

# Four Routes of Cognitive Evolution

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Four routes of cognitive evolution are distinguished: phylogenetic construction, in which natural selection produces qualitative change to the way a cognitive mechanism operates (language); phylogenetic inflection, in which natural selection biases the input to a cognitive mechanism (imprinting and spatial memory); ontogenetic construction, in which developmental selection alters the way a cognitive mechanism operates (face recognition and theory of mind); and ontogenetic inflection, in which developmental selection changes the input to a cognitive mechanism (imitation). This framework integrates findings from evolutionary psychology (i.e., all research on the evolution of mentality and behavior). In contrast with human nativist evolutionary psychology, it recognizes the adaptive significance of developmental processes, conserves the distinction between cognitive and noncognitive mechanisms, and encompasses research on human and nonhuman animals.

This article characterizes a problem for evolutionary psychology and proposes a framework for its solution. Human nativist evolutionary psychology (HNEP), which claims that the mind consists of many innate cognitive modules, is currently the most prominent and influential approach to the evolutionary analysis of cognition. The problem is that this relatively isolated research enterprise is having a disproportionate impact on the internal direction and external perception of the field, and yet its central claim is based on controversial assumptions and weak empirical evidence. Two kinds of errors are likely in this situation; there is a risk that examples of adaptive specialization will be forced into the modularity mold, regardless of whether the data genuinely support this interpretation, and that all evolutionary psychology, not just HNEP, will begin to be seen as flawed. The four routes framework presented here allows these errors to be avoided because it acknowledges the existence of cognitive modules, and thereby the valid claims of HNEP, but also provides a simple taxonomy enabling identification of other kinds of adaptive specialization. It can be used by all evolutionary psychologists—those that study human and nonhuman animals, constructivists, and selection theorists as well as nativists—to frame research questions, to communicate empirical claims, and to compare and integrate their findings. The four routes framework may, therefore, play a heuristic role in the reorientation of evolutionary psychology away from module hunting and toward broader and more integrative analyses of the effects of evolution on cognition.

HNEP asserts that cognition is typically adaptive because phylogenesis, the process of evolution through natural selection,<sup>1</sup> has constructed a variety of domain-specific cognitive modules that

are distinctive in terms of both their input (what information they process) and their mechanisms (how processing occurs; e.g., Cosmides & Tooby, 1992; Hirschfeld & Gelman, 1994; Pinker, 1997). Each module processes information primarily or exclusively from one environmental domain (in which domains correspond to common-sense functional categories; e.g., language, social exchange, and faces), and crucially, this information is processed by a cognitive mechanism that is distinctive in terms of the kinds of representations that it produces and manipulates and/or in relation to the rules that govern the production and manipulation of those representations.

HNEP represents a small subset of research that could be accurately described as evolutionary psychology (Daly & Wilson, 1999; Heyes, 2000; Karmiloff-Smith, 1992; Lang, Sober, & Strier, 2001; Shettleworth, 1998). The universal set includes a variety of disciplines investigating the behavior and mentality of human and nonhuman animals without exclusive commitment to symbolism, adaptationism, or nativism (e.g., animal cognition, animal learning, behavioral ecology, behavioral neuroscience, comparative psychology, evolutionary epistemology, ethology, and primatology). There are also many research projects in developmental psychology, cognitive psychology, and cognitive neuroscience that, although they do not address evolutionary issues explicitly, have a direct bearing on questions about the evolution of cognition.

The framework presented in this article rests on several assumptions that are broadly compatible with those of HNEP: (a) Computationalism, or the information processing approach, provides an appropriate level of explanation for the proximal causes of a broad range of behavior; (b) not all characteristics have evolved, and not all evolved characteristics are adaptive (Futuyma, 1998), but questions about adaptive function have heuristic value in psychology; and (c) cognitive processes are products of natural selection—their

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<sup>1</sup> The term *natural selection* is used here, as in most textbooks of biology, to encompass selection for survival and for reproductive benefits (sexual selection). Miller (2000) argued that it is important to distinguish natural and sexual selection when considering the adaptiveness of human moral and artistic qualities.

existence, like that of other highly complex phenotypic attributes, currently has no other plausible scientific explanation.<sup>2</sup> However, HNEP tends to make two further assumptions that are not shared by the present analysis: (a) The distinction between cognitive and noncognitive mechanisms is unimportant—it is profitable to characterize all behavior-control mechanisms as symbolic, as involving rule-governed transformation of representations (Cosmides & Tooby, 1994; Shapiro & Epstein, 1998); and (b) natural selection is the only source of adaptive properties of cognitive processes—ontogenetic processes are merely means through which natural selection achieves adaptive change (Pinker, 1997).

