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# 1 Evolutionary Psychology in the Round

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When I first encountered the term “evolutionary psychology,” I thought it referred to the study of how mind and behavior have evolved. But I was mistaken. In the last decade, evolutionary psychology has come to refer exclusively to research on human mentality and behavior, motivated by a very specific, nativist-adaptationist interpretation of how evolution operates (e.g., Cosmides and Tooby, 1994; Buss, 1999; Daly and Wilson, 1999). This is a strange, anthropocentric usage, akin to identifying human biology with “biology” generally, or describing geography as “astronomy.” This book is about evolutionary psychology more broadly and more transparently construed; about evolutionary psychology “in the round.” It encompasses the behavior and mentality of nonhuman as well as human animals, and a full range of contemporary evolutionary approaches. Rather than a campaign volume by and for the like-minded, it is a debate among authoritative researchers about the ways in which evolutionary processes have shaped cognition.

The debate is presented under five broad section headings: Orientations, Categorization, Causality, Consciousness, and Culture. In the first of these, the chapters by Huber, Shettleworth, and Bitterman provide general arguments in favor of distinct conceptual and methodological approaches to investigating the evolution of cognition: phylogenetic, ecological, and psychological/comparative. In each of the remaining chapters, the author(s) adopt one or a combination of these approaches in addressing a specific issue, or set of issues, relating to the evolution of cognition.

The chapters on “Categorization” are concerned with how various animals parse their environments, how they think about, or represent, objects and events and the relations among them. Those chapters under “Causality” focus on a particular kind of relationship, that of cause and effect, asking which nonhuman animals, if any, represent this kind of relation, and how they do it. The discussions of “Consciousness” consider whether it makes sense to talk about the evolution of consciousness, and how, if at all, this phenomenon can be investigated in nonhuman animals. The final section, on “Culture,” examines the cognitive requirements for nongenetic transmission of information, and the evolutionary consequences of such cultural exchange.

To help readers follow the debate, each contribution cross-references other chapters and concludes with an abstract-like summary. In addition, each section begins with a short overview identifying the main points of agreement and disagreement among the contributors to that section, and among their views and those expressed elsewhere in the volume.

The purpose of this introductory chapter is both to integrate and to propose. It addresses three elementary questions about the evolution of cognition, surveys the

various answers offered by the contributors to this volume, and, at the end, combines these in a general hypothesis about the evolution of cognition. The questions are: What is cognition? What is the difference among "different" cognitive processes? What makes research on cognition "evolutionary"?

### What Is Cognition?

Fortunately, a rough and ready definition is sufficient to support interesting research on the evolution of cognition, and for the present purposes I need only outline what most of the contributors to this volume assume about the nature of cognition, and to identify points of potentially confusing contention.

Most of the authors would probably agree that cognitive states and processes are (1) theoretical entities, which (2) provide a functional characterization of operations of the central nervous system, (3) may or may not be objects of conscious awareness, (4) receive inputs from other cognitive states and processes and from perception, and (5) have outputs to other cognitive states and processes and to behavior.

Regarding cognitive states and processes as theoretical entities that cause behavior distinguishes cognitive psychology from most varieties of behaviorism, and emphasizes that, unlike behavior or neural tissue, they cannot be observed directly. Hypotheses about cognition can be evaluated only by testing their predictions regarding the effects of various environmental manipulations on behavior. These theoretical entities are said to provide a functional characterization of the central nervous system (CNS) to flag the fact that most of contributors to this volume assume that the same cognitive process could be implemented or instantiated in a variety of different neuroanatomical structures or neurophysiological processes. In other words, this characterization of cognition is materialist, but it does not assume a simple one-to-one mapping between cognitive and neural states and processes. Similarly, although the foregoing characterization of cognition allows that some cognitive processes may be conscious, and that their subjective status may depend on their functional role, it does not identify cognitive processes with conscious processes; consciousness plays no part in the definition of what is and is not cognitive.

Dickinson and Balleine, Bitterman, and Shettleworth are the only contributors to this book who clearly depart from the usage outlined above. Dickinson and Balleine prefer to reserve the term "cognitive" for processes that support *goal-directed* behavior, excluding, for example, associative learning from the cognitive domain. Bitterman and Shettleworth, on the other hand, favor more inclusive definitions of cognition. Bitterman equates it with "knowing" in the classical sense of the term,

encompassing perception, learning, and understanding," whereas for Shettleworth cognition subsumes "all mechanisms that invertebrates and vertebrates have for taking in information through the senses, retaining it, and using it to adjust behavior to local conditions." These characterizations are incompatible with (4) and (5) above, which imply that cognitive processes are distinct from perceptual processes that are directly involved in dealing with sensory input and motor processes responsible for preparing effector movements. These dissenting voices highlight a truism: it matters little how we label our distinctions, but we would be unwise to let them get lost. Points 1–5 above circumscribe a set of properties of the CNS that are physically related to, but conceptually distinct from, its neurobiological and behavioral properties. Whether we label these properties "cognitive," "mental," or "intelligent" is unimportant in itself, but if we were to lose sight of their distinctiveness, there would not only be confusion, but research on the evolution of cognition/mentality/intelligence would move outside the domain of contemporary psychology. It would be reduced to an examination of the way in which evolution has affected nervous systems and motor physiology.

