ESF-Exploratory Workshop The contribution of animal research to the study of human cognition





Marseille, December 7-9, 2005

Organizers: Joël Fagot (INCM, CNRS, Marseille), Anne Reboul (ISC, CNRS, Lyon)

Executive summary

The real workshop occurred very much as we, as organizers, had thought it would, though there were two last minute defections: both Peter Gärdenfors from Sweden (chairperson of the symposium "Relations and causality") and Yadin Dudai from Israël (a speaker in the symposium "Memory") fell ill before the meeting and were unable to come. This led to some slight reorganisation of the meeting schedule.

After the meeting opening (Wednesday december 7, 9h30), including both a presentation of the meeting scientific goals and a few practical information given by the organizers and a brief presentation of the ESF by the ESF representatives (Dr. Agnes Gruart i Masso and Dr. Maria del Carmen Picallo Soler), the symposium "Memory" chaired by Anne Reboul began with Nicola Clayton's talk. The absence of Yadin Dudai led to the general discussion on memory (focused on episodic memory in animals and humans) taking place after the coffee break (see final program, below) and to the beginning of the symposium "Perceptual bases of cognition", chaired by Göran Sonesson, with the talk given by Giorgio Vallortigara. After lunch, the workshop participants went for a two-hour walk to the Calanques. After a coffee break, the symposium resumed with two talks by Ludwig Huber and Joël Fagot, followed by a general discussion on animal perception and categorization. The participants then took a bus which first led them to Joël Fagot's animal laboratory, where he was able to demonstrate the work being done on perception in baboons, as well as introduce a new subject of study, the microcebus, a small lemur. The participants were then conducted to the first conference dinner at the Restaurant les Arcenaulx in the old harbor of Marseille.

The third symposium of the workshop, "Relations and causality", opened on Thursday morning, chaired by Jordan Zlatev, who replaced Peter Gärdenfors. It began with a talk by Michèle Fabre-Thorpe, which, because her talk related more directly to perception than to causality proper, was a good transition between the two symposia on perception and causality. She was followed by Daniel Povinelli and Anthony Dickinson. A general discussion on causality and association in humans and animals followed.

The fourth symposium, on "Attentions and intentions", chaired by Anne Reboul, began with two talks by Jim Anderson and Josep Call, on gaze following and joint attention in primates. After a coffee break, the symposium closed with a talk by Pierfrancesco Ferrari on mirror neurons, followed by a general discussion.

Lawrence Weiskrantz had asked if his talk, initially scheduled at 8 AM on the Friday morning as an opening for the symposium "Animal models of human neuropathologies", could be rescheduled on Thursday afternoon. All participants being in agreement with this suggestion, it took place on Thursday at 5h30 PM. After

a discussion on blindsight, chaired by Tatjana Nazir, the participants were driven to the harbour of Cassis (about 15 km from Marseille) where they had dinner at a seaside restaurant.

The symposium "Animal models of human neuropathologies", chaired by Tatjana Nazir, resumed on friday morning with Sabrina Davis' talk on Alzheimer disease, followed by a final discussion.

The final lecture was given by Daniel Dennett who proposed a philosophical vision of animal cognition and its differences and similarities with human cognition. This was followed by a very lively round table, chaired and animated by Joëlle Proust. Then the two organizers, Joël Fagot and Anne Reboul, closed the meeting, thanking the participants for their contributions.

Scientific content of the event

Let us begin by a short reminder of the conference's aims, as outlined in the project and in the conference booklet:

"The aim of this workshop will be to determine the limits and importance of animal models for the study of human cognition. Part of this concerns the similarities and differences between animal and human cognition, with the possible description of human cognitive specificities. Theory of mind, causal reasoning and episodic memory are central issues for the workshop because they are representative of domains of human psychology that have largely been investigated in animal research. Bringing together leading figures in the field of comparative psychology, cognitive neuroscience and philosophy, this interdisciplinary workshop is expected to bring new ideas and theories of potential practical significance for the study of human (normal and pathological) psychology."

The conference seems to us to have fulfilled its aims, as well as to have opened areas of thought which may well contribute to future research and theories, notably in the booming field of the evolution of the cognitive specificities of humankind. We will shortly outline the content of each talk below, show the articulation between them and their contribution to the overall results of the conference, which will be summarized in conclusion.

