THE EMERGENCE OF MODERN COGNITION. *Sarah Wurz, Department of Archaeology, University of Stellenbosch, South Africa.*

Paleolithic archaeology presents us with an unique opportunity to investigate the evolution of human cognition or the modern mind. Changes in life history parameters of Homo sapiens ancestors were set in train with the emergence of stone tool technologies and ground dwelling. One of the most important aspects of this process is the enlargement of the brain. Near modern brain capacities were reached by 0.5 million years. Since then there has been selection for the re-organization of the brain and this may have increased the importance of the prefrontal area. Primate morphology and ethology is used to describe the evolutionary circumstances that were driving human encephalisation. The emergence of modern cognition would correlate with a speciation event some 250 000 years ago. It is argued that modern cognition is characterized by the ability to manipulate and communicate in symbols.. Symbolic communication can be traced by symbolic investment in artefact production and products for use in reciprocal exchanges, the use of red ochre as well as the occurrence of distinct regional industries reflecting modern-type linguistic groupings.

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THE NAPOLI SOCIAL LEARNING CONFERENCE

June 30 - July 5, 1998, Naples, ITALY

INTRODUCTION

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In 1898, exactly 100 years prior to the Napoli Social Learning Conference, Edward Thorndike published the first experiments investigating whether nonhuman animals are capable of learning by imitation. The results of these experiments, using cats, dogs and chickens as subjects and apparatus of Thorndike's own, somewhat ramshackle construction, housed in Thorndike's own living quarters (Boakes 1984), led him to a strong negative conclusion that was to have a profound effect on the future of comparative psychology. Thorndike inferred from his data that animals, with the possible exception of primates, could not "from an act witnessed, learn to do the act" (Thorndike 1898).

In striking contrast with this image of the young Thorndike as a struggling, isolated, sceptical scholar, the Napoli conference confirmed that, a century later, social learning is a thriving, progressive, international field of enquiry. In the course of five days, researchers from 13 countries, and at least five disciplines (comparative psychology, behavioural ecology, neurobiology, ethology, primatology) gave talks and presented posters indicating that, after a long gestation period, research on social learning has become not only methodologically sophisticated, but also theoretically integrated with a

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number of domains of enquiry concerned with the evolution of both mind and behaviour. The field is formulating important questions, many quite distinct from Thorndike's preoccupations, and arriving at answers that are both clear and of interest to researchers and scholars working in a variety of disciplines.

Two Thorndikean legacies conspicuously apparent at the meeting were the predominance of experimental and comparative methodologies. Indeed, the official title of the conference, "Social learning and cultural transmission: from invertebrates to great apes and humans. Towards a biological synthesis", emphasised its comparative focus. The proceedings included studies from every major class of vertebrates as well as several invertebrate classes. Such comparative emphasis is historically appropriate, as it was Romanes, another turn of the century scholar interested in social learning, who coined the term 'comparative psychology'.

Printed on the following pages are the abstracts of each oral presentation at the Napoli Social Learning Conference. The abstracts appear under four headings: Cognitive mechanisms of social learning; Functional interplay between individual and social learning; Communication; and Roles of social learning in behavioural adaptation.

The papers on cognitive mechanisms, including studies of chimpanzees, rats, marmosets, starlings, capuchins and pigeons, reflected the growing consensus that "two-action" tests are the most effective means of demonstrating and analysing imitation learning in nonhuman animals. At their strongest, these procedures control for non-imitative varieties of social learning (e.g. stimulus/local enhancement, social facilitation, emulation, observational conditioning) by contrasting the performance of 'observers' that have seen single objects manipulated by a 'demonstrator' (conspecific or human) using different appendages and/or response topographies. Work with this method has indicated that a range of species can imitate.

Current research investigates the degree to which imitative performance reflects cognitive complexity by examining whether animals can acquire by observation information about 'novel' behaviour, and the serial order of actions (Heyes, Huber, Whiten, Zentall). Other contributors in this section argued compellingly that the distinction between individual and social learning has been over-emphasised (Visalberghi, Fragaszy & Galloway), and that associative learning theory has substantial heuristic potential in the investigation of both psychological and neurobiological mechanisms of social learning (Fragaszy, Ray & Heyes).

