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Program:

PROLEGOMENA

Robert J. Richards The Linguistic Creation of Man, or the Missing Link in 19th Century Evolutionary Theory

OVERVIEW

Cecilia Heyes Questions about the Evolution of Cognition
M.E. Bitterman Cognitive Evolution: A Psychological Perspective

ECOLOGY & PHYLOGENY

Sara J. Shettleworth Modularity, Specialization and the Evolution of Cognition
Ludwig Huber The Evolution of Cognition: 25 Years after "the Mirror"

SPATIAL MEMORY

Nicola S. Clayton Memory and the avian hippocampus: Food-caching birds as a model system
Daniel C. Dennett Intelligence and Cultural Evolution

CONSCIOUSNESS

Nicholas K. Humphrey The Privatization of Sensation

Euan M. MacPhail The search for a mental Rubicon

IMPRINTING

Patrick P.G. Bateson What do we need to know in order to understand imprinting?
Adolf Heschl Imprinting and the nature of learning

ABSTRACTION

Juan Delius Equivalence relations in concept learning by pigeons
Nicholas J. Mackintosh Abstract Rules and Abstract Representations

CAUSALITY

Duane M. Rumbaugh Cause-Effect Reasoning - Brain, Rearing, and Emergents
Anthony Dickinson Causal Cognition and Goal-Directed Action

LANGUAGE

Terrence W. Deacon
Friedhart Klix Evolutionary impacts on the imprinting of learning mechanisms and language development

MENTALITY

Bernd Heinrich Problem-solving by raven
Louis Lefebvre The origin and cultural transmission of feeding innovations in birds

SOCIAL LEARNING & CULTURE

Peter J. Richerson
Michael Tomasello Cumulative Cultural Evolution

THEORY OF MIND

Kim Sterelny Primate Worlds
Robin I.M. Dunbar The Social Brain and the Evolution of Culture

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Abstracts

What do we need to know in order to understand imprinting?

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A long debate has revolved around whether imprinting is special. Over the years my own position has moved much closer to that adopted by Konrad Lorenz. The timing of the process, the features that most readily trigger learning and the motor systems that are linked to representations stored as a result of learning are all specific to the functional context of forming a social attachment. Of course, the underlying neural mechanisms might be the same as those involved other learning processes. Nevertheless, it is worth asking whether the rules involved in learning about the causal structure of the environment are different from those used in perceptual learning (of which imprinting is a special case). Time plays a different role in classical or instrumental conditioning than it does in perceptual learning. The order in which different events are experienced matters a lot when one event causes the other. However, the order does not matter at all when the experiences are different views of the same object. Some experimental evidence from studies of imprinting in chicks sug-gests that these two broad functions are served by different sub-processes which are, nevertheless, in touch with each other..

To understand imprinting properly from a behavioral standpoint, we do not need to know how genes are switched on and off or any of the other intricate mechanisms of cellular machinery, interesting though such details might be. However, we do need to have a good understanding of how the various sub-processes are activated in development and how they fit together. That means we need answers to at least the following questions: (a) In what ways does the animal play an active role in organizing its own experience. (b) What features are of special importance in attracting the animal? (c) How do effective features operating through different sensory modalities interact? (d) What mechanisms switch in some of the available detectors but not others? (e) Do all of the detectors feed into the representations of the imprinting ob-ject? (f) What aspects of behavior are elicited by imprinting stimuli and how are these executive functions linked? (g) How does the transfer of experience from imprinting to other learning processes take place?

Although it is not necessarily part of a focused inquiry into mechanism, comparisons of species living in different ecological conditions would high-light how particular sub-processes vary in character or importance.

Cognitive Evolution: A Psychological Perspective

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Comparative psychologists have long been interested in perception and in insight (that is, in creative as distinct from purely reproductive intelligence), but their main contribution thus far to the understanding of cognitive evolution has been an intensive analysis of learning and memory. Conditioning experiments with a small number of widely divergent vertebrate species have yielded a lengthy list of phenomena that may reasonably be assumed on the basis of the taxonomic diversity of the subjects to

be general phenomena of vertebrate learning; the results vary quantitatively with species and with training techniques, but there are common qualitative patterns that are understandable in terms of common functional principles and may well reflect the operation of homologous mechanisms of information storage and retrieval. Despite the remoteness of the evolutionary relationship, many of the vertebrate principles seem to hold also for honeybees, whose performance in conditioning experiments shows detailed similarities to that of vertebrates, although here we may suspect that the similarities are, at least in large measure, convergent; it is difficult to believe that like results would be obtained in analogous experiments (if at all feasible) with extant species resembling even the most advanced common ancestor. In the learning of vertebrates, there is not only extensive commonality, but evidence as well of a broad evolu-tionary divergence; the evidence is provided by a set of experiments on the control of instrumental behavior by its remembered consequences, whose results for mammals are qualitatively different from those for animals of older verte-brate lines. This promising work has been largely descriptive, with little opportunity as yet for systematic func-tional analysis.

Some familiar objections to the way in which comparative psychologists have approached the problem of cognitive evolution and the conclusions to which they have been led are reviewed and evaluated.

