumn 2009

## Course Organiser

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## Lecturers

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## AIMS

The overall aim of this course is to develop your understanding of what it means for an animal or a machine to behave intelligently, and how brain and behavioural systems are adapted to enable an animal to cope effectively within its environment. You explore this topic in lectures and seminars through a number of case studies that are designed to acquaint you with recent behavioural and AI literature.

## COURSE OUTLINE

Animals engage in a variety of complex behaviours that are intelligent in the sense of being well-adapted to particular situations. Thus, intelligence should perhaps not be thought of as a unitary phenomenon. Rather animals have multiple, specialised intelligences each of which is designed for particular tasks. Animals go in for computational economy and often do not build up detailed internal models of the world, using instead sensory information on-line to guide actions.

Developments in behavioural neuroscience and in artificial intelligence over the last decade have led to some convergence of the aims and methods of the two disciplines. In studies of behaviour, there is increasing acceptance of robot and computer modelling as experimental tools. In artificial intelligence and cognitive science, the focus has shifted from exploring high-level human intellectual capabilities toward detailed studies of the basic behaviours that are common to most animals, and that are required of autonomous robots. Our interdisciplinary course reflects this movement and aims to show how the two fields can inform each other, to give an understanding of the subtleties of cognition in simple animals and the challenges faced by scientists trying to create artificial systems with the same behavioural capabilities as these animals.

We begin by discussing the evolution of views on animal intelligence and robot building. The modern approach emphasises complete systems acting in the real world. This aims to avoid

the pitfalls of earlier methods, even if it means confining ourselves to relatively simple systems. Recent experiments are used to illustrate the developing methodology by which computer simulations and robotic experiments can stimulate biology (and vice versa).

We will consider in detail several examples of 'specialised or adaptive intelligences' in invertebrates and vertebrates. The study of relatively simple animals (such as insects) turns out to be challenging rather than restrictive. Their capabilities often exceed what can be achieved in artificial systems or fully understood by biologists. We concentrate on navigation and foraging, and we will examine the behavioural and memory strategies that insects and other animals have evolved to accomplish these tasks.

Difficulties in controlling behaviour can be lessened by appropriate design of sense organs and effectors, and by exploiting properties of the environment in which the animal/machine operates. A telling example is the way in which the insect visual system has adapted to interpret the visual consequences of an animal's own movements. We look at optic flow in insects and the specialised neural mechanisms that decode it.

The synaptic computations performed by real neurones in the insect visual system serve as an introduction to artificial neural networks (ANNs). ANNs are computer simulations or electronic circuits, at least partially based on observations of the structure and operation of animals' nervous systems. As we will see, they turn out to be very powerful computational devices for prediction, categorisation and learning and are becoming widely used in engineering and industry. They have also revolutionised our understanding of the brain in that appropriately configured and trained neural nets can in many cases substitute for explanations of behaviour that are cast in terms of rules and symbol manipulation.

We then consider what might be thought of as higher-level faculties and how they may have relatively simple antecedents, taking as an example the human ability to count and use number. This is put into a biological context by examining its possible origins in non-human animals and its neural basis.

Intelligence does not only exist at the individual level. Some tasks demand group co-ordination and intelligent algorithms can be implemented at the level of a group. Animals can obtain information and learn from observing and interacting with other members of a social group. Indeed one of the selection pressures driving the evolution of some high-level cognitive skills is thought to be a need to solve problems posed by social interactions. The course ends with a look at three aspects of social intelligence: i) the social organisation of foraging in bees; ii) culture and observational learning; iii) social intelligence and mind reading.

## TEACHING

Teaching is through compulsory lectures and seminars. **Lectures** are used to introduce a topic from where you are expected to develop knowledge and analytical skills through critically reading the recommended items. It is especially important that you integrate the different topics of the course. Again, lectures can only give pointers, developing a conceptual framework of your own is something that requires both individual thought and discussion with friends and colleagues. **Seminars** are an essential part of the course and may present material not covered in lectures. They are held primarily for group discussion about research papers.