Consistent with the idea that common mechanisms underlie individual and social learning, papers in the second section reported evidence of social learning in every invertebrate class (Fiorito & Webster; Traniello) and data showing that capacities for individual and social learning are highly correlated within and across a range of bird species (Lefebvre). However, the papers in this section were primarily concerned, not with mechanism, but with the functional interplay between individual and social learning and the ecological variables favouring each. Giraldeau proposes a general framework for research in this area, incorporating a taxonomy of levels of social learning, experimental methods and mathematical modelling techniques. Other contributors, using such modelling techniques (Best) combined with experiments on replicate populations of guppies (Laland, Reader & Laland), provided evidence that the benefits of social learning depend on reproductive strategies, the individual's potential to innovate, and, more generally, the degree to which a species' adaptive landscape permits 'deviation' from the socially-transmitted norm.

Oral presentations concerning communication were as varied as is the topic itself. Both Freeberg, King and West and Gajdon and Stauffacher focussed on the role of social interaction between naive and knowledgeable animals in determining what is communicated. While Gajdon emphasised the importance of understanding the behaviour of the tutor and possible insights that study of 'coaching' might play in understanding animal imitation, Freeberg focussed on the necessity of examining the structure of social interactions to determine where, when and how social learning occurs. Gardner described parallels in the spontaneous acquisition of models' behaviour by infant humans and chimpanzees, while Schuster described studies of cooperative behaviour in animals and their potential contribution to the field. Last, but certainly not least, Susswein reviewed an elegant series of studies of the effect of chemicals released by conspecifics on feeding behaviour and learning and memory processes in Aplysia.

Papers on the functional significance of social learning were equally varied. Ribes-Inesta introduced a Wittgensteinian conceptualisation of cultural learning in humans. The role of social learning in feeding and nest material choice by rabbits (Altbacker & Bilko), in choice of a sexual partner by Japanese quail (Galef & White), and selection of medicinally active plants by African great apes responding to illness (Huffman) each received attention. Perhaps most striking was Huffman's report of painstakingly collected field data indicating local and regional traditions in chimpanzees in the plants

they select for ingestion when ill.

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REFERENCES

Boakes, R. (1984) *From Darwin to Behaviourism: Psychology and the Mind of Animals.* Cambridge: Cambridge University Press.

Thorndike, E. L. (1898) Animal Intelligence: An Experimental Study of the Associative Processes in Animals. *Psychological Review, Monograph Supplement No. 8*, 68-72.

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ABSTRACTS OF PAPERS

COGNITIVE MECHANISMS

THE TIES THAT (MIGHT) BIND. *D.M. Fragaszy, Psychology Department, University of Georgia, Athens, USA.*

Can social learning and neurobiology be combined meaningfully in the same sentence? That depends on what the conversation is about. Social learning, to paraphrase L.-A. Giraldeau, is learning about the value of events, objects, or alternative courses of action, or learning how to achieve certain goals, from public information provided by another. Behavioral biologists distinguish social learning from other forms of learning by the source of information and perhaps the form of information (in the case of actions), but not the nature of the learning process. As B. Galef has pointed out many times, unless one posits a new mechanism of learning not yet imagined by neurobiologists or learning theorists, the same mechanisms (here, the same neural machinery and processes) must of necessity mediate all forms of learning, social and otherwise, in the individual.

Neurobiologists examine the ways neural systems work to achieve functional outcomes for the organism. Neurobiological models of learning span many levels of explanation, from the properties of receptors and membranes, to cell structure organization and patterned activity of circuits or regions. Can social learning be studied meaningfully at the levels of interest to the neurobiologist? Perhaps. It will be most interesting for both behavioral and neurobiologists if it can be. However, claiming something special for social learning at these levels requires distinguishing between social learning and "normal"

The e-mail addresses of corresponding authors and the titles of the 53 posters presented at the Napoli Social Learning Conference, organised phylogenetically according to subject species are available at the following Web site:
http://alpha.szn.it/~gfiorito/social.htm

(asocial) learning. This can be done *only* if there is some detectable and functionally significant difference (at the neural level) between socially provided information and information gained in other ways, as this is the only difference between social learning and asocial learning at the level of the organism. No such differences have yet been proposed, to my knowledge. In my view, if they exist, we are most likely to find them (first) in the organization of patterned activity, as it is the phylogenetically more diverse level of neurobiology, and social learning varies considerably across genera in its likelihood and manifestations.