Similarly, it doesn't really matter whether we call associative learning or perceptual processing "cognitive" or "noncognitive information processing," but we should be alert to the possibilities that the processes on either side of these divides show different evolutionary patterns. For example, over evolutionary time, associative learning may be more conservative, and perceptual processing more labile, than (other) cognitive processes.

### What Are the Differences Among "Different" Cognitive Processes?

#### Carving Cognition

The first question asked how we distinguish cognitive from other processes; the second examines how we distinguish one kind of cognitive process from another. The capacity to do this, the possession of conceptual knives that will carve cognition rationally and reliably into distinct pieces, is especially important in the context of an evolutionary analysis. At the most general level, evolutionary analysis uses synchronous patterns of similarity and diversity to infer historical continuity and change. Clearly, this cannot be achieved in the case of cognition unless we can work out where one kind of cognition stops and another begins.

All of the contributors to this volume carve cognition into different types, but few comment on the knives they are using, on what they consider to be the differences among different cognitive processes. If we first consider the pieces, we find that they

come in a range of shapes and sizes. At one extreme, Shettleworth mentions at least 14 types of cognition: spatial memory, circadian timing, interval timing, dead reckoning, landmark use, imprinting, song learning, motor imitation, associative learning (and components thereof), social intelligence, theory of mind (and components thereof), language, reasoning about social obligations, and consciousness. At the other extreme, several authors carve the cognitive pie into conscious and unconscious processes (Clayton et al., Heinrich, Humphrey, Macphail), and/or into two or three pieces, one of which corresponds loosely with what Shettleworth calls associative learning. Thus, Bitterman, Delius, and Huber distinguish associative learning from conceptual thought (and, in the case of Huber, from language); Dickinson and Balleine, Dunbar, Macphail, Rumbaugh, and Tomasello contrast it with the representation of intentional relations (and, in the latter case, with representation of relations more generally); Mackintosh leaves out representation of intentional relations and contrasts associative learning, based on invariant feature detection, with representation of relations generally; and Bateson opposes "learning involving external reward" with recognition learning. Dichotomies that apparently have nothing to do with associative learning are mentioned by Clayton et al. (remembering facts vs. personal experiences) and Sterelny (representing mental states vs. behavior); lists of cognitive processes, similar to, but shorter than, Shettleworth's can be found in the chapters by Lefebvre (spatial memory, imprinting, song learning, [associative?] learning, and imitation, but *not* social learning) and by Richerson and Boyd (decision making, [associative?] learning, social learning, imitation, and language).

This range of methods of carving cognition is representative of contemporary research on the evolution of cognition, and some of the diversity is almost certainly due to substantive disagreements about evidence. From a scientific perspective, these are the interesting disagreements, the unresolved empirical questions, but they are difficult to isolate from the diversity due to the use of different knives, different principles of classification. For example, circadian timing, interval timing, dead reckoning, and landmark use fall within Shettleworth's inclusive definition of cognition, but others may regard them as noncognitive, perceptual processes. In this example, it is the cut between cognitive and noncognitive processes that is at issue, but some of the remaining variation may be due to the use of different knives to distinguish among processes that are agreed to be cognitive.

#### What/When and How Rules

Extrapolating from the shapes and sizes of their pieces of cognition, and from occasional comments about principles of classification, it seems that the contributors to this volume, and evolutionary psychologists more generally, are using two sorts of

blades to carve cognition: "What/when" and "how" rules. What/when rules distinguish types of cognition according to their content (defined by inputs to or outputs from cognitive processes) and/or the time in ontogeny when they typically operate. How rules, by contrast, distinguish types of cognition in terms of the abstract principles (more or less formally specified) that characterize the way in which content information is processed.

When birdsong learning is identified as a distinct variety of cognition, it is primarily on the basis of a what/when rule something like, "Conspecific song, first season" (e.g., Catchpole and Slater, 1995). It specifies the content of what is usually learned (species-typical song) and when in ontogeny this learning usually takes place. Describing a cognitive process as "domain specific" (e.g., Shettleworth, this volume), implies that it is distinct *at least* in terms of its what/when rules. An example of a formally specified how rule is the Rescorla-Wagner equation (Bush and Mosteller, 1951; Rescorla and Wagner, 1972; Bitterman, this volume). How rules are what Sherry and Schacter (1987) describe as "rules of operation," Bitterman (this volume) as "equations," and Bateson (this volume) as "design rules."