**Lectures**                      Monday 14:00-15:00    SHAWCROSS-AS1  
    Tuesday 14:00-15:00    PEV1-1A6

**UG Seminars**              Thursday 9:00-11:00    CHI3-3R143

**Introductory workshop for UGs**              Friday 9<sup>th</sup> October 11:00-14:00    BSMS 3.07B

Week	Lectures		UG Seminar
1	Mon 5 <sup>th</sup> Oct	No Lecture	
	Tues 6 <sup>th</sup> Oct	Robots & Biology 1 (AT)	
	Fri 9 <sup>th</sup> Oct	Introductory workshop for UGs	
2	Mon 12 <sup>th</sup> Oct	Robots & Biology 2 (AT)	
	Tues 13 <sup>th</sup> Oct	Insect navigation 1 (TC)	
3	Mon 19 <sup>th</sup> Oct	Insect navigation 2 (TC)	Robot architecture (AT)
	Tues 20 <sup>th</sup> Oct	Path planning (TC)	
4	Mon 26 <sup>th</sup> Oct	Memory organization (TC)	Cognitive maps and spatial memories (TC)
	Tues 27 <sup>th</sup> Oct	Optic flow and direct perception (PG)	
5	Mon 2 <sup>nd</sup> Nov	Motion detection in insects (PG)	
	Tues 3 <sup>rd</sup> Nov	Motion detection in robots (PG)	
6	Mon 9 <sup>th</sup> Nov	Artificial neural networks 1 (AT)	Optic flow in insects and robots (PG)
	Tues 10 <sup>th</sup> Nov	Artificial neural networks 2 (AT)	
7	Mon 16 <sup>th</sup> Nov	Artificial neural networks 3 (AT)	
	Tues 17 <sup>th</sup> Nov	Honeybee social foraging (TC)	
8	Mon 23 <sup>rd</sup> Nov	Social learning (TC)	Metacognition (TC)
	Tues 24 <sup>th</sup> Nov	Tool use (TC)	
9	Mon 30 <sup>th</sup> Nov	Brain evolution (DO)	
	Tues 1 <sup>st</sup> Dec	Brain evolution (DO)	

## UG ASSESSMENT

Type	Date Due
Unseen Exam	Week 5 Summer term
Essay	Week 2 Spring term
2 Presentations	Completed during term

There will be a three hour unseen examination at the end of the academic year that contributes to 70% of the marks for the course.

One 3000 (+/- 20%) word assessed essay contributes to 15%.

Contribution to seminars, including two presentations, is the remaining 15%.

**Essay Submission.** There is a strict deadline for submission and so that we can give you feedback on your essay, we would like you to put your name as well as your exam number on the essay. Sample essay titles are provided though if you prefer, you may choose your own title, but it should be approved by one of the lecturers. We recommend strongly that you give a detailed plan of your essay to one of the lecturers well before the end of this term so that we have time to provide comments and advice before you write it in full. Essays are double-marked and are retained in case the external examiner needs to see them in the summer. We will give you a grade and comments on your essay towards the end of the Spring term. All coursework should be handed in to the School Office, JMS 3B10 and you must sign in any Assessed Coursework on the Submission Sign In Sheet. It is important that you sign in the correct slot, and date and time your submission. Guidelines for assessment criteria can be found at the following web address: <http://www.sussex.ac.uk/biology/1-3-8.html>.

Deadlines for assessed coursework are absolute and no extensions are given. Coursework submitted up to 24 hours late will receive a penalty of 10% reduction of the marks available. Work submitted after 24 hours will receive zero marks. If you are experiencing difficulty in getting your work in on time, you should talk to your Student Advisor. A Mitigating Evidence Form must be completed and returned, along with any medical evidence and your work should be handed in to the School Office as soon as is possible. If the reason for your late submission is valid, the reduction in your mark may be altered or waived.