Symposium "Memory"

The symposium "Memory" was unfortunately reduced to a single talk by the absence of Yadin Dudai. However, Nicola Clayton's talk was squarely in the focus of the whole conference, being devoted to the existence or absence of episodic memory in animals. As she pointed out, episodic memory is evidenced in humans by linguistic reports, a method clearly unavailable for non-linguistic animals. A more modest — and more realistic from the point of view of animal research — definition of episodic memory, eschewing the problematic linguistic reports, identifies three core features of an episodic-like memory in animals: the where, when and what features integrated in a single remembered episode. Clayton's talk reported a series of experiments made with scrub jays and exploiting the cache behaviour of these birds. These experiments show that scrub jays do remember not only what kind of food they cached and where they cached it, but also when they cached it. This shows the existence, in at least some animal species, of what-where-when memories, or of an episodic-like memory, which is only distinguished from human episodic memory by the fact that the autonoetic (phenomenal) component cannot be evidenced in animals.

Symposium "Perceptual bases of cognition"

Giogio Vallortigara opened the symposium on perception by a talk on spatial perception in young chicks. Using the same paradigm as the Spelke's experiment on young children, i.e. disorientation in an environment with a distinctive geometry (a rectangular space), he shows that young chicks and fish perform as do human adults, i.e. they reorient by conjoining geometric and non-geometric (landmark) information. Thus the use of geometric information for spatial reorientation seems to be an ancient evolution and the flexibility in the use of different sources of information to reorient in space may depend in animals more on ecological adaptation than on phylogenetic distance from humans. Manipulating the visual field by occlusion of one eye as well as using lesions to the left or right hyppocampal formation yielded results suggesting that separate mechanisms exist for dealing with spatial reorientation problems in birds, the right hemisphere taking charge of geometrical information while the treatment of non-geometrical, local cues is done by both hemispheres. However, in case of conflict between the two types of information, the left hemisphere predominates.

Ludwig Huber concentrated on perception and categorization in pigeons. He argued, based on experimental reports, that categorization of natural stimuli is based on the extraction of category specific information, flexibility in feature creation and selection, usage of various features at different levels of complexity and the simultaneous storage of item and category specific information about a stimulus. He then described experiments in which scrambling parts of stimuli for a given category (humans) or deletions of some parts show that pigeons have representational insight in the category concerned rather than mere discrimination.

Joël Fagot followed, discussing perceptual and cognitive binding in baboons. He began by discussing the similarity between visual zones in the monkey and human cortex, showing that the similarity may well be less than usually thought. He then proceeded to describe experiments made with baboons, showing strong evidence of a marked preference for a local rather global treatment of visual information in these monkeys, a preference which strongly contrasts with the global advantage in human visual perception.

Symposium "Relations and causality"

Michèle Fabre-Thorpe described a series of experiments comparing humans and monkeys on fast categorization of visual scenes (presented for 30 ms), with a view to assessing the similarity of treatment in such tasks where the temporal constraints are devised to prevent humans from using specifically human cognitive mechanisms. The results speak in favour of a similarity of treatment between humans and monkeys, with humans being slightly more accurate but much slower than monkeys (possibly as a result of brain size), while performance in both species is similarly affected by familiarity, achromaticity and low contrast. Use of low level cues augmented speed and accuracy in both species, while the presentation of subordinate categories decreases speed and accuracy in basic level categorization for both species.

Daniel Povinelli showed that despite some similarities between humans and chimpanzees — both are associative learners —, cognitive differences dominate.

Specifically, humans seem to form concepts which are not available to other species, notably concepts for unobservable properties of objects, possibly as a result of the unique evolution of language in humans. These concepts, in some cases at least, can be paired with observable 'ambassadors' and Povinelli takes the example of weight. Basically, his claims is that though chimpanzees can recognize specific colors, shapes, etc., they do not have a representation of objects properties as such. He shows this for weight through the description of a series of experiments comparing chimpanzees and human children (2 years +). Not only was the learning process protracted for chimpanzees (\approx 900 trials), they did not transfer their knowledge to new objects for which they had to be retrained. By contrast, in children, learning was immediate as was transfer. A conclusion is that whereas humans represent properties of objects as such, chimpanzees do not, which makes for highly different cognitive ontologies between the two species.

In his talk, Anthony Dickinson concentrated on goal-directed action, defined as a representation of the causal relation between action and outcome, accompanied by a representation of the outcome. He approached it through a reevaluation task, comparing the performances of children of three age-groups and rats, outlining an executive processing effect manifest in the fact that the two younger age groups were not able to disengage.