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Memory and the avian hippocampus: Food-caching birds as a model system

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Comparative studies of memory and the hippocampus in food-caching birds provide a unique source of evidence for in-vestigating hippocampal structure and function. Food-caching birds rely on memory to recover their hidden, scatter- hoarded caches of food. The results of laboratory tests show that food-storing members of the Corvidae (crows, magpies, jays and nutcrackers) and Paridae (titmice and chickadees) have a better spatial memory and/or rely more heavily on spatial cues than do their non-storing counterparts (e.g. Clayton & Krebs 1994). While the most critical component about a cache site may be its spatial location, there is mounting evidence that food-caching birds remember additional information about the contents and status of cache sites (Clayton in press; Clayton & Dickinson in review a & b). The hippo-cam-pus, a brain structure known to play a role in successful retrieval of stored food, is enlarged in species which cache food relative to those which do not. Studies of the development of behavior and brain show that the hippocampus is extremely plastic. Memory for food caches triggers a dramatic increase in the total number of number of neurons within the avian hippocampus by altering the rate at which these cells are born and die (e.g. Clayton & Krebs 1995). The find-ing that the specific experience of storing and retrieving food triggers dramatic changes in hippocampal morphology has led to the development of the food-storing system as an exciting model for studying fundamental questions about mem-ory and the hippocampus in a naturalistic environment.

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Abstract and title of abstract currently unavailable

Equivalence relations in concept learning by pigeons

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The ability of animals to learn to distinguish exemplars belonging to a category of stimuli, and to then generalize this dis-crimination to novel exemplars without additional training, was for a long time considered to be sufficient evidence for concept formation. Lea (1984), however, pointed out that human psychologists use the term concept is in a more restric-tive sense. He argued that it was additionally necessary to show that the stimuli pertaining to a category were functionally equivalent. Lea proposed a procedure with which this property could be taught to and demonstrated in ani-mals. Among the first to use it was Vaughan (1988). He trained pigeons to discriminate different slides that all depicted trees but which were arbitrarily divided into a set of rewarded and another set of non-rewarded slides. When the pigeons had learned to distinguish these arbitrary sets, the allocation of reward and non-reward between the two sets of slides was exchanged. Such reinforcement reversals were repeated until the birds became proficient at switching their choice re-sponding. Vaughan could then show that a reinforcement reversal training involving only half of the slides of each set was sufficient to get the pigeons to respond correctly to the remaining half without any special training. That is, when the pigeons noticed that some of the slides of the sets had exchanged their functional significance, they spontaneously transferred the adequate mode of responding to the remainder of the slides. Several other studies using variations of this basic design, however, were not, or no so successful in demonstrating the presence or development of functional equiva-lence. We shall report the results of three own studies that were aimed at finding out what factors might be causing these variable results. The talk will also touch upon the relationships that might exist between functional equivalence and symbolic equivalence as studied by Sidman (1992) and his followers using matching to sample procedures.

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Intelligence and Cultural Evolution

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As we learn more about the gulf between the cognitive powers of normal human beings and the cognitive powers of all other species, we can BEGIN to see shapes therein: hints about shared features that are, say, mammalian or vertebrate heritages which H. sapiens enjoys in relatively modest measure, and hints about which features are due quite directly to species-specific genetically transmitted differences, and which are secondary to our species' capacity to speak, which opens the floodgates to cultural evolution. We are neither just cultured apes, nor are we natural born geniuses. Two normal human powers that are not clearly present in any other species, and that will repay a careful evolutionary analysis in terms of reverse engineering, are the capacities for episodic memory (in a strong sense) and reflection.

Causal Cognition and Goal-Directed Action

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I shall argue that the capacity for causal cognition evolved to support goal-directed behavior. Whereas simple Pavlovian conditioned responses and instrumental habits can modeled by associative /connectionist systems that can be mapped directly onto neurobiological mechanisms, such systems have failed to provide a satisfactory account of goal-directed action. These actions warrant a cognitive explanation in terms of the interaction of a causal belief about the action-outcome relationship with a representation of the incentive value of the outcome (Heyes & Dickinson, 1990). Two lines of evidence will be offered in support of the role for causal cognition. The first consists of the concordance between hu-man causal judgments and animal instrumental action across variations in the parameters of the action-outcome relation-ship (Dickinson & Shanks, 1995). Secondly, the phenomenon of incentive learning in animals supports the predicted dissoci-ation between the cognitive representation of the outcome value controlling goal-directed action and the biological pro-cesses that determine this value (Dickinson & Balleine, 1993).

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- Heyes, C., & Dickinson, A. (1990). The intentionality of animal action. Mind & Language, 5, 87-104.

The Social Brain and the Evolution of Culture

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Primates have unusually large brains for their body size. I will review evidence suggesting that the need to evolve social skills to maintain social coherence in large groups has been the principal selection pressure favoring the evolution of large brains in primates. Detailed analysis of the patterns of brain size evolution suggest that, at the body size of great apes, there is a phase shift in the balance between visual and non-visual areas in the neocortex that frees up a disproportionate amount of cortical tissue for social functions. This appears to explain why great apes and humans (but not monkeys) possess Theory of Mind (or its immediate precursors). Since Theory of Mind is necessary to engage in any of the activities commonly described as culture, there appear to neuro-anatomical constraints on species' abilities to acquire or develop culture.