**Do you have a problem?** If a problem arises relating to this course, in the first instance you should talk to the Course Organiser, as many problems are easily resolved. If you and the Course Organiser feel that the problem cannot be easily resolved, only then should you take it to your student rep and/or the Head of Department.

## READING

There isn't a suitable general textbook for the course and we don't recommend buying the following, but useful perspectives are to be found in:

D. McFarland and T. Bösner. *Intelligent behaviour in animals and robots* MIT Press;

R. Pfeifer and C. Scheier, *Understanding intelligence*, MIT Press;

S. Shettleworth, *Cognition evolution and behaviour*. Oxford University Press.

R. A. Brooks. *Flesh and machines: how robots will change us*. Penguin.

S. Nolfi & D. Floreano (2001). *Evolutionary Robotics: The Biology, Intelligence, and Technology of Self-organizing Machines*, MIT Press Bradford Book.

Also, Whitby, B.R. (2003), *AI a beginner's guide*, Oxford University Press, is said to be a good introduction to AI for neophytes.

Essential articles, usually one per lecture are placed on Study Direct (let Paul Graham know if you cannot access this site) and should be read. The other papers on the reading list shouldn't be ignored, but you aren't expected to read them all! Many of the items are listed to help with essay writing. Most of these items can be obtained on-line through the University Library electronic journals. If you have problems getting hold of material or need extra sources, please contact the lecturer concerned.

## LECTURE SYNOPSIS

### **1. Thinking about Intelligent Behaviour.**

Intelligence, adaptive behaviour, adaptation. Some key historical frameworks (with special attention to vision): Cartesianism, Evolution, Cybernetics and dynamical systems theory, 'classical' AI, connectionism, Behaviour-based, 'Artificial Life.' Relationship between anatomy and function; functional localisation. Interface between biology and engineering. How much do we currently understand all this?

#### **Reading:**

(Available on the web: <http://www.ai.mit.edu/people/brooks/papers.html>)

- Extracts from Brooks, R.A. (1995). "Intelligence Without Reason". In Steels, L. and Brooks, R. (eds.) *The Artificial Life Route to Artificial Intelligence: Building embodied, situated agents*, 25-81, Lawrence Erlbaum Associates.
- Arkin R.C. (1998) *Behavior-based robotics*. MIT Press.
- Boden, M. (ed) (1996) *The philosophy of artificial life*. Oxford University Press
- Braitenberg, V. (1984). "Vehicles: Experiments in Synthetic Psychology", MIT Press. Library: QU 4588 Bra (1 copy in MAIN).
- Ashby, W.R. (1960). "Design for a brain: the origin of adaptive behaviour", Chapman. Library: QE 230 Ash (1 copy in RESERVE).
- Gibson, J.J. (1979). "The ecological approach to visual perception", Houghton Mifflin. Library: QZ 314 Gib (1 copy in RESERVE, 3 in SHORT).
- Gray Walter: see [http://www.epub.org.br/cm/n09/historia/turtles\\_i.htm](http://www.epub.org.br/cm/n09/historia/turtles_i.htm) (follow links)
- Proceedings of the four "Simulation of Adaptive Behaviour (SAB): From animals to animats" conferences. Library: QZ 1250 Fro (Several copies in MAIN and RESERVE).

### **2. Designing Intelligent Behaviour**

Special focus on Brooks' approach. Reactive and non-reactive control. Situatedness, embodiment and emergence; behaviour-based robotics; the subsumption architecture. Top-down vs. bottom-up design; hierarchical control structures. General purpose vs. niche-specific; Horswill's 'habitatconstrained' vision. The battles: Pros and cons of information processing and internal representation perspectives. Robots and simulations as models of nature.