#### Examples

Closer examination of two examples of behavior will, I hope, clarify the distinction between what/when and how rules. If the first, snake fear learning in rhesus monkeys (e.g., Cook and Mineka, 1990), is based on a distinctive type of cognition, then it is distinctive in terms of its what/when rules. The second, same-different categorisation by Alex the parrot (Pepperberg, 1987), seems to be based on a cognitive process with distinctive how rules.

**Snake Fear** Cook and Mineka (1987, 1989, 1990) have shown that rhesus monkeys acquire fear of snakes more readily than fear of flowers through exposure to a conspecific behaving fearfully in the presence of the target stimuli, that is, snakes or flowers. To check whether this effect is due to the content or identity of the stimuli (snakes vs. flowers), rather than to the differential salience of the snake and flower stimuli employed (e.g., differences in color or brightness), they did an experiment in which snake and flower stimuli were paired with food rather than fear (Cook and Mineka, 1990, experiment 3). They predicted that if the fear effect was due to differential salience, the monkeys would still learn about the snakes more readily than about the flowers, but that if it was due to the identity of the stimuli, they would, if anything, learn more slowly that the snakes signalled a positive event.

In each trial in this experiment, a monkey was shown one of four pairs of stimuli on a video screen. If it reached toward one of the stimuli (+) it was rewarded with

food; reaching toward the other was not rewarded (-). Thus, the monkeys had four discrimination problems: coiled snake + / red square - (snake positive); long snake - / red square + (snake negative); chrysanthemums + / blue diamond - (flower positive); silk flowers - / blue diamond + (flower negative). The results indicated that the monkeys solved the flower problems at least as fast as the snake problems, and in some cases the flower problems were solved more quickly.

There are three things to note about this example. First, it does not show that the cognitive process underlying snake fear in monkeys differs in terms of its how rules from the kind of associative learning mediating (other) Pavlovian conditioning. Indeed, snake fear acquisition is subject to the overshadowing and latent inhibition effects (Mineka and Cook, 1986; Cook and Mineka, 1987; Heyes 1994) that are characteristic of Pavlovian conditioning more generally, and which have played a key role in the formulation of its how rules.

Second, snake fear acquisition is a distinct form of associative learning in terms of its what/when rules only if it is the content, not the salience, of the snake stimuli that is responsible for faster learning. Thus, not all variations in learning that are typically described as "quantitative" rather than "qualitative," or as being due to changes in "constants" rather than "equations" (Bitterman, this volume), provide evidence of cognition with distinctive what/when rules. More generally, the what/when vs. how distinction is *not* equivalent to the quantitative vs. qualitative distinction.

Finally, the snake fear example illustrates how difficult it can be to find out whether different rates of learning about stimuli are due to the identity, rather than the salience of the stimuli. Even the results of Cook and Mineka's (1990) subtle experiment do not show this conclusively because (1) the snake and flower stimuli in this study were not identical to those used to test observational conditioning of fear, and (2) the monkeys were required to discriminate snakes and flowers from different, arbitrary stimuli. It may have been more difficult to discriminate the red square from the snake stimuli than to discriminate the blue diamond from the flower stimuli and, if this was the case, the monkeys might have solved the snake problems more slowly even if the snake stimuli were more salient than the flower stimuli.

**Alex the Parrot** Pepperberg's African Grey parrot, Alex, appears to be able to represent relations among objects in what could be described, for the want of a better word, as an "abstract" way (Pepperberg, 1987; Mackintosh, this volume). In the training phase of the relevant experiment, Alex was shown pairs of objects varying in color, material, and/or shape (e.g., a red wooden triangle and a blue wooden oval), and asked, in spoken English, "What same?" or "What different?" In the former case

he was rewarded for naming a dimension on which the stimuli had a common attribute (material), and in the latter for naming a dimension on which they had different attributes (e.g., color or shape). Alex not only succeeded in learning these discriminations, but was accurate on 82 percent of transfer trials involving novel objects (e.g., a gray wooden cube and a gray woollen ball).

The process forming Alex's representations of similarity and difference (but not necessarily that linking these representations with the experimenter's questions and with reward) seems to have how rules distinct from those that characterize Pavlovian conditioning. These equations (see Dickinson, 1980 for a survey) cannot fabricate from absolute values of stimuli (e.g., redness) a representation that does not function according to its absolute values. Thus, when Alex is shown two red objects, Pavlovian processes would allow him to represent double-redness, but not in a way that he spontaneously, without further training, treats as equivalent to double-greenness. However, there is no reason to suppose that the processes mediating Alex's representation of relations are distinctive in terms of their what/when rules, no evidence that he is able to represent relations among only a subset of the stimuli he can perceive, or that he has used this capacity more during a certain phase of his ontogeny than at other times. The foregoing experiment involved arbitrary stimuli and was conducted when Alex was already mature.