Drawing from a comparative psychologist's selective familiarity with current neurobiological thinking, I will suggest why socially provided information may differ from other forms of information at the level of patterned activity within and across brain regions or circuits. Perhaps the neurobiologists in the audience will have views on the likelihood of such differences, or will have others to suggest, or ideas about how postulated differences might be identified empirically. Although it is too early for a productive synthesis of the neurobiology of learning and social learning, it is not too early to consider the merits of such a project together. Let the conversation begin!

SOCIAL VERSUS INDIVIDUAL LEARNING: SIMILARITIES AND DIFFERENCES. *E. Visalberghi[1], D. Fragaszy[2] and A. Galloway[2], [1]Istituto di Psicologia, CNR, Roma, Italy, [2]Psychology Department, University of Georgia, Athens, GA, USA.*

In the last few years, social learning has been the focus of renewed interest. We welcome this interest, but are concerned about three major weaknesses in current research. 1) The surge of newly published definitions of social learning phenomena often lack operational criteria. This is problematic for comparisons across species and especially across higher taxa. 2) The biological significance of social learning is not always an initiating focus of research. This is unsatisfactory for behavioral biologists, who, we believe, represent the majority of social learning researchers. Difficulties in interpreting social learning from an evolutionary or comparative standpoint may be overcome by developing metrics of the potential fitness consequences of social learning. For example, biological significance might be measured by the time an individual requires to learn X, or by the rate of transmission of X in a group. Other proposed measures of biological significance examine what is learned, and direction of behavior transmission. 3) Claims that social learning is unique or special in process or outcome are often accompanied by inadequate evidence.

To illustrate these points, we will consider the status of operational definitions, and evidence of both the biological significance and putatively unique properties of documented social influences on feeding. Through the analysis of literature on human and nonhuman primates, domesticated species, birds, and rodents, we will explore whether the initiation of consumption or selection of foods is affected by the feeding activity or food choices of conspecifics.

TRANSFORMATIONAL AND ASSOCIATIVE THEORIES OF IMITATION. *C. M. Heyes, Department of Psychology, University College London.*

Actions vary on a dimension of perceptual opacity. Perceptually transparent actions give rise to similar patterns of sensation when observed and executed, while perceptually opaque actions yield sensory input in different perceptual frames and/or modalities when observed and executed.

The most significant challenge for any theory of the psychological mechanisms of imitation is to explain reproduction of perceptually opaque actions. Theories that have tackled this problem in the last century are of two kinds: Transformational theories suggest that complex (and largely unspecified) operations are performed on sensory input from the model, recoding it for motor output. In contrast, associative theories claim that mapping between sensory input from the model and motor output is achieved on the basis of correlated experience of observing and executing actions or action components.

An Associative Sequence Learning (ASL) model of imitation will be used as a contemporary example of a theory of the latter kind, and it will be argued that the importance of research on imitation of perceptually opaque actions in infants and nonhuman animals lies in its potential to provide evidence favouring transformational over associative theories of imitation.

UNDERSTANDING THE EMERGENCE OF NOVEL FORMS IN IMITATIVE LEARNING. *Ludwig Huber, Bernhard Voelkl and Sabine Rechberger, Institute of Zoology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria.*

The artificial-fruit method was used in a comparative study of movement imitation in marmosets (*Callithrix jacchus*) and keas *(Nestor notabilis*). Regardless of whether the animals had any insight into the causal structure of the foraging problem, they faithfully reproduced the observed technique; solving the problem both faster and with fewer

errors than did control groups not exposed to a demonstrator.