It is argued, by contrast, that evidence from evolutionary psychology as a whole indicates that it is important for evolutionary analysis to conserve the distinction between cognitive and noncognitive mechanisms and between behavior-control mechanisms that are guided by knowledge or expectancies and are subject to interference (e.g., reasoning and decision making) and those that are controlled by stimulation and are relatively immune to interference (e.g., early feature detection and orienting reflexes). This latter distinction is important not only because it marks substantial differences between the way behavior-control mechanisms operate online and is especially useful in comparisons between human and nonhuman animals but also because cognitive and noncognitive mechanisms may differ in the degree to which they are prone to adaptive modification. In addition to being products of natural selection, some ontogenetic processes are themselves sources of adaptive change to cognitive mechanisms. In other words, HNEP's monolithic conception of cognitive evolution, the view that cognitive evolution occurs through phylogenetic construction alone, ignores two important distinctions: between change to cognitive and noncognitive mechanisms and between phylogenetic and ontogenetic sources of adaptive modification. In combination, these distinctions circumscribe four major routes of cognitive evolution: phylogenetic construction, phylogenetic inflection, ontogenetic construction, and ontogenetic inflection.

The first section of this article presents the four routes framework in more detail, discusses potential objections, and considers in general terms the evidence required to classify examples of adaptive modification. The subsequent core of the article scrutinizes evidence relating to a series of phenomena that have been claimed to be products of phylogenetic construction: imprinting, spatial memory, face processing, theory of mind, and imitation. In each case, it is argued that the proposed evidence of phylogenetic construction is at least equally compatible with the phenomenon having evolved via another, specified route. Thus, the second, third, and fourth sections present potential examples of phylogenetic inflection, ontogenetic construction, and ontogenetic inflection, respectively. Together, these sections illustrate the four routes framework and raise the possibility that phylogenetic construction is a relatively rare form of cognitive evolution.

#### Four Routes

Four routes of cognitive evolution, four ways in which a cognitive process can change such that it produces more adaptive behavior, are distinguished here using two variables: the evolutionary *source* and the *locus* of the adaptive change (see Figure 1). The sources of change are natural selection, a gene-based evolutionary process, and developmental selection, a process of inter-

		LOCUS	
		MECHANISM	INPUT
SOURCE	NATURAL SELECTION	Phylogenetic construction	Phylogenetic inflection
	DEVELOPMENTAL SELECTION	Ontogenetic construction	Ontogenetic inflection

Figure 1. The four routes framework.

action between the developing organism and its environment during ontogeny. The loci of change are the cognitive mechanism itself, the computational device that processes information, and the input to the cognitive mechanism, the type or range of information processed.<sup>3</sup>

A route is described as *phylogenetic* when the source is natural selection and as *ontogenetic* when the source is developmental selection. It is called *construction* when the locus is a cognitive mechanism and *inflection* when the locus is input to the cognitive mechanism. Thus, in *phylogenetic construction*, natural selection changes the mechanism of a cognitive process; in *phylogenetic inflection*, natural selection biases the input to an unchanged cognitive mechanism; in *ontogenetic construction*, developmental selection effects change to a cognitive mechanism; and in *ontogenetic inflection*, developmental selection biases input without changing the mechanism.