Problem-solving by raven

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Ravens are often considered to be "intelligent" birds, yet almost n data exist that explore the nature and extent of this pre-sumed intelligence. It is difficult to demonstrate intelligence since the main criteria most commonly implied is men-tal visualization of alternative choices which can be repeated in and for ourselves through language. A second indirect what to examine potential intelligence is by the demonstration of those complex problem-solving behaviors that cannot be accounted for exclusively by innate programming and learning. Any one behavior presumably involves a mix of all three alternatives that vary in degree from one behavior to the next. I will explore primarily three different problem solv-ing behaviors in ravens that involve different degrees of programmed (innate and learned) and unprogrammed compo-nents. The first includes the responses that allow ravens from a great diversity of habitats to "solve" the problem of diet choice by a combination of innate and learned responses.

The second category of problem solving will center on awareness of objects that are out of sight. Ravens cache food in both social and solitary contexts. They keep track of food hidden by themselves and by others but also show evidence of anticipating the "trajectory" of others approaching hidden food. Finally, I will explore the reactions of naive ravens confronting food suspended by string, Can they access such food and if so does it involve primarily innate program-ming, learning or mental "visualization"?

Imprinting and the nature of learning

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Since Lorenz' discovery of filial imprinting in 1935, the interpretation of this behavioral phenomenon has changed several times. Lorenz himself always emphasized the distinctive nature of imprinting

processes (main variants: filial, sex-ual, food, habitat) when compared with other kinds of learning. However, today, we speak of sensitive, rather than criti-cal periods, and we now know that secondary imprinted attachments can be as stable as primary ones, thereby limiting the impact of assumed irreversibility. Nevertheless, in his study of imprinting, Lorenz did more than describe a new and special category of behavior, he was the first to understand how specific genetic constraints can define the structure of a learning mechanism. Consistent with there being specialized learning mechanisms, twenty years later, using ray -treated rats, John Garcia (1955) demonstrated for the first time that not every case of associative learning can be explained by simply referring to a small set of general (or even universal) learning rules. Meanwhile, it has been argued that it is pos-si-ble to conclusively resolve the misleading innate/acquired dichotomy by treating phylogeny as the exclusive source of ontogenetic novelties (Heschl 1990). This explains how, once the ultimate function of a behavior pattern in a particular species is understood, it is possible to predict the necessary proximate structure of that behavior.

The basic relationship between the survival function of a concrete behavior and its structure is exemplified by all types of imprinting: Filial imprinting in ducks and geese must guarantee that the young follow only their mother. Hence chicks preferentially attend to moving objects which produce a certain sound and they do this shortly after hatch-ing. Sex-ual imprinting in many birds and mammals has to guarantee that genetically closely related individuals are cho-sen as potential partners for both reproduction and cooperation after sexual maturity. Hence animals from these groups become perceptionally fixed on the characteristics of individuals with whom they socialize during early infancy. Food imprinting must guarantee that the next generation of a species uses the food sources which their parents have success-fully exploited for survival. Hence, juveniles often develop preferences for the foods they have eaten together with their parents. Habitat imprinting must guarantee that the young profit from remembering the qualities of the site where they were successfully reared. Hence, when they encounter new environments, the off spring of certain species will prefer those which resemble their birthplace. Now, I propose that the structure of any putative example of associative learning is the result of exactly the same selection principles. Consequently, by applying evolutionary theory to learning re-search, the so-called "general laws of association" become nothing but the highly specific genetic result of natural selec-tion, as different or similar as species in which the learning occurs.

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Questions about the Evolution of Cognition

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Surveying contemporary views of the evolution of cognition, and using examples from social and spatial cognition, it will be suggested that the current focus of empiricist-nativist debate is the degree to which specialization of cognitive function is achieved ontogenetically, through experience, or phylogenetically, via natural selection. Research emphasiz-ing the contribution of phylogeny is often conducted in the ethological tradition or under the auspices of "evolutionary psychology", but ontogenetic specialization is equally compatible with evolutionary thinking. Contemporary empiri-cists in comparative psychology and animal cognitive psychology embrace mental continuity, assume that natural selec-tion is the source of domain- and taxon-general cognitive processes, and, in some cases, postulate that variation and se-lective retention processes are responsible for ontogenetic specialization.

The truly contentious issues center on: 1) the validity of the distinction between central (cognitive) and peripheral (sensory, motor) processes, 2) the range and power of domain-general cognitive processes, and 3) the type of psychological theory which offers default / parsimonious ex-plana-tions for adaptive behavior.

The Evolution of Cognition: 25 Years after "the Mirror"

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"Nothing in biology makes sense except when it is viewed from an evolutionary perspective" (Dobzhansky). Since it is widely accepted that cognitive phenomena are the result of evolutionary processes, evolutionary biology has a great deal to offer animal learning theory. However, the current diversity of explanations of evolutionary development means that there is no straightforward way in which to reconstruct the evolution of cognitive systems.