In both of these examples and in many others, associative learning of the kind that mediates Pavlovian conditioning features as a kind of bench mark, as that from which potentially distinct cognitive processes are shown to differ. There are probably two sound reasons for this, as well as a third that is more contentious. The first reason is pragmatic: the how rules of associative learning are relatively well specified, and therefore in many cases the only evidence currently available that *different* how rules underlie a behavior, is that the behavior in question cannot be explained with reference to associative learning. The alternative rules have not been formulated. Second, there is evidence to suggest that the capacity for Pavlovian associative learning is present in a very broad range of vertebrate and invertebrate species (e.g., Bitterman, this volume; Mackintosh, this volume; Macphail, this volume), and therefore it is a natural contender to explain a broad range of behaviors. Third, it is sometimes claimed that it is more "parsimonious" to attribute behavior to associative learning than to an alternative cognitive process (e.g., Macphail, 1985). This reason is problematic if, going beyond the second, it assumes that associative mechanisms are necessarily simpler than nonassociative processes, or that evolution is so conservative that any behavioral adaptation that *can* be achieved by associative learning *will* be so achieved (Sober, 1998).

### Inferring How from What/When

Most of the varieties of cognition discussed in this book seem, on the surface, to be circumscribed by their what/when rules. The names they are given identify a category of environmental input (e.g., spatial memory, circadian timing, interval timing, landmark use, song learning, social learning, social intelligence, reasoning about social obligations, language), of cognitive product (e.g., representations of relations, intentional relations, behavior, and mental states; remembering facts and personal experiences; decision making; recognition learning), or of behavioral product (e.g., imprinting, imitation, language). Possible exceptions are associative learning, conceptual thought, theory of mind, and consciousness, but even some of these can be construed as characterizing types of information processed rather than processing operations.

This way of labeling types of cognition may give the impression that what/when rules are considered more important than how rules, but the reverse is true. The vast majority of contributors to this volume, and to research on the evolution of cognition generally, use differences in what/when rules as markers for putative differences in how rules, and consider distinctions of the latter kind to be of primary significance in evolutionary analysis. Shettleworth makes this priority very clear: "When distinct classes of input (domains) are computed on in distinct ways as inferred from behavior, we have a distinct mental module or memory system. Computational distinctiveness is the primary criterion for cognitive modularity." Other contributors are less explicit, and do not use the language of modularity, but they seem to have a common purpose. For example, it is unlikely that Tomasello would distinguish "intentional/causal cognition" from understanding the relationship between one's own actions and their outcomes if he believed that these two differ only in terms of what is understood, and not with respect to how that understanding is achieved.

In addition to being used as markers for distinctive how rules, what/when rules are sometimes used to infer the existence of distinctive how rules. A what/when rule acts as a simple marker if, of the many slices into which cognition could be cut by characterizing its inputs or products, a researcher delineates only those types that he or she believes, on the basis of independent evidence, also to be distinctive in terms of their how rules. By contrast, a difference in what/when rules is used to infer a difference in how rules when the former is itself treated as evidence of the latter.

The chapters in this book suggest that differences in how rules can sometimes be inferred from differences in the kind of what/when rules that circumscribe cognitive products (e.g., understanding causality, representing relations, representing intentional relations), but rarely if ever from what/when rules that characterize envi-

ronmental inputs (e.g., social learning) or behavioral products (e.g., imprinting). In the former case, it requires painstaking empirical work (e.g., Delius, this volume; Dickinson and Balleine, this volume; Mackintosh, this volume) to establish that the cognitive product is really of the specified kind—for example, that the animals in question are really representing causality, relations, or intentional relations—but, if this information can be secured, in conjunction with knowledge of inputs, it may provide the basis for inferring the presence of distinctive how rules. This is possible because in principle one can work out which how rules could, and which could not, generate specified outputs from specified inputs.

In contrast, at least three chapters in this volume (Bateson, Clayton et al., and Lefebvre) make it clear that, as they are currently circumscribed, how rules do not coincide with behavioral products and environmental inputs in a way that allows the former to be inferred reliably from the latter. Bateson's model of imprinting implies that this type of cognition differs from (other) recognition learning in terms of its what/when rules, but not in terms of its how rules. The experiments reported by Clayton et al. raise the intriguing possibility that spatial memory in food-storing birds, although it is distinctive in terms of what is remembered (cache locations) and when encoding takes place (during seasonal gluts), occurs via the same how rules as episodic memory in humans. Similarly, Lefebvre's demonstration that social learning ability covaries with (other) learning ability suggests that, at least in avian taxa, these two may differ in terms of whether their environmental inputs are or are not from social interactants, but not in their how rules.