A simple physiological analogy, in which a stomach stands for a cognitive mechanism, may clarify these distinctions. The amount of energy produced by the operation of a stomach could increase as a result of change in the activity of the enzymes that convert ingested material into nutrients (construction) or through alteration in the type and/or quantity of ingested material (inflection). A change in enzyme activity would be an example of phylogenetic construction if individuals with the new enzyme action had out-reproduced those with the old system because they have the new system. It would be ontogenetic construction if the shift from the old to the new system occurred within the lifetime of individuals and as a consequence of the material they ingested. Perhaps in this hypothetical digestive system, enzymes that are underused become unavailable, and those that are overused develop new properties. In the case of inflection, alteration in the type and/or quantity of ingested material would be phylogenetic inflection if it was due to

<sup>2</sup> Chomsky (1986) and Fodor (2000) apparently denied that language and other cognitive processes are products of natural selection, but closer reading of their arguments suggests that they are supporting saltationist over gradualist accounts of the evolution of cognitive processes rather than denying the importance of natural selection (Gould, 1991).

<sup>3</sup> In this article, as in HNEP, cognitive mechanisms are individuated relative to content domains, but it is not assumed here that cognitive mechanisms, thus distinguished, differ in terms of their rules and/or representations. For example, a mechanism that processes face stimuli is a face recognition process even if faces are processed in the same way as other visual objects. An input process is a noncognitive process that supplies information to a cognitive mechanism thus defined.

the effects of natural selection on the creature's jaws or dentition, structures that modulate input to the stomach. It would be ontogenetic inflection if the change in type and/or quantity of ingested material occurred within the lifetime of individuals and as a consequence of the material ingested. For example, consumption of the original set of materials may make owners of the stomach so big and strong that they can obtain a broader range or a new type of food.

Use of a variety of different taxonomic principles would make room for exploration of diversity in cognitive evolution. For example, cases could be classified according to whether adaptation occurs under cultural influence, according to whether it consists in alteration of cortical or subcortical mechanisms, or according to the range of taxa in which the adaptation occurs. The four routes framework uses the source (phylogenetic vs. ontogenetic) and locus (mechanism vs. input) of change because these are the broadest and most foundational distinctions already used by evolutionary psychologists in their research. What is distinctive about evolutionary analysis is that it investigates not just mature form but origins, and phylogenetic and ontogenetic processes are the two major alternative sources of mature form.<sup>4</sup> Similarly, although many finer distinctions are possible, the divide between cognitive and noncognitive mechanisms is a fundamental division in post-behaviorist psychology (Neumann, 1984).

#### *Source: Phylogenetic Versus Ontogenetic*

The source of an adaptive feature of a cognitive process is phylogenetic if that feature was specifically favored by natural selection—if, in the course of evolutionary history, cognitive phenotypes that included the target feature out-reproduced those that lacked the feature and did so because they possessed the target feature. By contrast, the source of an adaptive feature of a cognitive process is ontogenetic if the feature was not specifically favored by natural selection but is instead generated in the course of development as a product of cognitive and other behavior-control processes operating on environmental input. In other words, the information that enables a system feature to fit its environment comes from natural selection in the case of phylogenetic evolution and development in the case of ontogenetic evolution (D. T. Campbell, 1974).

In line with HNEP (Pinker, 1997) and nativist views of cognition more generally (Chomsky, 1959; Fodor, 2000), an example of cognitive evolution is assumed to be phylogenetic if there is evidence of "poverty of the stimulus"—that the adaptive properties of the cognitive process could not have arisen through experience alone—or if there is evidence that the adaptive properties are genetically heritable. Conversely, it is classed as ontogenetic if the evidence suggests "wealth of the stimulus"—that the adaptive properties could be products of experience—and if there is no evidence that the adaptive properties are genetically heritable. Research relevant to the poverty or wealth of the stimulus compares the development of cognitive processes across species, cultures, and subgroups within a population. Wealth is indicated by correlated variation in experience and development, whereas poverty is implied by invariant development in the face of experiential diversity.

This distinction between phylogenetic and ontogenetic sources is not a crude nature–nurture dichotomy. It acknowledges that, like

all other phenotypic attributes, cognitive processes are produced jointly by genetic and developmental processes (Mayr, 1974). The information obtained through natural selection and stored in the genotype cannot produce a phenotype without developmental processes of some kind, and development cannot yield phenotypic outcomes that are outside the potential of the genotype. However, development is not always tightly genetically constrained or canalized (Waddington, 1959) such that it does all and only what natural selection "desires." Development can produce outcomes, some of them adaptive, that were not anticipated (not specifically favored) by natural selection, and these outcomes may be said to have an ontogenetic source (D. T. Campbell, 1974; Karmiloff-Smith, 1992).