In fact, a historic fallacy prevents such an endeavor. Paradoxically, in the disciplines of both comparative psychology and ethology, the temptation has been to trust intuitions about intellectual continuity. The shortcomings of the former discipline have been sufficiently well debated. It has led to a polarization between the view that intellectual development follows a linear sequence and the denial of the existence of any intellectual differences in the non-human world. The few ethologically motivated attempts to order cognitive phenomena in an evolutionary plausible way have been under-repre-sented in the cognitive sciences.

This contribution aims to give a brief review of Lorenz's attempt to identify a natural history of human knowledge (1944-48/92, 1973). His approach of "looking behind the mirror" can be characterized as an analysis of the hierarchies of cognitive structures and their functions in various species of animals. This requires a systems approach rather than an iso-lated view of specific learning mechanisms. In discussing the heuristic value of this analysis I will address the fol-lowing topics:

(1) How can the adaptionist and the constructivist perspectives of the evolution of mind be reconciled?

(2) How does Lorenz's "knowledge-gaining processes" fit into the "state-of-the-art" view of learning mechanisms?

(3) How can we properly reconstruct the timing and order in which particular characteristics appear during the history of life?

(4) How can we link the selective forces acting on structure (coherence) to those acting on function (correspondence) since the two do not necessarily evolve in parallel?

(5) How can we determine the degree of specificity that exists in "higher" brain areas within the range of narrowly adapted to generally applicable?

(6) How can our understanding of the human mind profit from the evolution-of-cognition approach (the evolutionary epistemology tenet)?

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The Privatization of Sensation

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It is the ambition of evolutionary psychology to explain how the basic features of human mental life came to be se-lected in the course of evolution because of their contribution to biological survival. Counted among the most basic, surely, should be the subjective qualities of the qualia - of conscious sensory experience: the felt redness we experience on look-ing at a ripe tomato, the felt saltiness on tasting an anchovy, the felt pain on being pricked by a thorn. But, as many theo-rists acknowledge, with these qualia, the ambition of evolutionary psychology may have met its match.

True, it may be possible for us to point to the survival value of there being any such thing as sensory experience (although even this may not present a trivial problem .. among the better ideas, perhaps, being my own and Gregory's proposal that the role of sensory experience in human beings is to "flag the present"). Nonetheless, it will be much harder for us to show how any survival value at all can attach to the subjective quality of sensory experience as such.

The difficulty is obvious. Everyone agrees that a mental trait can only contribute to an organism's biological sur-vival in so far as it operates in the public domain so as to affect the individual's objective relations with the world. Yet almost everyone also agrees that the subjective quality of sensory experience is (at least for all practical purposes) pri-vate and without influence on objective relationships. As Wittgenstein remarked, "The assumption would be possible - though unverifiable - that one section of mankind has one sensation of red and another section another". And ó if true - this "unverifiable" clearly spells death to any explanation of the subjective red quality of the sensation in terms of bio-logical survival.

Then, what is to be done? On the one hand, perhaps we should concede that the subjective quality of sensations cannot after all have been determined by natural selection at any level whatsoever. (But this, I think, would be theoretically depressing) ... Or, on the other hand, perhaps we should challenge the received view that the quality of sensations is as private as it seems to be. (But this, I think, would be intuitively unconvincing.)

I believe neither of these solutions to the puzzle is in fact the right one. The truth, I shall argue, is that the subjec-tive quality of sensations has indeed been shaped by selection in the past - even though it is today effectively private. And this situation has come about as a result of a remarkable evolutionary progression, whereby the primitive activity of sensing slowly became "privatized" - that's to say, removed from the domain of overt public behavior and transformed into a mental activity that is now, in humans, largely if not exclusively internal to the subject's mind.

The evolution of cognitive models in behavioral ecology

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Cognition came as an afterthought for behavioral ecologists. At its inception, their program was clear-cut: the goal was to focus on ecological problems that involved individual behavior, and hence within-subject processes were not within the remit. Behavior was predicted as a function of ecological circumstances, but the processes by which individuals gen-erated actions were not of interest. The implicit hope was that just one of Tinbergen's four levels of analysis (func-tion) would suffice. The theory developed was refreshingly a priori: behavior was predicted without influence from pre-vious descriptions. References to internal representation, to information processing, to biased systems of decision, to mecha-nisms of perception and many other cognitive or quasi-cognitive concepts were gradually introduced as a conse-quence of predictive failures: if an animal did not do as expected, there was a good reason to ask why, and cognitive pro-cesses often did provide good answers.

I believe that this reaction was healthy, but that it can go beyond. Cognitive processes invoked to account for failure to perform optimally in some problem lead us to re-think the problem itself. In the case of foraging behavior, a large num-ber of observations in which animals did not follow models' predictions can be interpreted at the light of the proper-ties of perception, memory or associative learning. Evolutionarily oriented researchers now face the task of investigating why (in the functional sense) these systems have their properties.