Novelty is commonly used as a cardinal requirement for both insightful imitation and slavish copying. However, neither the learning process nor the experimental analysis allows emergence of novel patterns of behaviour to be identified in an all-or-none fashion. Rather, assimilation and accommodation of functional behavior, during which novel forms emerge, is based on a dynamic process of neuronal re-organization. Consequently, a conceptual shift is required to describe both the effects and the processes of imitative learning. This could be achieved through use of a dynamic systems approach. There is also a need for improved methods for dissecting the mechanisms underlying imitation. This was attempted by employing sophisticated video analysis techniques and mathematical descriptions of movement; the first results of which are presented here.

IMPLICATIONS OF CONTEMPORARY LEARNING THEORY FOR SOCIAL LEARNING RESEARCH. *E. D. Ray and C. M. Heyes, Department of Psychology, University College London, UK.*

It has been assumed that the formation of S-R links, whereby stimuli previously experienced contiguously with the execution of a response come to elicit that response, is either sufficient to explain social learning or, particularly in the case of observational learning, that it is inadequate to do so. Contemporary learning theory conceives of learning rather differently; as the formation and association of mental representations. It is argued that the problems which affected learning theory in the behaviourist era are those which arise in trying to understand social learning today. Therefore, social learning theory might similarly benefit by understanding learning to involve the cognitive processes that contemporary associative learning theory proposes. Conceiving of learning as the acquisition of information has many theoretical and empirical implications for social learning research and these will be illustrated by reinterpreting effects documented in the literature and data from new experiments. For example, a cognitive social learning theory acknowledges that the ability to learn about stimuli confers considerable behavioural flexibility, casts observational conditioning as a functionally important and pervasive social learning process, and suggests that social learning is likely to result in conditioned responses other than matching behaviour. A cognitive social learning theory also predicts the occurrence of socially mediated inhibitory learning.

COGNITIVE ISSUES IN IMITATION. *Andrew Whiten, Scottish Primate Research Group, School of Psychology, University of St Andrews, UK.*

To date, the objective of most imitation research has been simply to establish whether the phenomenon exists in the species studied: relatively little work has explicitly addressed questions of underlying cognition. This applies even to the case of imitation, which is understood to involve a distinctive, but largely unspecified, type of cognition. In this paper I consider a series of cognitive issues in the study of imitation. Empirical material comes principally from new studies of the imitation of "artificial fruit" processing in chimpanzees. The issues analysed are: 1) Copying sequential structure; 2) Copying hierarchical structure; 3) Imitation versus emulation; 4) How novel acts are imitated; 5) The nature of feedback in imitation; 6) Existence of a concept of imitation; 7) The role of imitation in culture; and 8) The role of enculturation in imitation. Empirical results now cast some light on nearly all of these, but the aim of the presentation is also to highlight gaps in our knowledge and discuss possible ways of filling them.

THE SEARCH FOR A THEORY OF IMITATIVE LEARNING IN ANIMALS. *Thomas R. Zentall, University of Kentucky, USA.*

The recent publication of refined demonstrations of imitative learning in a variety of species has led to renewed interest in understanding the mechanisms responsible for this behavior. Imitative learning has been explained by developmental psychologists either in terms of simple learning principles (e.g. instrumental learning), or in terms of complex cognitive principles (e.g. perspective taking). Research suggests that simple learning principles are insufficient to account for imitation. Furthermore, many animals that appear to be capable of imitative learning show little evidence that they are capable of perspective taking, or even mirror-image recognition, proposed by some to underlie perspective taking. Biologists, on the other hand, tend to view the various forms of social learning, including imitation, as genetically predisposed. However, predispositions of the type generally proposed (e.g. contagion) are unlikely to account for the relatively arbitrary nature of behaviour that can be imitated. Although it is likely that imitative learning has been evolutionarily selected in certain species because it allows for rapid behavioural plasticity without the need to suffer the consequences of 'trial and error learning', such an account does little to clarify its underlying mechanisms. An adequate theoretical account of imitative learning in animals remains a challenge to researchers in the this field.