Symposium "Attentions and intentions"

JimAnderson opened the symposium concentrating on three subjects: the use of gaze in object choice tasks, gaze alternation in 'pointing', and mutual gaze in infants. He showed that primates are sensitive to eye-contact, with both gibbon and chimpanzee infants preferring direct eye contact, though chimpanzees are sensitive to the fact that presented faces are scrambled while gibbons are not. Monkeys show visual co-orientation, while lemurs do not. Macaques follow orientation even without visual contact. Regarding combined attention (i.e. following collective gazes) is better than following individual attention, though there are differences among species. In object choice, however, gaze alone or even pointing alone do not yield any result, though a combination of gaze and pointing does work. This should not, however, be taken to imply that pointing is understood by non-human primates as it is in humans, including young children. By contrast, human children are very good at using gaze cues in object choice, while even great apes do not show very good results. Though squirrel monkeys do show some gaze alternation, the general results suggest that non-human primates follow attention, rather than gaze as such.

Josep Call also concentrated on gaze following, discussing two families of models: the *ecological* models (centering on attention) and the *mentalist* models (centering on eyes and gaze). There is a wide distribution of attention following among species, especially among domestic species, including goats. In great apes, chimpanzees and bonobos are better at gaze following than are gorillas and orangutans. Gaze following in chimpanzees begins at around 45 months, while bonobos show gaze alternation from 5 years on. However, though some behaviours are shared between the great apes and humans, there seems to be a major difference in that gaze and

gestures in apes seem limited to request: there is no evidence at any point for the declarative gestures which, in humans, appear fairly early.

Gianfrancesco Ferrari closed the symposium by a talk dedicated to the role of the mirror neurons system in the treatment of attention and intentions. From the point of view of the mirror system, action recognition corresponds to an internal description of an external event achieved by a direct mapping through mirror neurons. Motor neurons encode goal-directed actions, which should lead to an expectation of imitation. This is not commonly found in monkeys, but macaques are able of recognition of imitation of their own actions. On the whole, the mirror system in monkeys seems to facilitate recognized action and there is a very short temporal window (third day) during which infant macaques can imitate lip smacking and tongue protusion. Imitation in humans presumably involves learning and goes through the mirror system. The reason why monkeys cannot imitate could lie in limitations of the motor organization.

Symposium "Animal models of human neuropathologies"

Lawrence Weiskrantz opened the session by an outline of the work on blindsight, with its alternation between human and monkey research. Though the existence of blindsight had been shown in humans since the XIXth century, William James' adverse comments discouraged scientists to further explore the phenomenon in humans. Humphrey's work on the monkey Helena brought the subject back from oblivion, opening the path to the work on human subjects. The existence of blindsight was shown (Weiskrantz presented a short video of a human blindsight subject faithfully reproducing the trajectory of a light spot in his blind field while disclaiming any precise perception) in human subjects, before being once again shown in monkeys. The history of blindsight research is thus the history of a constant interaction between human and animal research.

Sabrina Davis then talked about the animal models of Alzheimer disease (transgenic mice), insisting on the importance of the reliability of such models for research. She began by a short description of Alzheimer disease, which can be defined as a general brain shrinkage, accompanied by neuritic plaques and neurofibriary tangles. The attack begins in the entorhinal cortex and hippocampus before spreading to the rest of the brain. Symptoms center on memory impairment with an insidious onset. Transgenic mice however seem to be a partial rather than a total model, though the accuracy of the model increases with the 2nd and 3rd generations. Limitations associated with testing mice mean that most tests target spatial, procedural and fear learning, showing deficits in learning abilities in aged animals. However, testing procedures are problematic in that there is no individual testing along aging, lack of a reliable group of tests and that their relations to the pathology in humans seem tentative. Another problem is that the relation between plaques and Alzheimer disease is a not a straightforward causal one and it is not thus clear that these mice are a good model, especially considering the fact that there is no progression in cognitive decline, contrary to what is found in humans. However, such mice might be a good model for an especially critical period of the disease, i.e. early onset. An expansion of current tests to include delayed recall is necessary to verify that hypothesis.

Closing session "Prospective"

Dan Dennett opened the closing session with a talk intituled "When should we ask what it is like to be an animal". His main topic was how we assess similarities and differences between animal and human cognition. He pointed out that we tend to use the human model, i.e. we extrapolate from our own case to other species. Basically, our reasoning goes like this: 'they're thinking, they're just not talking about it'. But that is a mistake and the very question 'what is it like to be a...' is dubious as can be seen when it is applied to a brace of oxen, an ant colony, a football team or even, given the extreme specialisation of birds' cerebral hemispheres, a bird... Coming back to the previous talks, there is no reason in the case of Clayton's scrubjay to think that it appreciates the rationality of its own action. Given Povinelli's talk, if chimpanzees are so different in cognitive ontology from us, we also ought to be cautious. Indeed, the very number of learning trials needed to obtain a response from animals should make us doubtful: are the mental structures involved really similar? It does not seem to be a mere matter of getting the animal to understand what it is supposed to do... So what about the role of language? One observation seems obvious: imagination is far from straightforward without language because language directs imagination. On higher-order matching to sample, chimpanzees do much better with symbols for 'some' and'different', which act not so much as labels as cognitive crutches. In the same way, correctly sorting images is not the same as having a concept and discrimination is different from understanding. It is known that people tend to extend pictures (i.e. remember pictures as including more material, spacewise, than they actually do). This speaks for a global bias which it is doubtful that animals have. Extrapolation is the dividing factor between discrimination and understanding: concepts are isotropic in the sense that you can apply them everywhere (no encapsulation). Thus understanding something must be concept independent. In the same way, there is no consciousness without access consciousness contrary to Block's distinction.