Evolutionary impacts on the imprinting of learning mechanisms and language development

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1. Anthropogenesis has been driven by different geophysical factors. Irregular periodicities in our planetary system generated the Pleistocene age on earth. During this period the volume of the hominid skull increased by up to four times its original size. The reasons for this and what its effects were will be discussed.

2. A decline in food resources during the ice age meant that the hominids had to move into the widely extended savanna areas. The resulting change in biotops required a high degree of flexibility in the control of hominid behavior, especially with regard to the organization of social behavior. A flexible system is one that is capable of learning and forgetting. Learning and forgetting rely upon memory. Information can be stored in a rational manner by efficient information processing systems. This is where cognitive modes of learning came into being. Examples include the compression of in-for-mation by chunking, the shortening of sequences, and mapping between memory entries. These processes are charac-teristic of the earliest forms of modular thinking.

3. Between 180 000 and 120 000 BC the 'Em warming up' happened on earth. During this period the modern human being (Homo sapiens sapiens) originated from the H. erectus or Heidelbergensis-type. This probably took place both in Central and Northern Africa, and the new form of social organization was likely to have been tribes with totem and ta-boo (Freud). A new ice age (105 000 BC) then lead to a new migration "out of Africa". The results of which are reflected in the new kind of tools found in the neolithic caves of Israel, Jordania, and South and West Europe (90 000 - 20 000 BC). The construction of these tools was based on principles similar to those depicted in the cave paintings found in Spain and in France. They reflect a hierarchically organized combination of well-defined mental procedures or modules.

4. There is sufficient evidence to suggest that prehuman primates did not develop a precursor to human language. The evolutionary steps that this would require cannot be identified. However, I would like to

introduce a new hypothesis. This hypothesis is based on the assumption that there is an endosymbiotic interaction between different, but well-defined, brain areas. The nerve nets in these different areas developed separately, at different times, and for different pur-poses. The outcome of this anatomically identifiable interaction was a new kind of combinatory thinking by construc-tive mod-ules. This slightly cryptic statement will be made clearer in my report.

The origin and cultural transmission of feeding innovations in birds

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When new behaviors originate and spread in animal populations through non-genetic means, three types of questions can be asked: (a) what determines the appearance of the new behavior in its originator(s), (b) what potential is there for oth-ers to learn the new behavior and (c) how does this potential translate into actual transmission of the innovation in the population. Each of these three steps may be governed by different rules.

(a) In birds, taxonomic variation in behavioral novelty can be quantified by collating reports of new feeding behav-iors published in the short notes sections of ornithology journals. Relative size of the forebrain appears to be an important predictor of innovation rate in different avian taxa.

(b) Learning potential can be assessed through comparative experiments on wild-caught animals.

Tests on pigeons, doves and grackles show that scramble competition in the field is the best predictor of social learning potential in single cage experiments. This ecological variable affects the type of innovator one is most likely learn from; its effect on the overall probability of learning is very broad, leading to differences in both social and individual learning, as well as in intervening variables like neophobia and tameness. The experiments highlight three difficulties with comparative learning tests: (1) does response to novel problems in captivity reflect response to novelty in the field? (2) Do differences in performance on captive tests specifically reflect learning or other, more basic, intervening variables? (3) Are differences in both captive and field performance due to divergent natural selection or divergent experience?

(c) Field and aviary experiments on pigeons suggest that the most important predictors of cultural transmission rate are the relative payoff and salience of new vs. old behaviors. Even if single cage experiments show that practically all pigeons have the potential for learning new feeding behaviors from others, this can translate into limited transmission in real populations. When an innovation can be shared, the payoffs to new (learn the innovation for yourself) vs. old (join the innovator and share) behaviors are linked by frequency-dependence; transmission rate in pigeon flocks is predicted by the frequency-dependent equilibrium between the alternatives, not by the learning potential determined in single cage tests. When payoffs are kept constant, relative salience of the new vs. old behaviors determines transmission: both the simple presence of inactive bystanders and scramble competition with other scroungers inhibit learning.

Abstract Rules and Abstract Representations

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When people or other animals have solved a particular problem, they can be tested to see whether what they have learned transfers to other problems. Successful transfer or generalization implies that the training and test problems share features in common, and that those features came to control behavior during the course of initial training. Associative learning theories thus have no difficulty in predicting successful transfer of a learned discrimination, whether between a single S+ and S-, or between numerous exemplars of two categories, to novel instances.

There is evidence from both categorization and function learning tasks, however, that people are capable of abstracting the rules describing the structure of a given problem, and using such rules as a basis for transfer that would not be readily accounted for by any such associative model (e.g. Delosh et al., 1997). But associative models can certainly predict more transfer in some situations, if they are allowed the luxury of representing stimuli in more complex, perhaps abstract, ways. What representations do we need to ascribe to various animals? Pigeons can learn whether a stimulus is (relatively) novel or (relatively) familiar, and use this as the basis for transfer from one problem to another. It seems likely that a similar type of representation would be sufficient to account for transfer in artificial grammar learning tasks, based largely on the detection of repetitions (Brooks & Vokey, 1991). But claims for yet more abstract or rela-tional rep-resentations in birds such as pigeons should probably be treated with some caution, since their detection of even physical relationships, such as brighter, larger than etc. is probably based on nothing more than sensory mecha-nisms of contrast (Wills & Mackintosh, submitted).