#### **Reading :**

- Webb, B. (1996). "A Cricket Robot". *Scientific American*, December 1996, 62-67.
- Franceschini, N., Pichon, J.M., and Blanes, C. (1997). "Bionics of Visuo motor Control". In: *Evolutionary Robotics: From intelligent robots to artificial life (ER'97)*, Gomi, T. (ed.), 49-67, AAI Books.
- Deneubourg, J.L., et al. (1991). "The dynamics of collective sorting: Robot like ants and ant like robots". In Meyer, J A., and Wilson, S.W. (eds.), *Proc 1st Int. Conf. on Simulation of Adaptive Behaviour: From Animals to Animats*, 356-363, MIT Press.

### **3. Navigation in Insects**

Ants and bees are impressive navigators. They leave their nest to collect food from sites that may be located hundreds (ants) or thousands (bees) of metres away. They then return accurately to their nest. To do this, they have at their disposal a repertoire of navigational strategies that must be properly co-ordinated. A primary one is path integration or dead reckoning. Unavoidable inaccuracies arising from path integration are reduced by the insects' use of visual landmarks to specify stereotyped routes. The study of navigation can tell us much about sensori-motor control and 'situated cognition' in these animals.

#### **Reading:**

- Wehner, R. Michel, B., Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J exp Biol* 199, 129-140.
- Wehner, R. (1992) *The arthropods*. In *Animal Homing* (ed. F. Papi). pp. 45-144. Chapman and Hall.
- Wehner, R. and Srinivasan M. V. (1981) Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. comp. Physiol A*, 142:315-338.

- Journal of Experimental Biology, Symposium volume on Navigation. Jan 1996 vol 199. (Downloadable from the web: [www.biologists.com](http://www.biologists.com))
- Srinivasan MV, Zhang SW, Bidwell NJ: Visually mediated odometry in honeybees navigation en route to the goal: visual flight control and odometry. J exp Biol 1997 200:2513-2522.
- Srinivasan MV, Zhang SW, Altwein M Tautz J (2000), Honeybee navigation: nature and calibration of the 'odometer'. Science 287, 851 - 853.
- Ronacher, B., Gallizi, R., Wohlgemuth, S., Wehner, R. (2000). Lateral optic flow does not influence distance estimation in the desert ant. J. exp. Biol. 203, 1113-1121.
- Wohlgemuth S, Ronacher B, Wehner R (2001) Ant odometry in the third dimension. Nature 141, 795-798.
- Riley, J.R. et al (2005) The flight paths of honeybees recruited by the waggle dance. Nature. 435,205-7.
- Vickerstaff, R. J. and Di Paolo, E. A. (2005). Evolving neural models of path integration. J Exp Biol 208, 3349-3366.

#### **4. Defining Places by Landmarks**

Bees and ants use landmarks to specify a place. What kinds of representations of landmarks do these insects have, how do they acquire these representations and how do they use them for navigation? Answers to these questions show how apparently complex tasks can be accomplished in relatively simple ways and mimicked by model navigational systems simulated through artificial evolution.

##### **Reading:**

- Collett, T.S. (1992) Landmark learning and guidance in insects. Phil. Trans R. Soc. B 337:295-303.
- Journal of Experimental Biology, Symposium volume on Navigation. Jan 1996 vol 199 (Downloadable from the web: [www.biologists.com](http://www.biologists.com))
- Dale, K., Collett, T.S. (2001) Using artificial evolution and selection to model insect navigation. Current Biology 11, 1305-1316.
- Collett, T.S., Collett, M. (2002) Memory use in insect visual navigation. Nature Reviews Neuroscience 3, 545-552.

#### **5. Path Planning**

Many animals must plan efficient routes through cluttered environments and the methods that they use give insights into what they 'know' about their 3-D environment and how this knowledge is used in intelligent planning. We will see the very different strategies and mechanisms adopted by spiders planning routes through complex 3-D mazes and frogs and toads planning detours round barriers, and how planning strategies can be implemented neurally in simple structures.