FUNCTIONAL INTERPLAY BETWEEN SOCIAL AND INDIVIDUAL LEARNING

GENES, INDIVIDUAL LEARNING, AND SOCIAL LEARNING. *Michael Best, Massachusetts Institute of Technology, Media Laboratory, Cambridge, MA, USA.*

We studied the relationship between genes, individual learning, and social learning. We started with the simulation environment of Hinton and Nowlan in which individual learning was shown to guide organic evolution towards a difficult adaptive goal. We add to this environment "culture" in the form of social learning via imitation.

Our results demonstrate that when genes and culture cooperate, or enhance one another, culture is able to guide organic evolution towards an adaptive goal. Further, we show that social learning is superior to individual learning insofar as it converges more quickly on the goal than does individual learning. However, the social-learning algorithm results in slower genetic assimilation of adaptive alleles than does individual learning. It is as if, we argue, adaptive values are stored in culture rather then in genes. Finally, we consider when culture and genes pursue diametrically opposed goals. We show that when the two algorithms are opposed, culture, in the form of social learning, is no match for organic evolution with individual learning. In fact, only the most Herculean of social learning algorithms is able to keep a neutralizing toe-hold against the slow, plodding force of organic evolution. Our results suggest that both when in opposition and in agreement, transmission forces, such as the ratio of teacher to learner, are central to the success of social learning. Finally, in new results, we consider the relative force of horizontal, vertical, and oblique transmission modes.

WHEN IS SOCIAL LEARNING ADAPTIVE? *K.N. Laland and K. Williams, Sub-Department of Animal Behaviour, University of Cambridge.*

Social learning is clearly an important adaptation that allows animals to acquire information about their local environments rapidly, efficiently, and at low cost. Moreover, socially acquired information is typically expressed in adaptive behaviour. However, in a changing and variable world, theoretical models suggest that social learners risk picking up outdated or inappropriate information. This talk brings together theoretical and empirical insights to discuss the circumstances under which social learning is adaptive.

In order to fully understand the adaptive significance of social learning distinctions must be made between: (1) the capacity for social learning, (2) the behaviour of an individual influenced by, or resulting from, social learning, (3) the socially acquired information, and (4) the behavioural tradition. Theoretical models have shed light on the circumstances under which a capacity for social learning would or would not be favoured by natural selection. Human learned behaviour is frequently maladaptive, but this is rarely the case for animals, and the difference can be understood in light of findings from evolutionary models. However, animals may frequently acquire and express maladaptive information, and may maintain maladaptive traditions.

What constitutes adaptive behaviour for an individual depends on the behaviour of others. Transmission chain experiments on the social learning of foraging information in guppies provides empirical support for this position. It is concluded that selectively neutral and sub-optimal behavioural alternatives may be maintained as short-term traditions in animal populations.

THE COMPARATIVE ECOLOGY OF SOCIAL LEARNING. *Louis Lefebvre, Department of Biology, McGill University, Montreal, PQ, Canada.*

Comparative studies have identified three types of learning characterized by a robust association between neural substrate, evolutionary co-variates and readiness to learn: parental imprinting, song imitation and spatial memory. Attempts to apply this comparative logic to social learning have produced disappointing results: (1) ecologically-correlated differences in social learning do not appear to be specialized; they also extend to individual learning; (2) intervening variables, like neophobia and tameness, co-vary with differences in learning; (3) ecologically-correlated learning differences may be learned, and not due to divergent natural selection. Similar problems occur if we look at the overall link between learning and the exploitation strategy most logically associated with it, opportunistic generalism. One solution is to bypass captive learning experiments altogether and to test directly in the field the predicted link between opportunistic generalism, neural substrate, and developmental costs. Three new ways to operationalize and quantify opportunistic generalism will be presented: rate of feeding innovations, use of modified habitats, and pair-wise prediction matrices. Field and laboratory reports of social learning could be treated in a similar comparative way, without regard for mechanistic distinctions, in a search for broad evolutionary correlates, either phyletic or ecological.