A morphological example may clarify the distinction between phylogenetic and ontogenetic sources of adaptive change: Many people who worked in the ancient Chinese silk industry had serrated finger nails. The end of each nail had a zigzag shape, and the points were used to tease silk fibers. There is no doubt that the silk workers' fingernails were joint products of natural selection and developmental processes, but it is still legitimate to ask which of these kinds of processes was responsible for the serrated shape. In principle, this feature could have had a phylogenetic source. Over generations in a silk-working subpopulation, people who inherited a mutation for serrated nails may have out-reproduced those who did not because they were more efficient at silk processing. Alternatively, and much more plausibly, the serrated shape may have had an ontogenetic source. The silk workers had the same fingernail-relevant genes as other members of the population, and these genes had not been favored by natural selection because they contributed to the development of nails that could, in certain environments, become serrated and assist in silk production. Instead, the silk workers learned, initially by trial and error and subsequently through social learning, that serrated nails facilitate silk teasing and therefore adopted the practice of clipping their nails into multiple points. In an analogous sense, whereas every cognitive process is a joint product of natural selection and developmental processes, a feature of a cognitive process, such as its input domain or some property of its mechanism, may be adaptive by virtue of either phylogenesis or ontogenesis.

<sup>4</sup> Fitness-enhancing psychological attributes have been classified as adaptations, when "natural selection shapes the character for current use," or exaptations, when the character has been "co-opted" for its current use, whether or not it was previously shaped by natural selection (Gould & Vrba, 1982, p. 6). This distinction has been used effectively to argue, as I do in this article, that the fitness-enhancing properties of psychological processes should not automatically be attributed to natural selection (Gould, 1991). However, it is less likely to capture the current concerns of evolutionary psychologists than the distinction between phylogenetic and ontogenetic sources of adaptive change for several related reasons. First, some evolutionary psychologists find the concept of exaptation confusingly ambiguous (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). Second, the adaptation–exaptation distinction is associated with a battle between gradualists and saltationists, which is a focus of empirical investigation among relatively few evolutionary psychologists. In contrast, and this is the third reason, the systematic (and possibly selection-based) processes through which psychological characters are co-opted are foci of intensive study among evolutionary psychologists, and therefore it is more appropriate to identify them positively as ontogenetic, developmental processes than merely to indicate that they are not natural selection.

### *Ontogenetic Evolution?*

In this article, a cognitive process is said to have evolved when there is reason to believe that it has changed systematically over time in a way that increases the adaptedness of the cognitive system's behavior. According to this usage, both phylogenetically and ontogenetically generated change to cognitive processes is evolutionary. Some readers may prefer to reserve the term *evolution* for change guided by natural selection, but this is a purely terminological issue. Phylogenetic construction, phylogenetic inflection, ontogenetic construction, and ontogenetic inflection may be regarded as four routes to the *adaptive modification* or *adaptive specialization* (Rozin & Kalat, 1971) rather than the evolution of cognitive processes, without alteration to the substance of the debate. However, it is important to note that the present usage is not eccentric and does not vacuously equate evolution with change.

There is a long tradition in evolutionary psychology that describes ontogenetic adaptive modification as evolution (e.g., D. T. Campbell, 1974; Edelman, 1987; Heyes & Hull, 2001; Hull, Langman, & Glenn, 2001; James, 1880; Plotkin & Odling-Smee, 1981; Skinner, 1981, 1984),<sup>5</sup> and this terminology does not entail that all developmental changes in behavior are examples of cognitive evolution. Experience-based changes in behavior do not represent cognitive evolution when (a) they result from acquisition of information via cognitive processes but are not associated with systematic, adaptive change to the input or mechanisms of cognitive processes (e.g., learning facts such as that the pyramids are in Egypt) and (b) they involve systematic change in the input to, or mechanisms of, a cognitive process, but this change is unlikely to promote reproductive fitness (e.g., becoming an expert train spotter). Thus, if there are systematic, experience-based changes to cognitive processes that are neutral or deleterious with respect to fitness, they would not constitute examples of ontogenetic evolution.