##### **Reading:**

- Arbib, M. A. and Liaw, J.-S. (1995). Sensorimotor transformations in the worlds of frogs and robots. Artificial Intelligence 72:53-79.
- Jackson, R. R. (1985) A web-building jumping spider. Scientific American 253 (Sept):106-113.
- Hill, D.E. (1979) Orientation by jumping spiders of the genus Phidippus during the pursuit of prey. Behav. Ecol. Sociobiol. 5:301-322.
- Tarsitano, M.S., Jackson, R.R. (1997) Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey. Anim. Behav. 53: 257-266.
- Tarsitano, M.S., Andrew, R. (1999) Scanning and route selection in the jumping spider *Portia labiata*. Anim. Behav. 58, 255-265.
- Collett, T.S. (1982) Do toads plan routes? J. comp Physiol. 146:261-271.
- Menzel E.W. (1973) Chimpanzee spatial memory organisation. Science 182:943-945.

#### **6. Memory organisation: procedural, contextual and episodic**

Most intelligent behaviour relies on remembering and utilising previous experiences, both in the short term (working memory) and in the longer term. The importance of long-term memory in allowing flexible behaviour is already seen in insects. We will first consider the use of spatial and

temporal context in helping bees and ants retrieve appropriate navigational memories. Vertebrates have more elaborate memory mechanisms. Psychologists divide long-term memories into two very different functional classes: procedural (skills and habits) and episodic (memory of individual events). Until recently it was believed that episodic memory is restricted to humans. However, detailed study of the memory requirements of caching behaviour in birds reveals that birds also have the ability to remember and utilise information about specific events, and similar studies show that rats do too.

**Reading:**

- Griffiths, H, Dickinson, A. Clayton, N. (1999) Episodic memory: what animals can remember about their past. *Trends in Cognitive Science* 3, 74-80.
- Clayton, N.S., Yu, K. S., Dickinson, A. (2003). Interacting cache memories: evidence for flexible memory use by western scrub jays (*Aphelcoma californica*). *J. exp. Psychol. Anim. Behav. Processes* 29, 14-22.
- Clayton, N.S., Dickinson A. (1998) Episodic-like memory during cache recovery by scrub jays. *Nature* 395, 272-274.
- Clayton, N.S., Dickinson A. (1999) Memory for the content of caches by scrub jays (*Aphelocoma coerulescens*). *J. exp. Psychol. Anim. Behav. Processes* 25, 82-91.
- Emery, N.J., Clayton, N.S. (2001). Effect of experience and social context on prospective caching strategies by scrub jays. *Nature* 414, 443-446.
- Squire, L.R. & Kandel E.R. (1999) *Memory: from mind to molecule*. Scientific American Library.
- Symposium on episodic memory in *Philosophical Transactions of the Royal Society* 2001, vol 356, pp 1341-1515.
- Ergorul, C. and Eichenbaum, H. (2004) The hippocampus and memory for "What," "Where," and "When". *Learning and Memory* 11: 397-405.
- Roberts, W.A. (2009). The comparative study of mental time travel. *Trends in Cogn. Sci.* 13, 271-277.

**7-9. Direct perception and motion detection. Neural Pathways, Behaviour, and Algorithms.**

A fundamental question that motivates comparisons between animal and machine intelligence is: Can we make a machine that exactly mimics a human or animal brain? The 1940's saw mathematicians make major developments in our understanding of computation, with the development of universal computing machines based on simple logical operations. At the same time, biologists were also making important advances in our understanding of synapses in the brain. Workers such as Alan Turing and the biologist/philosopher Warren McCulloch asked whether the logical operations required for a universal computer could be implemented by a brain, and whether there is more to brains than formal logic. This approach to neural computation is illustrated by work on visual motion, which asks how neural circuits solve specific computational problems. Later lectures consider neural networks, which make more general comparisons between the computational architectures of machines and brains.