The round table was quite lively thanks to Joëlle Proust who did an excellent job of summing up shortly and fairly the major topics of the conference in a quick presentation. She identified the central question as that of both similarities and differences between humans and animals. Though similarities can be explained, in some cases at least, through a common evolution, differences need an explanation. A major question is how, assuming — reasonably — that evolution was the factor behind the cognitive differences, evolution worked: did it just preserve what cognitive capacities existed in the common ancestor of both chimpanzees and humans and add other capacities in the evolution of both species (the *continuity* hypothesis) or did it change the existing capacities beyond recognition (the *discontinuity* hypothesis)? This led to a lively debate with some contributors (e.g. Povinelli) defending continuity and insisting that the question could not be as simple as such a simple dichotomy, but with no enthusiasts for the discontinuity hypothesis. An important issue that emerged, raised by Fabre-Thorpe, was that of the validity of 'unecological' testing, as represented for instance by the difference between

Clayton's experiments, exploiting a natural tendency of scrub jays (e.g. caching) and Fagot's experiments (presenting monkeys with black and white, often geometrical drawings). However, it is far from clear that presenting animals with photographs on a screen is ecological either. And in experiments such as Povinelli, it might be said that it is not notably more ecological for young children to be asked to sort tin cans according to weigh through holes in a plexiglas screen than it is to ask chimpanzees with plenty of experience of such experiments to do it. Thus, the general issue of the ecological, or not, quality of laboratory experiments is presumably a slippery issue in which no experiments can hope to escape criticism.

Assessment of the results, contribution to the future direction of the field

One major idea when looking at animal research as a contribution to the knowledge of human cognition is that differences are as important as similarities. Though neuroscientific studies tend to assume cognitive and functional similarities between human and animal mind, for obvious reasons, and though they presumably fairly often are right in their assumptions, there is no denying that human cognition is very often highly different from animal cognition, as is shown not only by the fact that the human species is the only one to build a (variety of) skyscrapers, but also by the fact that it is the only species to wonder about its cognitive similarities and differences with other species. This does not detract, obviously, from the possibility that humans may be very similar to other species in other, more basic, for instance, perceptual, abilities. However, in every specific case, assuming similarity will not do: similarity has to be shown to exist and, given Fagot and others' result, it is not clear that it is straightforward even for such presumably basic abilities as visual perception. This might seem to be a rather pessimistic result: i.e. given such possibly extensive differences between human and animal cognition, the study of animal cognition has nothing of import to bring to the study of human cognition. This, however, is plainly a myopic view. The human lineage separated from the chimpanzee lineage fairly recently in geological terms (between 7 and 5 millions years ago) and both lineages share more than 98.5 of their genes: from that vintage point, similarities are not astonishing, but differences are. Yet differences are present. This calls for both an evolutionary and a genetic story (as well as, presumably, a cultural story, as advocated by Tomasello), a story which can only be based on a fair assessment of both differences and similarities between species and that can only be done through experimental comparative studies at both a behavioural and a cellular level.

Final programme

Wednesday Dec. 7th

9h30-10h: Meeting opening (Joël Fagot & Anne Reboul, organizers; Agnès Gruart i Masso, Maria del Carmen Picallo Soler, ESF representatives)

Symposium "Memory" (chaired by Anne Reboul, ISC, CNRS, Lyon, France)

10h00-10h45: Nicola Clayton (University of Cambridge, UK): Mental Time Travel in Animals? A Western Scrub-Jay's Perspective

10h45-11h15: Coffee break

11h15-11h45: Discussion

Symposium "Perceptual bases of cognition" (chaired by Göran Sonesson, Lund University, Sweden)

11h45-12h30: Giorgio Vallortigara (University of Trieste, Italy): *Animals as Natural Geometers*

12h30-14h00: Lunch break

14h-16h30: Visit of the calanques (2 hours of easy hicking for a wonderful landscape + coffee pause on coming back)