Ontogenetic evolution/developmental selection occurs in the immune system (Hull et al., 2001). Natural selection, gene-based evolution, provides the body with a basic set of B cells, the cells that produce antibodies against infection. However, this set is wholly inadequate as a defense against the millions of pathogens to which a body can be exposed. To deal with the full range, in the course of an individual's lifetime, B cells from the original set that find their pathogens undergo mutation and division. Some of the new B cells that result from this process of developmental selection are better able than the originals to engage with pathogens, and these are available in large numbers to deal with reinfection.

Little is known about developmental selection of cognitive processes. There are few general theories (e.g., D. T. Campbell, 1974; Karmiloff-Smith, 1992), and in individual cases (e.g., face processing and theory of mind), it would be desirable to know much more about the type of experience that is important, the kinds of environment in which this experience is obtained, the sequence of states traversed by the cognitive process in the course of its evolution, and the principles that govern transition between these states. These are research priorities for evolutionary psychology and developmental psychology alike. However, to ascribe cognitive change to ontogenetic evolution begs no more questions—it is no more of a promissory note (Sperber, 1996) than ascribing cognitive change to phylogenetic evolution. Phyloge-

netic accounts of the evolution of cognitive processes seldom if ever specify a genetic mechanism, identify with any precision the environmental conditions that provided selection pressure, or indicate transitional stages between the ancestral and the current state of the cognitive process (Davies, 1999; Richardson, 1996). Relative to the study of morphological and anatomical characteristics, ontogenetic and phylogenetic evolutionary analyses of cognition are in their infancy.

### *Locus: Input Versus Mechanism*

Changes to the input of a cognitive process consist of alterations in its “catchment area”—in the identity or extent of the environmental domain from which it typically receives information or in the amount of information it receives from a given domain. By contrast, changes to the mechanism of a cognitive process alter the way in which information is processed, the way in which the mechanism operates.

Cases of adaptive specialization of cognitive processes are classed as constructive when there is evidence that the cognitive mechanism in question is qualitatively different from those that process different information in the same species or the same information in different species. This typically consists of experiments showing that for the focal process the relations between environmental input and behavioral output are distinctive in a way that can be explained only by supposing that the cognitive mechanism processes information using distinctive rules and/or representations. Neurobiological research contributes to this enterprise, but neural localization of a cognitive mechanism is not, in itself, evidence that the mechanism is qualitatively distinct (Sherry & Schacter, 1987). Cases are identified as inflectional if there is no compelling evidence that the target cognitive mechanism is qualitatively distinct but there is evidence that input to the cognitive mechanism is being biased in favor of a particular environmental domain.<sup>6</sup>

In contemporary psychology, the operation of a cognitive mechanism is typically characterized with reference to its rules and representations. Accordingly, the four routes framework assumes

<sup>5</sup> The same “evolutionary epistemological” or “selection theoretic” tradition proposes that the ontogenetic processes that give rise to adaptive change in cognitive phenotypes are based on a Darwinian, variation-and-selective-retention algorithm, operating on nongenetic variants. This idea is implicit in my choice of the term *developmental selection* to describe the source of adaptive, ontogenetic change in cognitive processes, but it is not pursued further in the present article, and the analysis presented here does not depend on its validity.

<sup>6</sup> Sherry and Schacter's (1987) distinction between the “type of information” handled by a memory system and its “rules of operation” is similar to the distinction between input and mechanism used here. However, in their discussions of animal memory, Sherry and Schacter adopted a more black box approach, assuming that two memory systems or cognitive processes have different rules of operation if, for example, one receives input throughout ontogeny, whereas the other is a sensitive period phenomenon. Here, as in Sherry and Schacter's discussion of human memory, it is understood that temporal variation of this kind could indicate a difference between upstream noncognitive processes or between cognitive mechanisms; that is, it does not necessarily reflect variation in the way the information is represented by the cognitive system or the rules that operate on these representations (see the *Imprinting* section).