SOCIAL LEARNING: A BEHAVIOURAL ECOLOGICAL APPROACH. *Luc-Alain Giraldeau, Department of Biology, Concordia University, Montreal, PQ, Canada.*

Learning requires the use, processing, storage and retrieval of information. This information can be used to learn about the value of alternative courses of action or to learn how to accomplish certain tasks. In the context of foraging behaviour, for instance, "learning about" may involve estimating the value of alternative prey types while "learning how" involves acquiring the skills required to handle, find or uncover each prey type.

The information upon which learning how or about depends can come from either of two sources. In one instance, the information originates from an individual's personal transactions with the environment leading to individual, non-social learning. Information can also originate in transactions of other individuals with the environment. Such information is public, in the sense that it is available to all. Social learning involves instances of learning based on the use of public information.

I review instances of social learning how and about, and propose a functional classification of social learning how into three categories: area copying, object copying and behaviour copying. I review some adaptive hypotheses for each, and propose that future studies should investigate the conditions under which these forms of learning are used.

INVESTMENT ASYMMETRIES, INNOVATION AND THE SOCIAL TRANSMISSION OF INFORMATION. *Simon Reader and Kevin Laland, Sub-Department of Animal Behaviour, University of Cambridge, UK.*

Theoretical models of the social transmission of information have tended to neglect the effects of differences in the abilities or propensities of individuals to innovate and learn from others. Evidence from the guppy (*Poecilia reticulata*) suggests that the sex, size and motivational state of an individual can strongly bias both the likelihood that an individual will innovate and the spread of such novel behaviour patterns. We propose that this may be the result of parental investment asymmetries and differences in competitive ability. Since such asymmetries are common to many vertebrate species, similar effects may be widespread and may help to explain why relatively few innovations appear to spread in the wild.

Mathematical models predict that the cumulative number of individuals displaying a novel behaviour will follow a sigmoidal pattern

over time. A sigmoidal diffusion curve may also result from individual variation in asocial learning. However, analysis of the diffusion curves in replicate experimental populations of guppies found the hyperbolic sine function provided the best fit. It is likely that both asocial and social learning processes were operating in these experimental populations. To understand fully the dynamics of information flow, it may be necessary for models to allow for the dual processes of individual and social learning.

THE ECOLOGY AND EVOLUTION OF INDIVIDUAL AND COLONY LEARNING IN ANTS. *James Traniello, Boston University, Department of Biology, Boston, Massachusetts 02215, USA.*

Dividing labor and scheduling tasks such as brood care and foraging according to worker morphology and age has historically been regarded as an example of the programmed simplicity of worker behavior in social insects, such as ants. Recent research, however, has shown that behavior changes adaptively in response to individual experience and the social environment. Task specialization, which is achieved through programmed behavioral development and learning, is thought to improve the efficiency of individual labor and thus colony fitness. Foraging efficiency, for example, has been shown to increase with individual experience in seed-harvesting ants, and individual and colony-level learning and memory appear to be adaptive. Also, colonies of leaf-cutter ants show conditioned feeding responses that are based upon the foraging decisions of scouts that locate new sources of leaves. Additionally, learning at the colony level may concern the recognition of and social response to neighbouring and competing ant species.

Studies of the search behavior of the ant *Formica Scyphozoa* show that worker task specialization and learning ability appear to be influenced by the distribution of food resources in time and space. Resources with different distributions (protein and carbohydrate food) elicit individual search responses that appear to enhance foraging efficiency. In particular, workers tend to concentrate their search effort close to the site of a prior carbohydrate, but not a protein, food load. Resource-related search behaviors appear to be innate and workers cannot be conditioned to increase area-restricted search behavior using consecutive rewards of protein food. Ecology, therefore, seems to set limits on individual learning ability. However, individual ants may increase food collection by stimulating other individuals to forage.

Considering the phylogeny and sociobiology of ants as a whole,

there appears to be an inverse relationship between the degree of social complexity and individual learning ability. Collective action, mediated by chemical signals, may compensate socially for limits on individual learning ability in ants.