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The search for a mental Rubicon

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We adult human beings are conscious, and most of us believe that at least some nonhuman organisms are conscious: not all living organisms, but animals; and perhaps not all animals, but some multicellular animals. It may seem that to ques-tion this belief is to question the Darwinian account of human evolution. But difficulties arise when we attempt to envis-age the evolution of consciousness, because there is as yet no universally acceptable account of the survival value of consciousness. Plausible accounts can be developed of the evolution of animal behavior, accounts in which animals would come to behave precisely as they are seen to behave, and that make no assumption of consciousness in them. But since we are conscious, the similarity of behavior in species closely related to us suggests that, by analogy, those spe-cies must be conscious also. If we do suppose that some, but not necessarily all, animals are conscious, this in turn raises the question of what differences we should find between species that are conscious and those that are not: how should we distinguish between a conscious and a nonconscious animal?. A common and reasonable assumption is that conscious-ness is associated with a minimal degree of complexity - complexity of behavior rather than of neural connectivity. And the most plausibly relevant aspect of behavioral complexity is complexity of cognition - of intelligence. Comparative psychologists have, however, found it surprisingly difficult to establish substantive differences in intelli-gence between groups of animals. Many psychologists believe that language is a peculiarly human competence, and I have suggested (e.g. Macphail 1996) that whereas the intelligence of nonhumans is dominated by association formation, the human intel-lect is transformed by the capacity for language. Language may, then, be a mental Rubicon and so, a candidate for the leap in cognitive capacity that resulted in consciousness. The plausibility of this possibility is strengthened by evidence, from studies of implicit learning, that when humans employ the associative system that we have inherited from nonhu-mans, we are not conscious of its operation. A role for language in consciousness is also suggested by the phenomenon of infantile amnesia, whose offset coincides with the onset of language: conscious recall, that is, may depend upon the mat-uration of language. But how could the development of language result in conscious-ness? I shall suggest (Macphail, 1998) that the capacity to entertain subject-predicate relationships is a prerequisite for development of a concept of self, and that the self-concept is a necessary condition for any form of consciousness.

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The Linguistic Creation of Man, or the Missing Link in 19th Century Evolutionary Theory

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Darwin used the development of language as a model for species development. He also argued that language was responsible for distinctly human mind. Charles Lyel, the great geologist and Darwin's friend, further explored the model, show-ing how Darwin's devices could be applied to language. Lyel, however, could not go the whole orang: he thought that language was that barrier the distinguished man from the animals, and that no animal of itself could cross that Rubicon. August Schleicher, the great German linguist and friend of Ernst Haeckel, fully endorsed Darwin's theory and showed how it could explain the descent of language from primitive animal sounds. Schleicher solved two critical problems for Haeckel's theory of human evolution: Haeckel argued, of course, that man came up from ape-like ancestors. But he had no theory of the transition from ape-like intelligence to human reason. Further he believed that human beings formed several species, some being more advanced than others--the Germans and English leading the pack. But he had no good theory of the traits that provided the superiority. He found the solutions to his problems in Schleicher's conception of the evolution of language: some languages, Schleicher held, were superior to others, more perfect, and these led to the dif-ferential evolution of mind. What Haeckel didn't realize was that the essential structure of Schleicher's theory was not due to Darwinian evolutionary considerations but to Hegelian romantic considerations. Thus the missing link in 19th- evolutionary thought was Hegel.

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Cause-Effect Reasoning - Brain, Rearing, and Emergents

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Cause-effect relations are imputed on the basis of perceptions in relation to an organism's prior experience. They are like hypotheses--tentatively affirmed, tested, altered, and subject to belief. Belief systems are dynamic and produce prob-abil-ity estimations regarding the reliability and truthfulness of cause-effect hypotheses. With the evolution of life, neu-ral control of behavior has tended to become more complex, equipping species with highly complex nervous systems and brains. Elaborated central nervous systems and magnificent brains, notably in the great apes and human, have en-abled the emergence of cognition, symbolism, referential communication, reasoning, and language--all of which serve the for-mulation of cause-effect relations and their reliability and validity. Posited cause-effect relationships can serve to struc-ture the world so as to afford a leveling of the environment's gaming fields in which the do-or-die survival games of life are pursed. Evolution of the brain has been more rapid than evolution of the body, at least for primates, in that the brain has become disproportionately larger and more complex than has the body. Even within primates there is robust evi-dence that with evolution of the brain from prosimian to ape and human the essence of learning process has shifted, probabilistically, from basic stimulus-response (S-R) associative learning (reminiscent of Thorndike and Hull's psychology) to a more comprehensive and hypothesis-based form of learning that here will be termed relational. Relational learning processes are emergents, (Rumbaugh, Washburn, & Hillix, 1996), in that they transcend the more basic processes of respondent and operant conditioning. Emergents are not reducible to respondents and emergents. Emergent processes can afford organisms over-arching frameworks within which they pursue, insofar as possible, the "good life" con-strained only by the parameters of survival and reproductive fitness. Emergents may be studied from the perspective of cognitive operations and structures; or they may be studied from the perspective of more traditional behaviorism in that their antecedents are sought and defined as are their consequences, in the elaborations of behavioral skills and varied pat-terns of creativity for which they provide.