that qualitative change to a cognitive mechanism consists of alteration of the kinds of representations it produces and/or the rules that describe the production and manipulation of those representations. However, this characterization does not assume that all cognitive mechanisms are rule following, that is, that they embody or “know” the rules of their own operation in the way that a cook knows a recipe. Nor, therefore, does it assume that representations are symbolic, that is, that they are representations by virtue of the way in which they are treated by rules internal to the system (contra, e.g., Cosmides & Tooby, 1994; Fodor, 1975). Instead of adopting this symbolist view, which is committed to a digital computer metaphor, the present analysis assumes that rules describe the operation of a cognitive mechanism but that, like the rules of planetary motion, they are not necessarily consulted by the system. Accordingly, the present analysis assumes that a state of a system is a representation if it stands for another state of the system or of the environment and if it is the biological function of the system in question to produce such representations (Dretske, 1988; Hatfield, 1991; Kosslyn & Hatfield, 1984; Millikan, 1984). For example, a pattern of neural activation in the visual system represents certain spatial properties of the environment because the pattern is a state of a system whose function it is to represent such properties (Hatfield, 1991). This “biopsychological” conception of representations is compatible with integrative evolutionary analysis because it focuses attention on function (Shapiro & Epstein, 1998), embraces both connectionist and symbolist uses of the term in psychology, and avoids exclusive commitment to the symbolist explanatory framework that is alien to many biologists.

Inflection, adaptive change to the input of a cognitive mechanism, can result solely from processing of earlier input (without any alteration in the way that cognitive or noncognitive mechanisms operate), or it can be a consequence of changes to a noncognitive mechanism that modulates input to the cognitive mechanism. Although they may be described with reference to rules and representations (as defined above), noncognitive mechanisms differ from cognitive mechanisms in being automatic or bottom up. They are controlled by stimulation rather than by knowledge or expectancies, are relatively immune to interference, and do not necessarily give rise to conscious awareness. The primary examples of noncognitive mechanisms are those involved in sensory and motor processes such as early feature detection, orienting reflexes, and control of bodily functions (Neumann, 1984).

Adaptive change to the input of a cognitive mechanism can also be a consequence of change to the mechanism itself. For example, by virtue of having new rules and/or representations, a cognitive mechanism may be more selective, that is, capable of processing information from one domain exclusively or at a higher rate than information from other domains. In these cases, the four routes framework would classify the change as constructive rather than inflectional. Adaptive change to the input of a cognitive process is classified as inflection when it is not a consequence of change to the cognitive mechanism.

Proponents of HNEP sometimes write as if the division of minds into domain-specific cognitive modules, and therefore the widespread occurrence of phylogenetic construction, could be deduced from the theory of evolution by natural selection (e.g., Cosmides & Tooby, 1994). However, whereas there are arguments for and against the adaptive value of phylogenetic construction (and each of the other three evolutionary routes), the extent of its influence

on cognitive phenotypes is understood ultimately to be an empirical question and one that can be resolved only on a case by case basis (Cosmides, 1989; Shapiro & Epstein, 1998). Therefore, the remainder of this article focuses on cases, both to demonstrate how examples of cognitive evolution can be classified as phylogenetic or ontogenetic and constructive or inflectional and to show that the occurrence of phylogenetic construction is typically inferred from weak empirical evidence. Language is exceptional in this respect. Although this case is not conclusive (e.g., Bates & MacWhinney, 1982; Chomsky, 1986; Elman et al., 1996; Fodor, 2000; Gould, 1991), there is strong evidence that human language acquisition is guided by a phylogenetically constructed cognitive mechanism (Pinker, 1994).

### Phylogenetic Inflection

Phylogenetic inflection occurs when natural selection biases the input to a cognitive mechanism by changing an upstream noncognitive process. Two examples will be discussed in this section: filial imprinting and spatial memory in food-storing birds. These cases are of particular interest because they are, respectively, the oldest and best potential examples of phylogenetic construction in nonhuman animals (Lorenz, 1937; Sherry & Schacter, 1987; Shettleworth, 1993, 1998), and yet many decades of elegant, interdisciplinary research has failed to provide compelling evidence that either involves a qualitatively distinct cognitive mechanism.