Specifically these three lectures concern the neural circuitry beneath the insect eye that process visual motion. The way local motion signals are abstracted and integrated into behaviour have been a test-bed for ideas at the interface of neurobiology, behaviour, formal modelling and machine vision. We will look at how bees and other insects use visual motion signals to control flight and to perform tasks such as obstacle avoidance and landing. Where known, we will examine how these tasks are performed by the nervous system and study how similar algorithms are implemented by designers of autonomous robots.

**Reading:**

- Franceschini, N., Pichon, J. M. and Blanes, C. (1992) From insect vision to robot vision. *Phil. Trans. R. Soc. Lond. B.* 337:283-293. Describes one of the first robots inspired by studies of insect vision.
- Egelhaaf, M. and Borst, A. (1993) Motion computation and visual orientation in flies. *Comp. Biochem. Physiol.*, 104A: 659-473. Good survey of the biological mechanisms underlying visual motion detection in insects.

- Rind FC, Simmons PJ (1999) Seeing what is coming: building collision-sensitive neurones Trends Neurosci 22 215-220: a short review of the neural mechanisms involved in detecting (and avoiding) collisions.
- Clifford, C. W. G. and Ibbotson, M. R. (2003), "Fundamental mechanisms of visual motion detection: models, cells and functions", Progress in Neurobiology, 68, 409-437: Good review describing several algorithms for detecting visual motion and what we know about the corresponding neural circuitry in vertebrates and invertebrates
- Krapp, H. G. and Hengstenberg, R. (1996), "Estimation of self-motion by optic flow processing in single visual interneurons", Nature, 384, 463-466: An elegant paper describing "matched filtering" by individual neurons in the fly's visual system to particular patterns of optic flow.
- Poggio, T. and Koch, C. (1987) Synapses that compute motion. Scientific American, May 1987, pp.42-48: an easy read about synaptic mechanisms that may provide the non-linear properties needed for motion detection.

## **10 to 12. Artificial Neural Nets (ANNs)**

**10. Basics and History.** What ANNs are. Feedforward and recurrent nets. Learning vs. hardwired. The Perceptron; training, testing and generalisation. Weight vectors and error surfaces; gradient-descent learning. The need for a hidden layer. NETtalk as an example. What ANNs are good for? **11. Some details of learning mechanisms.**

Backpropagation. Kohonen's self-organising maps. Reinforcement learning (Barto's pole balancer).

### **Reading for 10 and 11:**

- Elman, J.L. et al. (1996) Rethinking Innateness. MIT Press. chap 2: Why connectionism? Pp 47-106.
- Sejnowski, T.J. and Rosenberg, C.R. (1986). "NETtalk: a parallel network that learns to read aloud". Reprinted in the book below, Chapter 40
- Anderson, J.A. and Rosenfeld, E. (eds) (1988). "Neurocomputing: foundations of research", MIT Press. Library: QU 4550 Neu (1 copy in MAIN, 1 in SHORT).
- McCord Nelson, M. and Illingworth, W.T. (1991). "A Practical Guide to Neural Nets", Addison Wesley. Library: QZ1335Nel, (1 copy MAIN, 1 SHORT).
- Browse section QZ 1335 in the library.

### **12. ANNs and nature.**

What's the relation between ANNs and brain function, anatomy and psychology? "Biological Plausibility" of architectures and learning regimes. Hebbian learning. Local and distributed representations in ANNs. Graceful degradation. Symbolic vs. non-symbolic, semantic grounding. Computational Neuroethology, ANNs as "artificial nervous systems"; time and dynamics. Artificial evolution of ANN designs.