We now know, at the turn of the millennium, that the complexities and plasticity of the ape's brain, in equally complex interactions with the parameters of early rearing and environmental vectors of influence, can instate capacities and skills which, until only a few years ago, were thought to be the exclusive domain of "being human" Thus, young chim-panzees and bonobos, if reared in a language-structured environment provided by skilled caregivers, spontaneously (e.g., without formal discrete-trial training and the selective reinforcement of responses) comprehend human speech--first indi-vidual words and then even the meaning encoded with the syntax of novel sentences of request (Savage-Rumbaugh, Mur-phy, Sevcik, Brakke, Williams, & Rumbaugh, 1993). Their comprehension of speech is well beyond that of the average 2-1/2 year old child, though their language production is somewhat less. These advanced capacities of the im-mature ape surely are founded in its capacities to discern and organize predictive probabilities regarding the relationships between things and events of its world. And those relationships that are perceived as reliable and probably valid are used as guide-lines for the building of belief systems and future-oriented frameworks from which, then, the ape (and even human!) ven-ture forth as agents for action within interactive environments. (NICHD-O6016)

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Modularity, Specialization and the Evolution of Cognition

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This contribution sketches an adaptationist, ecological, approach to the evolution of cognition (Shettleworth, 1993; in press). It has two major ingredients. First, it construes cognition as information processing in the broadest sense, i.e. all of the ways in which animals from the simplest to the most complex adjust their behavior to local conditions, from gath-ering information through the senses to making decisions and performing functionally appropriate actions. "Simple" forms of adjustment to the environment such as habituation and other forms of recognition memory are considered as well as possibly more complex representational and learning processes, simple organisms as well as birds and mammals. In contrast to traditional psychological research on isolated individuals of a few species solving problems about physical causality in the laboratory, this approach includes analysis of how animals of all species process and use information in their natural environments.

Second, cognition is modular. Cognitive modules process restricted domains of information in functionally appropriate ways, and are largely preprogrammed to do so. A completely generalized and undifferentiated information processor simply could not survive long enough to reproduce in the real world (Cosmides & Tooby, 1994). To use Lorenz's term, animals need an "innate schoolmarm" to select which information is used and how. The paradigm examples of cognitive modularity are found in perception. Vision, hearing, olfaction, electroreception, and so on, each evolved to deal with a different kind of input. Other candidates for distinct information-processing modules include physical cognition (associative learning) vs. social cognition, circadian vs. interval timing, imprinting, song learning, imitation, theory of mind, the various sub-processes of spatial cognition such as dead reckoning, landmark use, beacon homing, the sun compass, the geometric module, magnetic orientation. how and why these qualify as separable modules will be discussed.

Finally, this view implies that cognitive specialization and adaptation - evidence bearing on how cognition has evolved - can be seen in at least three ways. (1) Modules shared among many species because they deal with information important in a variety of niches (i.e. "general processes" such as habituation and associative learning) are tweaked in species-specific, adaptively relevant, ways just as are shared physical structures like beaks, eyes, and feet. Again, very striking examples come from perception, in sensory specializations of bats, owls, electric fish, and so on. To take an exam-ple from memory, birds that store food may have superior spatial memory but remember other kinds of material no bet-ter than other birds. (2) Entire modules may appear in some lineages, making possible ways of dealing with the world that are impossible or very limited otherwise. At the most basic level, species clearly differ enormously in the variety of sen-sory information available to them and the ways in which they can process and act on it. Candidates for cognitive mod-ules present in only some species include bird song and human language, theory of mind, imprinting, cognitive mapping, imitation. (3) Finally, the ways in which output of different modules is combined may vary adaptively. In the simplest case, modules are used one at a time, as when a disoriented rat disregards landmarks and uses geometry. In con-trast, information from different modules may be processed in parallel and then averaged. In associative learning in vertebrates, different sources of information may compete for control as described by the Rescorla-Wagner model, or they may be treated configurally or hierarchically, depending on the circumstances.

This view implies that cognition evolves through specialization of pre-existing, shared, modules, addition of new modules (ideas about how and why this might happen will be suggested), and appearance of new ways of combining information processed by separate modules.