#### *Imprinting*

Filial imprinting is the process by which the social behavior of a young animal, typically a bird, becomes limited to a particular object or class of objects, usually its mother or conspecifics (Bolhuis, 1991). Lorenz (1937) suggested that filial imprinting has three characteristics indicative of its occurring via a learning mechanism qualitatively distinct from those of instrumental and Pavlovian conditioning. He claimed that filial imprinting (a) occurs without reinforcement, (b) is confined to a *critical period* in development (that it is possible during the first few days of life and not subsequently), and (c) is irreversible—once formed a preference for an imprinted object cannot be changed.

Subsequent experimental research has led each of these conclusions to be revised. First, evidence that imprinting is susceptible to blocking and overshadowing suggests that it is a form of Pavlovian conditioning in which the motion of the imprinting object acts as an unconditioned stimulus, or reinforcer, that becomes associated with static properties of the object, such as color and shape (Bolhuis, De Vos, & Kruijt, 1990). Second, the critical period for imprinting, now described as a *sensitive period*, has turned out to be much more flexible than Lorenz anticipated and to be controlled to a large degree by experiential factors. There is evidence that the sensitive period is self-terminating; it is terminated by the establishment of an object preference because this preference entails that the bird will avoid exposure to alternative potential objects of imprinting (Bolhuis, 1991). Finally, under most conditions, imprinting is reversible. Birds subjected to two successive imprinting procedures in the laboratory shift their preference from the object of the first to the object of the second unless the former includes

head and neck features and the latter does not (Bolhuis, 1991; M. H. Johnson & Horn, 1988).

As a consequence of these discoveries and many others, contemporary models of imprinting cast it as a behavioral phenomenon mediated by species-general and domain-general mechanisms of learning. This is true even of Bateson and Horn's (Bateson, 2000; Bateson & Horn, 1994) model of imprinting, which is not only one of the strongest theories but also one of the most conservative in the degree to which it retains elements of Lorenz's (1937) original conception of imprinting (cf. McLaren, Kaye, & Mackintosh, 1989). Bateson and Horn's model implicates three processes in imprinting: analysis (sensory), recognition (cognitive), and execution (motor). The recognition process learns the features of the imprinting object, and according to the model, it achieves this end via the same mechanisms, the same learning rules, that mediate visual recognition of nonimprinting objects in birds and other vertebrates. It is a special characteristic of the noncognitive analysis process, not of the recognition process, that renders imprinting adaptive for precocial birds by making it more likely that they will form attachments to conspecifics than to other objects. The analysis process operates such that head and neck stimuli have privileged access to the recognition process (M. H. Johnson & Horn, 1988). The elements of the analysis process that are responsible for head and neck detection mature earlier than detectors of other features (M. H. Johnson, Bolhuis, & Horn, 1985) and thereby create an input bias to the recognition process favoring head and neck stimuli. Deprivation experiments have indicated that the early maturation of head and neck detectors does not depend on visual experience, and therefore it is likely that natural selection has scheduled their development as an adaptation promoting maintenance of contact with caregivers.

Thus, the original evidence that imprinting is a product of phylogenetic construction, which convinced Lorenz (1937) of the distinctiveness of imprinting, has been largely undermined, and the results of recent research are more consistent with the view that imprinting evolved through phylogenetic inflection. Therefore, current theory and evidence suggest that in the case of imprinting, natural selection has biased the input to a cognitive process by altering an upstream noncognitive process and that it has not changed the cognitive mechanism—in this case, the learning rules—that processes this input. It is possible, and indeed likely, that these learning rules, the same ones that mediate associative learning in a wide range of vertebrate and invertebrate taxa, were themselves products of phylogenetic construction early in evolutionary history, but current evidence suggests that it was phylogenetic inflection, rather than phylogenetic construction, that made imprinting distinctive with respect to other forms of associative learning.