#### **Reading:**

(Available on the web: <http://citeseer.nj.nec.com/cliff91computational.html>)

- Cliff, D. (1991). "Computational Neuroethology: A Provisional Manifesto". In Meyer, J A., and Wilson, S.W. (eds.), Proc 1st Int. Conf. on Simulation of Adaptive Behaviour: From Animals to Animats, 29 39, MIT Press.
- Beale, R. and Jackson, T. (1990). "Neural Computing an introduction", chapter "Kohonen Self Organising Networks", IOP Publishing.
- Roitblat, H.L. et al. (1991). "Biomimetic Sonar Processing: From dolphin echolocation to artificial neural networks." In Meyer, J A., and Wilson, S.W. (eds.), Proc 1st Int. Conf. on Simulation of Adaptive Behaviour: From Animals to Animats, 66 76, MIT Press.

### **13. Decision making by honeybee colonies: foraging and choosing a nest site**

The socially organised behaviour of a hive of honey bees during foraging is a wonderful example of how simple rules followed by individual bees leads to exquisitely organised and effective global behaviour without centralised control. Those working in this field like to consider individual bees as individual neurones and a hive of bees as a brain. We will emphasise how information concerning the availability and need for nectar is transferred through the waggle dance to distribute bees over a range of foraging sites, and how the same communication system is used to

choose a single nest site. Good decision making arises despite the limited knowledge available to individual bees.

**Reading:**

- Seeley, T.D., Camazine, S., J Sneyd, J.D. (1991) Collective decision making in honey bees: how colonies choose among nectar sources. *Behav. Ecol. Sociobiol.* 28:277-290.
- Seeley, T.D. (1992) Tactics of dance choice in honey bees: do foragers compare dances. *Behav. Ecol. Sociobiol.* 30:59-69.
- Michelsen, A., et al. (1992) How honeybees perceive communication dances, studied by means of a mechanical model. *Behav. Ecol. Sociobiol.* 130:143-150.
- Seeley, T.D. (1994) Honeybee foragers as sensory units of their colonies *Behav. Ecol. Sociobiol.* 34:51-62.
- Seeley, T.D. (1995) *The Wisdom of the hive: the social physiology of honey bee colonies.* Harvard University Press.
- Seeley, T.D. and P.K. Visscher. 2004. Group decision making in nest-site selection by honey bees. *Apidologie.* 35:1-16
- Seeley, T.D. and P.K. Visscher. 2004. Quorum sensing during nest-site selection by honeybee swarms. *Behavioral Ecology and Sociobiology* 56:594-601.
- Seeley, T.D. and Buhrman, S.C. (2001). Nest-site selection in honey bees: how well do swarms implement the "best-of-N " decision rule? *Behav Ecol Sociobiol* 49:416-427

**14. Observational learning and culture**

Observational learning speeds up the acquisition of environmental affordances and skills. Even in the absence of language, it allows information and skills to be transmitted between individuals and, over time, between generations. We will consider examples of observational learning in humans and other animals, possible neural mechanisms underlying imitative learning, and elements of culture in animals.

**Reading:**

- Brass, M., Hayes, C. (2005) Imitation: is cognitive neuroscience solving the correspondence problem? *Trends in Cog Sci* 9 489-495.
- Multi-authored feature article in *Science* 1999 vol 284, 2070-2076. Chimps in the wild show stirrings of culture.
- McGrew, W.C. (1998) Culture in non-human primates. *Ann. Rev. Anthropol* 27, 301-328.
- Wolpert, D.M., Doya, K., Kawato, M. (2003). A unifying framework for motor control and social interaction. *Phil. Trans. R. Soc. Lond.* 358, 593-602.
- Whiten, A (1998) Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *J. comp. Psychol.* 112, 270-271.
- Meltzoff, A.N., Decety, J. (2003). What imitation tells us about social cognition. *Phil. Trans. R. Soc. Lond.* 358, 491-500.
- Byrne, R.W. (2002) Imitation of novel complex actions: what does the evidence from animals mean. *Advances in the study of behavior* 31, 77-105.
- Horner, V. & Whiten, A. (2005). Imitation and emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition.* 8: 164-181
- Rizzolatti, G., Luppino, G. (2001). The Cortical Motor System. *Neuron* 31:6:889-901.
- Gallese, V, Christian Keysers, C and Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cogn. Sci.* 8, 369-403

**15. Tool use and insight**

Many animals from insects to apes are known to use tools in a variety of ways to gain access to food. Tool use has attracted the interest of comparative psychologists as examples of problem solving and insightful behaviour. It is possible to examine what different animals understand about the details of how a tool works and the problem that the tool solves. Recent work suggests that the competence of birds in this respect approaches that of primates.