Covariation between neural substrates and behavioral product or environmental input what/when rules is commonly interpreted as support for the suggestion that the former characterize important differences among cognitive processes. For example, Lefebvre (this volume) argues that the association of distinctive neural substrates with spatial memory in food-storing birds (hippocampus), parental imprinting (left intermediate medial hyperstriatum ventrale), and birdsong learning (high vocal center) contributes to making these what/when types of cognition more distinctive than social learning. This is undoubtedly true, but not because the discovery of a distinctive neural mechanism necessarily indicates that what/when rules are coincident with how rules. This would be the case only if we assumed that different neuro-anatomical structures necessarily implement different cognitive rules of operation, and that differences in what/when rules alone could not be associated with distinctive neural substrates; this assumption does not appear to be warranted. For example, food-storing birds may have larger hippocampi than related, nonstoring species (e.g., Clayton and Krebs, 1994; Clayton, 1996), not because the spatial memory of storing species operates according to distinctive how rules, but because in these birds a

system using how rules common to storing and nonstoring species processes a large volume of information about the locations of food caches. Covariation between what/when rules and neural mechanisms is significant, not as a short cut to discovering diversity in how rules, but in its own right; as an indicator of the effects of evolution on what/when rules of cognition.

Addressing the question "What is different about 'different' cognitive processes?" I have suggested that the contributors to this volume use a combination of what/when and how rules to distinguish types of cognition, and that most or all of them consider distinctions based on how rules, on the way in which information is processed, to be primary, and use differences in what/when rules as markers for these distinctions, or as a basis for inferring how rule diversity. Thus, at root, the authors that postulate different ranges of cognitive processes disagree about the variety of how rules found in the animal kingdom, and it is unlikely that these disagreements can be resolved except by generating hypothetical how rules for various categories of behavior and testing them empirically against other such rules. At present, research of this kind typically examines whether behavior can or cannot be explained in terms of how rules of Pavlovian associative learning, but there is no reason in principle why other how rules should not be formulated and tested.

The current preoccupation with differentiating cognitive processes according to their how rules is understandable in historical context. It may be a healthy reaction to the many years in which the "general process" tradition denied the existence of any such diversity, and the subsequent period in which "biological boundaries" or "constraints on learning" approaches fought for the recognition of what/when variation (e.g., Johnston, 1981). However, there is a risk of over-compensation, of exaggerating the extent of how rule diversity, and of underestimating the potential contribution to behavioral adaptation of what/when variation alone.

#### What Makes Research on Cognition "Evolutionary"?

All of the contributors to this volume subscribe to a broadly Darwinian account of evolution. Within this, however, at least four evolutionary approaches to the study of cognition are discernable. For convenience, I will call them the ecological, phylogenetic, comparative, and selection theoretic approaches.

#### Ecological and Phylogenetic

The ecological and phylogenetic approaches are, to a significant degree, complementary. Each has historical roots in ethology, and proceeds from a known fact

about evolution. The ecological approach focuses on the fact that evolution tends to produce adaptations, phenotypic characteristics that enable organisms to survive and reproduce in their unique environments; the phylogenetic approach emphasizes descent rather than adaptation. It concentrates on the fact that the phenotype of a given taxon depends not only on the selection pressures to which *those* animals or plants have been subjected, but also on the genetic variants that they inherited from their ancestral species.

As a consequence of this difference in emphasis, the two approaches seek evidence of different evolutionary footprints on cognition. The ecological approach anticipates that a species' cognitive capabilities will be correlated with the demands of its natural environment, and investigates the character and specificity of this correlation—which cognitive characteristics are tuned to environmental demand, and with what degree of precision. The phylogenetic approach, on the other hand, aims to chart the way in which cognitive capabilities vary with phylogenetic relatedness—to identify where in evolutionary lineages major cognitive change has occurred, and to specify the nature of these changes.

None of the contributors to this volume would deny that there are likely to be both ecological and phylogenetic trends in the evolution of cognition. Both patterns are so clearly apparent in the evolution of morphological, anatomical, and physiological characteristics, that, when we turn to cognition and behavior, the challenge is not to discover whether they are both present, but to uncover their relative contributions to particular cognitive characteristics in particular regions of the phylogenetic tree. Consequently, none of the chapters in this volume represent the ecological approach, or the phylogenetic approach, in pure form. However, Huber concentrates on the phylogenetic approach, examining its historical roots in the work of Konrad Lorenz and illuminating some of the methodological problems that make it difficult to pursue. Shettleworth, at the editors' request, makes a strong case in favor of modularity, a contemporary variant of the ecological approach.

The modularity approach is characteristic of what is currently known as "evolutionary psychology." In common with other ecological approaches, it is concerned with behavioral adaptations, but the modular approach is distinctive in that it attributes them to psychological mechanisms with specific properties. These psychological mechanisms or "modules" are thought to be "domain-specific," to have distinctive what/when rules, *and* to have distinctive how rules. Following Fodor (1983), it is often also assumed that modules are innate, have distinctive neural substrates, are automatically activated by input from the relevant domain, and are "informationally encapsulated." This means, roughly, that modules are relatively impermeable to information from central or more general cognitive processes.