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Primate Worlds

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Much of the early discussion on "primate theory of mind" implied that at issue was the transition to folk psychology; that "mind reading" primates had a theory of mind. In this paper I join a growing group that attempts to map the logical space between being a simple behavior reader and being equipped with folk psychology. In my view, an organism repre-sents a feature of its world, as distinct from merely responding to it, if it can track that environmental feature via more than one kind of proximal stimulus. Arthropods often respond to the world in adaptively complex ways but via a single informa-tion channel. They are (often) cue-bound with respect to the features of the world that matter to them, and only detect and respond to their world. Consider in contrast Mirror Self Recognition. Heyes has rightly argued that MSR does not dem-onstrate possession of a concept of the self. She points out that animals that find their way through physically cluttered environments have to adjust their behavior to the position of their body in space, so they must have a 'body concept' of some kind. Information about their body in space is used to control their behavior. In her view, MSR is just a less usual example of the same phenomenon, and no more shows self-consciousness than does the behavior of a nim-ble bull in a china shop. But while self-recognition does not demonstrate self-consciousness, it does show an ability to track bodily features using unusual perceptual inputs. So animals capable of MSR do not have a cue-bound body con-cept. Their body concept is a real representation of their body, for they can use unusual information channels to update it.

I use this representation/detection distinction to get a fix on representational capacities of primates. A primate re-sponds to the mental state of another if it can track - that is, it responds distinctively with some reliability - to some suite of behaviors that are actually caused by some specific mental state: for example anger or fear. If a bonobo appeases angry behavior by trading sex for peace, it's tracking anger. We investigate whether this is anger detection or anger representation through experimentally probing the robustness of the tracking. In particular, it's detection rather than representation if this capacity is cue-bound. At the same time, we can experimentally investigate the sophistication of this tracking by probing the breadth of the responses to anger. Does the anger-reader adapt to angry behavior differently in environments which cause that behavior to be expressed differently? So this picture defines two separate experimental investigations. We investigate a primate's capacity to represent a mental state by investigating the robustness of its ability to track that mental state. Robustness is the variety of observational cues it uses in tracking. And we can inves-tigate the breadth of its response to tracking. Breadth is the extent to which the tracker's expectations about the agent's behavior or its appropriate response are appropriately modified by the agent's environment and the other mental states the mind-reader tracks.

We can then think of an animal's social intelligence developing via two sorts of behavior rules. Recognition rules are rules that link a reader to tracked mental states. We search for the animal's recognition rules by fixing as far as we can the reader's environment, but varying behavioral cues of a single underlying cognitive state, to see whether the reader gives the same response to these different cues. An animal is mind-reading only if it has, for some mental states, a battery of recognition rules. Output rules are rules governing responses to the states a reader can track. We probe an animal's output rules by fixing the reader's cue, varying the environment, and testing for different responses.

Cumulative cultural evolution

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Many human cultural traditions show an accumulation of modifications over time. This is most readily apparent when material artifacts are involved. For example, upon examination of the shelters built by peoples of a given culture over time, what is typically seen is the adding on of structures for functions (e.g., windows for air and outside vision, doors for privacy, chimneys to eliminate smoke, etc.). We may thus say that the current artifact (including new instantiations) has a "history" that reflects the modifications made by many people over time. Symbolic artifacts such as language and reli-gious rituals have histories of this same type as well, although for obvious reasons they are not so easy to determine in detail. Two essential questions about cumulative cultural evolution of this type are:

(1) Is the process unique to humans? I will address this question by examining the cultural behaviors of human be-ings' nearest primate relatives, especially chimpanzees. I will also seek an explanation for the different types of cul-tural mechanisms observed among primates in terms of the kinds of social cognition employed by the different species.

(2) Does this special form of cultural process have evolutionary consequences? I will address this question by examining some of the characteristics that different types of behavioral and cultural traditions may have in terms of their vulnerability to changes in the physical and social environments for a given primate group.

Gossip and other forms of talk as multilevel cognitive adaptations

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Gossip is culturally universal and accounts for a large fraction of spoken language but it has been scientifically neglected for both conceptual and methodological reasons. We develop a conceptual framework based on multilevel selection theory and an empirical methodology involving the use of fictional gossip events whose elements can be systematically var-ied.

Gossip has been interpreted to benefit both groups (e.g., by enforcing social norms) and individuals (e.g., by deni-grat-ing rivals), and therefore is naturally suited to multilevel selection theory. The study of group-level adaptations has been marked by a decreased emphasis on genetic relatedness and an increased emphasis on mechanisms of social control. Higher-level units such as individual organisms and social insect colonies function as well as they do in part because their elements police each other, preventing forms of cheating that would otherwise be advantageous. Social control provides a way for human groups to function as adaptive units, even when their members are not genetically related, and gossip is one of the foremost mechanisms of social control. It is therefore possible to think about group-serving functions of language in addition to self-serving functions without being guilty of so-called "naive group-selectionism."

Just as an individual mind can be regarded as a cluster of interconnected modules that perform many adaptive functions, language must also perform many different functions to adaptively coordinate the activity of human groups. Three possible group-serving functions are a) policing members of the group, b) establishing the boundaries of the group, and c) evaluating the quality of information. Language must be richly context-sensitive for these and other functions to operate in parallel.

The use of fictional gossip events provides a way to test the predictions outlined above. Our preliminary results suggest that people respond to fictional gossip events much as they respond to gossip in everyday life. By systematically varying the contents of fictional gossip events, we test several hypotheses about the group-serving functions of gossip and other forms of talk.