A REVIEW OF SOCIAL LEARNING PHENOMENA IN INVERTEBRATES. *Sandra J. Webster[1] and Graziano Fiorito[2], [1]Department of Biological Sciences, McGill University, Quebec, Canada; [2]Laboratorio di Neurobiologia, Stazione Zoologica 'Anton Dohrn', Napoli, Italy.*

Most of the current literature on social learning focusses on vertebrate species. This paper reviews evidence of social facilitation and/or social learning in invertebrates. Our principal goals are to increase awareness of social learning phenomena in invertebrate groups, ranging from the simple Planaria to molluscs and arthropods, and to modernise their scientific interpretation. We will emphasis contrasts between the original interpretative frameworks and our contemporary view, and we will propose a potential "model" preparation for the investigation of invertebrate social learning.

COMMUNICATION

PROBING THE DEEP STRUCTURE OF SOCIAL EXPERIENCE: STUDIES OF THE DEVELOPMENT OF COMMUNICATING. *T.M. Freeberg, A.P. King and M.J. West, Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA; Department of Biology and Psychology, Indiana University, Bloomington, IN 47405, USA.*

Studies of the role of social learning in the development of avian communication have typically uncovered only the surface structure of social influences. Here we argue for probing deeper structures of social influences in studies of effects of social experience on vocal development and, more generally, in studies of social learning in animals. Traditionally, both "endpoint" and developmental studies of vocal ontogeny have focussed solely on the vocal signal itself. We believe researchers must broaden their focus to include the development of communicating, of which vocal signals are but one part. Assessing the development of communicating with the goal of elucidating the deeper structures of social experience requires that we study the very social interactions that induce, facilitate, and/or maintain

communicative competence in individuals. Study of these social interactions requires intensive analyses of individuals while communicating both as signallers and as receivers within their social group. Such analyses are no small task. However, we present data from previous and ongoing work with Brown-headed Cowbirds *(Molothrus after)* indicating that documenting deeper structures of social experience is absolutely necessary for full understanding of how, when, and perhaps why, social influences affect the development of both communication and communicating.

SHIFTING ATTENTION FROM QUESTIONS CONCERNING NAIVE ANIMALS TO QUESTIONS CONCERNING TUTORS- A NEGLECTED TOPIC IN SOCIAL LEARNING? *GK. Gajdon and M. Stauffacher, Swiss Federal Institute of Technology ETH, Institute of Animal Sciences INW, Schwerzenbach, Switzerland.*

Most studies in social learning focus on the bystander side of the bystander-tutor system. Research is, to a great extent, concerned with the cognitive level on which one animal learns from another. Tutors constitute an alternative, yet equally important, topic. Neglect of the role of the tutor in social learning is reflected in the fact that few studies are concerned with teaching. Examining corrective intervening behaviour ('coaching') suggests that there might be a link between limited knowledge of this form of teaching and the paucity of evidence for imitation. Common to both imitation and coaching is comparison of one's own behaviour with the perceived behaviour of a conspecific .

Lack of evidence for imitation seems to reflect an insensitivity to details of the performance of others. Why then should animals show such a sensitivity when coaching others? In fact, evidence of coaching is rare in animals. Research to determine whether animals even recognize a companion's mistakes would help to understand the lack of evidence of coaching. Further, if even animals that already know a behaviour pattern don't recognize divergence in the same behaviour pattern in other animals, evidence would be provided that imitation exceeds the animal's cognitive abilities. Another question is: What characteristics define the most effective tutors for which class of bystanders? Once best tutors are defined, experiments using such elite tutors, as well as especially competent bystanders may improve our understanding of the range of social learning abilities in animals.