The broader ecological approach is represented in the chapters by Bateson, Clayton et al., Dunbar, Heinrich, Lefebvre, Sterelny, and Tomasello. Bateson's topic, imprinting, is defined by its role in behavioral adaptation, and Clayton et al. were motivated to seek evidence of episodic memory in scrub jays by reflection on the demands of their natural ecology as food-storing birds. Dunbar, Heinrich, Sterelny, and Tomasello all express some support for the "social intelligence" or "social function of intellect" (Humphrey, 1976) hypothesis, the idea that complex social environments are a powerful stimulus for the evolution of complex cognitive capacities, and Lefebvre examines the relationship between an ecological variable, distribution of food resources, and learning and innovation in birds. However, like Dunbar's and Tomasello's chapters, Lefebvre's discussion also subsumes the phylogenetic approach, and integrates it with an ecological analysis. Dunbar and Tomasello are concerned with cognitive transitions in the primate lineage; Lefebvre examines avian taxa.

### Comparative

The comparative approach to the study of cognition is represented in this volume by Bitterman, Dickinson and Balleine, Delius, Mackintosh, and Macphail. Practitioners of this approach focus intensively on the how rules of cognition (e.g., associative learning, conceptualization, goal-directedness), study them with a high level of methodological rigor in a few nonhuman taxa (including rats, pigeons, rhesus monkeys, honeybees, ravens, goldfish, and chimpanzees), and compare the results, implicitly or explicitly, with each other and with what is known about human cognition. The outcome of this comparison process, unlike those of the ecological and phylogenetic approaches, is more commonly the discovery of similarities than of differences. But, while the comparative approach emphasizes evolutionary continuity over evolutionary diversity, and the role of ontogeny rather than of phylogeny in behavioral adaptation, it is no less "evolutionary" than the other approaches.

### Selection Theoretic

The selection theoretic approach, represented in this volume by Lefebvre, Richerson and Boyd, and Wilson et al., has much in common with the ecological approach. Like the latter, it is preoccupied with adaptation, with the fit between animals' behavioral and cognitive traits and the demands of their natural environments. However, the selection theoretic approach argues that this fit arises not from just one evolutionary process, natural selection operating on genetic variation, but from several (e.g., Campbell, 1974; Plotkin and Odling-Smee, 1981; Campbell et al., 1997; Sober and Wilson, 1998; Wilson et al., this volume). An evolutionary selection process, a

process involving variation and selective retention, operates not only on genetic variation, that is, at the phylogenetic level, but also at ontogenetic and cultural levels. In the ontogenetic case, cognitive variants—contents or processes of thought—arise from interaction between an individual animal and its environment, and are selectively lost/forgotten or retained/remembered according to the consequences of their behavioral expression for that individual. At the cultural level, the cognitive variants are contents or processes of thought characteristic of groups of individuals, and normally acquired by individuals through social interaction. They are generated within the group, or via the group's interaction with its environment, and selected according to their success in being transmitted to new individuals or groups, which may or may not be or contain biological descendants of the previous cultural generation. Thus, cultural selection may or may not constitute group selection (Sober and Wilson, 1998), and variants that are relatively successful in cultural selection may or may not enhance the reproductive fitness of the individual or group (Boyd and Richerson, 1985).

According to the selection theoretic approach, these ontogenetic and cultural processes are evolutionary in three senses: (1) Phylogenetic evolution, natural selection operating on genes, has shaped the cognitive processes that make them possible. (2) They make autonomous contributions to cognitive and behavioral adaptation. That is, phylogenetic evolution alone could not achieve the same degree of fit between cognitive systems and their environments, *and* ontogenetic and cultural processes sometimes perpetrate characteristics that are not "good for the genes," that would not be selected at the phylogenetic level. (3) The ontogenetic and cultural processes each promote adaptation through variation and selective retention, the fundamental Darwinian evolutionary algorithm.

These four approaches to studying the evolution of cognition are complementary rather than antagonistic. As figure 1.1 suggests, selection theoretic analysis can be seen as a subset of the ecological approach, the comparative perspective as a subset of the phylogenetic approach, and the combination of the ecological and phylogenetic approaches, broadly construed, as comprising the universal set of current evolutionary research on cognition. This picture is, of course, a very simple representation of complex conceptual geography. Each of the four main categories could be subdivided many times. Those adopting different perspectives often find themselves in healthy dispute, and many researchers productively combine approaches. For example, in this volume Tomasello, Dunbar, and Lefebvre combine ecological and phylogenetic perspectives, Bateson and Clayton et al. combine ecological with comparative analysis, and in their theoretical work Richerson and Boyd use the products of all four approaches. However, in spite of its simplicity, figure 1.1 provides some indication of what evolutionary psychology looks like "in the round."