## Reading:

- Bluff, L.A., Weir, A.S., Rutz, C., Wimpenny, J.H., Kacelnik, A. (2007) Tool-related Cognition in New Caledonian Crows. *Comp. Cogn. Behav. Rev* 2, 1-25
- Maravita, A. and Iriki, A (2004) Tools for the body (schema). (2004) *Trends in Cogn Sci.* 8, 79-86.
- Weir A.S, Kacelnik, A. (2006). A New Caledonian crow (*Corvus moneduloides*) creatively re-designs tools by bending or unbending aluminium strips. *Animal cognition* 9, 317-334

## **16-17. Brain size, intelligence and evolution**

It seems obvious that bigger brains will be better, and we know that compared to other primates humans have disproportionately large brains, and especially neocortex. These lectures will look in more detail the evolution and development of brains. For example: If bigger is better, what limits brain size? What specific faculty or cognitive tasks underlie the selection for differences in brain size in humans and other animals? Does natural selection act to regulate the development of the entire brain or on specific regions?

**16. Overall brain size.** Read Dunbar on the Social Brain Hypothesis. 1. Metabolic and other costs of having a large brain. Evidence that unused structures are lost. 2. Allometry, general relationships between body size and brain size. 3. Accounting for departures from allometric functions. Sensory systems or cognitive ability. Differences in the number of cortical areas, and their relative sizes

**17. Cortical specialization and brain development.** Control of the number and size of functional areas in mammal neocortex. Read papers by Purves and co-workers, and by Allman and co-workers and the recent review by Premack. 1. Regional specialization in the cortex, and differences between individuals and species. 2. Role of genetic and environmental processes in controlling relative size of different structures. Including ideas of Finlay & Darlington on developmental programmes, and the controversy over the role of the gene FoxP2 in language .

## Reading:

- Dunbar R. 1998. The social brain hypothesis. *Evolutionary Anthropology* 6:178-190.
- Dunbar, R. (2003). The social brain: mind, language and society in evolutionary perspective. *Annual Review of Anthropology* 32: 163-181
- Watson, K. K., Jones, T. K., and Allman, J. M. (2006) Dendritic architecture of the von Economo neurons. *Neuroscience*. 141:1107-1112
- Allman, J.M., Hakeem, A., Erwin, J.M., Nimchinsky, E., and Hof, P. (2001) Anterior cingulate cortex: The evolution of an interface between emotion and cognition. *Annals of the New York Academy of Sciences*. 935:107-17.
- Finlay BL, Darlington RB, Nicastro N. 2001. Developmental structure in brain evolution. *Behavioral And Brain Sciences* 24, 263–308
- Lai CS et al. 2003. FOXP2 expression during brain development coincides with adult sites of pathology in a severe speech and language disorder. *Brain*, 126, 2455-2462.
- Marcus GF, Fisher SE. 2003. FOXP2 in focus: what can genes tell us about speech and language? *Trends Cogn Sci.* 7: 257-262.
- Reader, S. M. & Laland, K. N. 2002. Social intelligence, innovation and enhanced brain size in primates. *Proceedings of the National Academy of Sciences, USA*, 99, 4436-4441
- Premack D. 2007. Human and animal cognition: continuity and discontinuity. *Proc Nat Acad Sci USA*. [www.pnas.org/cgi/doi/10.1073/pnas.0706147104](http://www.pnas.org/cgi/doi/10.1073/pnas.0706147104)