THE FUZZY LOGIC OF SOCIAL LEARNING. *R. Allen Gardner, University of Nevada, USA.*

Human children incorporate adult routines into their developing repertoires. Incorporation is usually partial and often fragmentary. Precise replication is unnecessary, often impossible, and probably unwise. Incorporation appears throughout ethology. Young birds must hear adult songs, but only incorporate elements into their own developing repertoires. Chimpanzees, cross-fostered in human homes, begin by incorporating fragments of adult routines. The chimpanzees' routines develop in a pattern much like that seen in human development. For example, after observing adults sweeping, infant chimpanzees, like children, begin by riding on the broom as an adult sweeps the floor or by helping to push the broom. Gradually, the chimpanzees and children develop into effective sweepers and work independently at the task. This paper focuses on a pattern of incorporation and expansion that fits the fuzzy logic of modern science better than the Aristotelian tradition of logic-tight categories.

THE COOPERATIVE BEHAVIOR OF DYADS. *Richard Schuster, Department of Psychology, University of Haifa, Israel.*

Many species engage in a type of cooperation, often termed mutualism, whereby individuals learn to coordinate behaviors for joint outcomes. According to theories in evolutionary biology, psychology and game theory, cooperation is expected when individuals experience more favorable outcomes when cooperating than when behaving alone. Field studies of mutualisms, however, sometimes fail to confirm that all participants benefit, raising questions about why and how animals cooperate. Our research asks whether part of the answer resides in social relationships and their consequences that cannot be addressed with experimental designs using animal or human subjects that minimize social interactions by isolating subjects in separate chambers. Using laboratory rats, pairs are rewarded for coordinating movements within a shared chamber. Coordination strategies emerge that typically incorporate asymmetries expressed in aggressive dominance, initiation of interactions, and division of obtained outcomes. These dyadic relationships influence the roles adopted by cooperators, the attractiveness of outcomes, competition over outcomes and choice between cooperation and individual action. We will be examining within-pair differences in physiological states associated with these asymmetries. More generally, this research addresses the design of laboratory paradigms appropriate for studying why and how cooperative behavior varies across individuals, sex, age and species.

SOCIAL STIMULI AFFECT MANY ASPECTS OF LEARNED AND UNLEARNED BEHAVIOR IN APLYSIA FASCIATA. *A.J. Susswein, M. Schwarz, S. Blumberg, M. Levy, I. Ziv, T. Haran and S. Markovich, Department of Life Sciences, Bar Ilan University, Ramat Gan, Israel.*

Aplysia fasciata are highly social animals. They sense one another's presence via the chemosensory rhinophores, which respond to pheromones affecting many behaviors. A number of peptides thought to be pheromones are synthesized and released from various tissues in the reproductive tract. Aplysia react differently to newly introduced individuals and to individuals to which they have been previously exposed, suggesting that they can distinguish novel and familiar conspecifics. One effect of pheromones is to facilitate feeding behavior. Pheromones also modulate performance in an instrumental learning task affecting feeding. In this task, animals stop responding to a palatable food which is too tough to eat. Long-term memory is shown by a decreased responsiveness 24 hours after training. Isolating animals from conspecifics during training obstructs learning, and isolating them for an hour after training blocks long-term memory. The effects of isolation are reminiscent of the modulation of learning and memory by trauma or stress in vertebrates, suggesting that social isolation in A. fasciata may be an analog of stress. In mammals, stress-evoked modulation of memory is affected by a number of modulatory neurotransmitters. These transmitters also modulate the neural circuitry controlling Aplysia feeding. Many neurons initiating and organizing Aplysia feeding are identified, opening the possibility of examining the physiological basis of how social stimuli affect learning and memory.

ROLES OF SOCIAL LEARNING IN BEHAVIOURAL ADAPTATION

FOOD PREFERENCES IN THE EUROPEAN RABBIT: LONGEVITY, DURABILITY AND ECOLOGICAL SIGNIFICANCE OF SOCIAL LEARNING. *V. Altbacker and A. Bilko, Department of Ethology, Eotvos University, Hungary.*

We have previously demonstrated that a rabbit mother's diet can influence her pups' food preferences at weaning. Supplementing a mother's diet during pregnancy and lactation with either 10% juniper berries or thyme leaves resulted in preference for that plant when weanling animals were tested in a three-choice situation. However, there was a rapid decrease in preference, presumably as a consequence of eating the less-nutritious, aromatic plants. We determined whether this decrease could be prevented by reducing the amount of aromatic