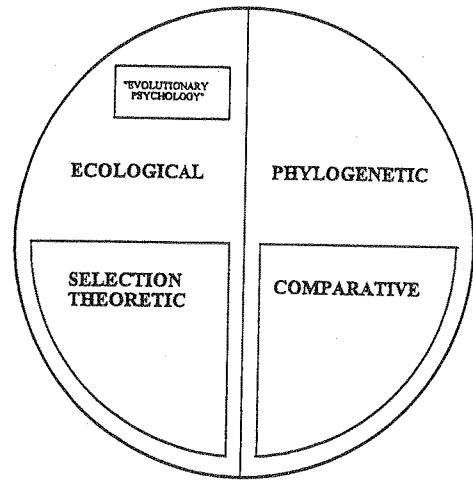


Figure 1.1  
Schematic representation of relationships among components of evolutionary psychology in the round.

### Evolutionary Psychology in the Round

At the beginning, I pointed out one prominent difference between the research enterprise currently known as “evolutionary psychology” (e.g., Buss, 1999), and that which is represented by this book, evolutionary psychology in the round: the former is concerned almost exclusively with human cognition and behavior; the latter investigates these phenotypic characteristics throughout the animal kingdom. Now that I have surveyed the contributors’ views on the nature of cognition, on variation among cognitive processes, and on the characteristics of evolutionary analysis, further differences between the two research enterprises have become apparent. These can be summarized: (1) Evolutionary psychology in the round is concerned with the phylogenetic history, as well as the adaptive characteristics, of behavior and cognition, descent as well as selection. (2) It recognizes that behavioral adaptation can be achieved via modification of perceptual and motor processes, instead of or in addition to modification of cognitive processes. (3) It investigates the contributions to cognitive adaptation of ontogenetic and cultural processes, as well as that of natural selection operating on genes. (4) Evolutionary psychology in the round seeks inde-

pendent evidence that variation in what/when rules of cognition is correlated with variation in how rules, resisting easy inferences from domain specificity to modularity. Two examples, taken from research on spatial memory in food-storing birds and motor imitation, will serve to illustrate these contrasts.

Certain birds, such as Clark’s nutcrackers and Marsh tits, which experience seasonal variation in the availability of food, scatter hoard for winter survival. Cache retrieval has been demonstrated to involve memory (e.g., Clayton and Krebs, 1994), and these birds have been reported to perform better on tests of spatial memory than related species that cache less assiduously (e.g., Kamil et al., 1994; Olson et al., 1995). Furthermore, lesions of the hippocampus impair memory for cache sites (e.g., Sherry and Vaccarino, 1989), and birds that depend heavily on food storing for winter survival have larger hippocampi than related species (e.g., Krebs et al., 1989).

One interpretation of these data is as follows. Food-storing birds have an innate, spatial memory module lodged in the hippocampus. That is, natural selection operating at the genetic level has given rise to a cognitive process, based in the hippocampus, which has distinct what/when rules *and* distinct how rules; it processes spatial information, and does so in a way that differs from the processing of non-spatial information. This kind of interpretation is characteristic of “evolutionary psychology.”

By its nature, evolutionary psychology in the round recognizes a range of plausible interpretations of these spatial memory data. It does not underestimate inferential complexity, even where the topic has been researched so extensively and so elegantly as spatial memory. One alternative account, which is consistent with recent evidence that the act of cache retrieval stimulates hippocampal growth (e.g., Clayton and Krebs, 1994; Lee et al., 1998), and of episodic-like memory in scrub jays (Clayton et al., this volume) is as follows. In response to selection pressure from seasonal variations in food supply, phylogenetic evolution (natural selection operating at the genetic level) has furnished certain birds with a specialized *behavior*, namely, scatter hoarding. There may be what/when distinctive perceptual and motor processes controlling this behavior, but the action of caching does not itself involve a significant cognitive component. From the point in ontogeny when hoarding behavior begins, higher than average demands are made on memory. Hoarding creates for the hoarder an environment in which food resources are scattered, and thereby exercises the memory system. This system, located in the hippocampus, grows as it deals with a higher volume of information, but neither its potential for growth, nor the how rules that it implements, have been changed by natural selection relative to those used by other species to remember spatial stimuli. Thus, according to this interpretation, the spatial memory performance of food-storing birds is a product of phylogenetic and



ontogenetic specialization. Phylogenetic evolution, natural selection, has yielded a behavioral, but not a cognitive adaptation, and, provoked by this behavioral adaptation, a cognitive system with specialized what/when rules, but not distinctive how rules, emerges in the course of ontogeny.

Research on motor imitation is more diffuse, and has provided much less reliable information than that on spatial memory in food-storing birds. However, it illustrates the contrasting attitudes toward culture of evolutionary psychology and evolutionary psychology in the round.