16h30-17h15: Ludwig Huber (Department for Behavior, Neurobiology and Cognition, University of Vienna, Austria): From Categories to Concepts: Bridging the Gap between Perception and Cognition

17h115-17h45 Coffee break

17h45-18h30: Joël Fagot (INCM, CNRS, Marseille, France): Perceptual and Cognitive Binding in Baboons

18h30-19h00: Discussion

19h15- visit of Joël Fagot's primate cognition laboratory

Dinner: Restaurant les Arcenaulx

Thursday Dec. 8th

Symposium "Relations and causality" (chaired by Jordan Zlatev, Lund University, Sweden)

9h30-10h15: Michèle Fabre-Thorpe (CERCO, CNRS, Toulouse, France): Fast Categorization of Natural Scenes by Humans and Monkeys: a Comparative Study

10h15-11h00: Daniel Povinelli (University of Louisiana at Lafayette, USA): Causal Reasoning in Chimpanzees: Lessons from their Concept of Weight

11h-11h30: Coffee Break

11h30-12h15: Anthony Dickinson (University of Cambridge, UK): *Animal Models of Instrumental Causality*

12h15-12h45: Discussion

12h45-14h00: Lunch break

Symposium "Attentions and intentions" (chaired by Anne Reboul, ISC, CNRS, Lyon, France)

14h00-14h45: James Anderson (University of Stirling, UK): Exploring Primates' Use of Others' Gaze

14h45-15h30: Josep Call (Max Planck Institute, Leipzig, Germany): Gaze Following and Joint Attention in Primates

15h30-16h00: Coffee break

16h00-16h45: Pierfrancesco Ferrari (University of Parma, Italy): *Mirror Neurons and Social Cognition in Primates. Findings, Implications and Speculations*

16h45-17h15: Discussion

17h15-17h30: Free time

Symposium "Animal models of human neuropathologies" (chaired by Tatjana Nazir, ISC, CNRS, Lyon, France)

17h30-18h-15: Larry Weiskrantz (Oxford University, UK): From Animal Research to Human Blindsight, and Back Again

19h: Dinner at the restaurant "Chez Gilbert", Cassis

Friday Dec 9th

08h45-09h30: Sabrina Davis (NAMC, CNRS, Orsay, France): Rodent Models of Cognitive Decline in Alzheimer's Disease

09h30-10h: Discussion

10h00-10h30: Coffee break

Closing session: "Prospective"

10h30-11h30: Special lecture by Daniel Dennett (Tufts University, USA): When Should We Ask 'What Is It Like' to Be an Animal?

11h30-12h15: Round table (chaired by Joëlle Proust, Institut Jean Nicod, CNRS, Paris, France)

12h15-12h30: Closing of the workshop (Joël Fagot, Anne Reboul)

12h30-14h00: Lunch

Final list of participants

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Statistical information on participants

Excluding the ESF representatives, here are three tables on countries of origin as well as age of the participants:

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|-----------------------|-------------|---------|-------|-----|
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| Anne Reboul | France | | 49 | |
| Michèle Fabre-Thorpe | France | | 53 | |
| Sabrina Davis | France | | 44 | |
| Joëlle Proust | France | | 56 | |
| Bruno Wicker | France | | 34 | |
| Tatjana Nazir | France | | 43 | |
| Nicola Clayton | UK | | 36 | |
| Anthony Dickinson | UK | | 54 | |
| James Anderson | UK | | 44 | |
| Larry Weiskrantz | UK | | 80 | |
| Jules Davidoff | UK | | 47 | |
| Chris Sinha | UK | | 54 | |
| Katja Liebal | UK | | 28 | |
| Carlo de Lillo | UK | | 39 | |
| Göran Sonesson | Sweden | | 46 | |
| Jordan Zlatev | Sweden | | 35 | |
| Giorgio Vallortigara | Italy | | 47 | |
| Pierfrancesco Ferrari | Italy | | 38 | |
| Giovanna Spinozzi | Italy | | 48 | |
| Ludwig Huber | Austria | | 39 | |
| Daniel Povinelli | USA | | 37 | |
| Daniel Dennett | USA | | 72 | |
| Josep Call | Germany | | 38 | |
| Daniel Haun | Netherlands | | 28 | |
| | | | 60 | and |
| Twenties Thirties | Forties | Fifties | above | |
| 2 | 8 | 9 | 4 | 2 |

| France | UK | Sweden | Italy | Austria | USA | Germany | Netherlands |
|--------|----|--------|-------|---------|-----|---------|-------------|
| 7 | 8 | 2 | 3 | 1 | 2 | 1 | 1 |