Motor imitation, the capacity to learn a novel body movement by seeing it done, has been clearly demonstrated only among humans. Many researchers believe that it occurs in other apes (e.g., Tomasello and Call, 1997), but, like all other putative evidence of imitation in nonhuman animals, the bases of these claims have been or could be challenged (e.g., Akins and Zentall, 1996; Moore, 1996; Lefebvre et al., 1997; Campbell et al., 1999). Furthermore, it is not clear how humans, or any other animals, could imitate certain "perceptually opaque" actions (Heyes and Ray, 2000). For example, imitation of novel facial expressions, which are seen in others but felt by oneself, would seem to require some kind of cross-modal transformation of information, and it is not clear what sort of cognitive how rules could achieve this transformation. This problem notwithstanding, it has been noted repeatedly that imitation learning could be the means by which many culture-specific behaviors are transmitted.

Evolutionary psychology has deduced from observations of this kind that imitation learning is a phylogenetically specialized cognitive module, which selectively processes sensory input from others' body movements according to distinctive rules of operation, is found only in humans and possibly other apes, and supports cultural transmission of information. An interpretation that is at least equally consistent with current evidence, and more in the spirit of evolutionary psychology in the round, suggests that the capacity to imitate arises from ontogenetic specialization, using cultural input, of phylogenetically general, associative learning processes (Heyes and Ray, 2000). According to this Associative Sequence Learning (ASL) hypothesis, children acquire the capacity to reproduce action units (fragments of what would normally be delineated as "an action") through contiguous experience of seeing and doing each unit, thereby forming associations between sensory and motor representations of each unit. These links establish an imitation repertoire. That is, when units in the repertoire are observed in a novel sequence, the sequence can be learned by observation alone, and the modeled movement can be reproduced. The most important sources of contiguous experience of seeing and doing action units, and therefore

the most significant influences on the development of an imitation repertoire, are optical mirrors and the adult tendency to imitate infants; both, broadly speaking, are cultural phenomena. Thus, ontogenetic specialization yields a cognitive process that is distinctive in its what/when rules (it reproduces body movements) and that both supports and is supported by culture.

For both of these examples—spatial memory and imitation—more evidence is needed to establish the relative merits of the alternative interpretations I have outlined. For example, we need to know whether the hippocampi of storing and non-storing species grow at comparable rates when they are given spatial memory tasks, and, to evaluate the ASL theory of imitation, whether prior experience of seeing and doing action units facilitates subsequent imitation of sequences of these units in humans and other animals. Whatever the results of these further experiments, the spatial memory and imitation examples illustrate the nature of the biases inherent in much evolutionary psychology, and, more generally, emphasize that evolutionary psychology in the round generates and tests more complex hypotheses. Many of the contributors to this volume, myself included, would argue that such complexity is necessary to capture even the basics of the evolution of cognition, but it certainly doesn't make life easy. It is much easier to attribute all adaptive variation among cognitive processes to phylogenetically evolved modules than to investigate the nature (what/when and/or how rules) and evolutionary sources (the relative contributions of phylogenetic, ontogenetic, and/or cultural processes) of such variation.

Perhaps this difficult (but rewarding) process of enquiry can be assisted by bold hypotheses about the evolution of cognition that take account of the different types and sources of variation. In this spirit, I offer, as a parting shot, my own bold hypotheses: What/when rules of cognition are more labile, more responsive to change in ecological demand, than how rules, and adaptive specialization of cognitive processes occurs more readily at the ontogenetic than the phylogenetic level. Therefore, we will find across the animal kingdom that most evolutionary variations in cognition arise through ontogenetic specialization of what/when rules; that ontogenetic specialization of how rules and phylogenetic specialization of what/when rules occur less often; and that phylogenetic specialization of how rules is very rare indeed.

### Summary

This chapter introduces the contents of this volume by addressing three fundamental questions about the evolution of cognition: What is cognition? What are the differences among "different" cognitive processes? What makes research on cognition

“evolutionary”? In answer to the first of these, cognitive states and processes are loosely defined as theoretical entities providing a functional characterization of the operations of the central nervous system, which may or may not be objects of conscious awareness, and that are distinct from perceptual and motor processes. In discussing the second question, it is suggested that contemporary researchers differentiate cognitive processes using what/when rules, which specify environmental inputs and/or cognitive products, and using how rules, which specify processing operations. Inferring how rules (which are of primary concern to contemporary investigators) from what/when rules is difficult under any circumstances, and may be impossible when the latter circumscribe environmental inputs rather than cognitive products. Addressing the third question, it is argued that there are four principal evolutionary approaches to the study of cognition—ecological, phylogenetic, comparative, and selection theoretic—and that together they comprise evolutionary psychology “in the round”. By contrast with what is currently known as evolutionary psychology, this research enterprise investigates phylogenetic, ontogenetic, and cultural contributions to behavioral adaptation in human and nonhuman animals. Also by contrast with the assumptions of evolutionary psychology, it is suggested in conclusion that most evolutionary variations in cognition arise through ontogenetic specialization of what/when rules; that ontogenetic specialization of how rules and phylogenetic specialization of what/when rules occur less often; and that phylogenetic specialization of how rules is exceptionally rare.

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