### *Spatial Memory in Food-Storing Birds*

Certain birds, such as Clark's nutcrackers and marsh tits, that experience seasonal variation in the availability of food scatter hoard for winter survival; they store food in small quantities at a large number of locations. Cache retrieval has been demonstrated to involve memory (Clayton & Krebs, 1994), and these birds have been reported to perform better on tests of spatial memory than related species that cache less assiduously (Kamil, Balda, & Olson, 1994; Olson, Kamil, Balda, & Nims, 1995). There is also evidence

that lesions of the hippocampus impair memory for cache sites (Sherry & Vaccarino, 1989) and that species that depend heavily on food storing for winter survival have larger hippocampi than related species (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989).

These data would provide evidence of phylogenetic construction if they showed that natural selection has given rise to a cognitive mechanism, based in the hippocampus, that processes spatial information using rules and/or representations that differ from those used to process nonspatial information. For example, the mechanism processing spatial information may be distinctive in generating and manipulating map-like representations, which allocentrically code unexplored space as well as objects (O'Keefe & Nadel, 1978).

A recent review of the experimental literature (Bolhuis & MacPhail, 2001; MacPhail & Bolhuis, 2001) casts doubt both on the claim that food-storing birds have superior spatial memory and on the hypothesis that any such superiority is due to the operation of a distinctive, hippocampus-based memory mechanism. The review found that the performance of food-storing birds in spatial memory tasks is not consistently superior to that of related nonstoring species (storsers showed significantly better performance in four types of task, whereas nonstorsers were superior in two others) and that in those studies in which storsers were better than nonstorsers, the effect did not vary with retention interval, implying that it was not due to a difference in memory. Furthermore, although there is solid evidence that in adulthood food-storing species have larger hippocampi than nonstorsers (Healy, Clayton, & Krebs, 1994; Healy & Krebs, 1993) and that experience in a spatial task promotes more hippocampal enlargement in storsers than in nonstorsers (Clayton, 1995), hippocampal growth has not been firmly linked with improvement in spatial memory. For example, marsh tits (storsers) are better than blue tits (nonstorsers) at revisiting locations where they previously saw food, but this effect is present before as well as after experience-dependent hippocampal growth (Clayton, 1995).

The phylogenetic inflection account of spatial memory in food-storing birds assumes, in common with most researchers in this field and in spite of the problems identified by MacPhail and Bolhuis (2001), that storsers are generally better than nonstorsers in spatial memory tasks and that this is connected in some way with hippocampal volume. However, the phylogenetic inflection hypothesis also takes account of the fact, underlined by MacPhail and Bolhuis (2001), that there is no compelling evidence that storer superiority in spatial tasks is due to the use of a qualitatively distinct memory mechanism to remember spatial rather than nonspatial information. The phylogenetic inflection account suggests that in response to pressure from seasonal variation in food supply, natural selection has produced storing behavior by changing noncognitive sensory and motor processes. These changes increase the total volume of information entering memory mechanisms that process both spatial and nonspatial stimuli, and they increase the proportion of this information that is spatial, by promoting detection of spatial stimuli and provoking behavior that scatters food. Performance of this behavior creates for the hoarder an environment in which there is a large amount of (spatial) information to be remembered. The hippocampus grows as it deals with the higher volume of information entering the memory system, but neither its potential to grow as spatial information is memorized nor the cognitive mechanisms that it implements have been changed by

natural selection relative to those used by nonstoring species to remember spatial and nonspatial information.

Thus, the phylogenetic inflection hypothesis does not assume that the hippocampus is a totally general memory mechanism or contradict the ecological view of spatial memory in food-storing birds. Rather, it suggests that at least in these species, the hippocampus processes nonspatial as well as spatial information and that the mechanisms that have been changed by natural selection to meet ecological demands are noncognitive input processes.

Support for the idea that storer superiority in spatial tasks is due to the effects of natural selection on sensory processes that promote detection of spatial stimuli, rather than on memory, comes from dissociation tests (Brodbeck, 1994; Brodbeck & Shettleworth, 1995; Clayton & Krebs, 1994). In these tests, birds see food hidden in a visually distinctive object at a specific location, and before they are allowed to search for and consume the bait, the object is moved to a new location and replaced with one of a different appearance. Nonstorsers go as often to the object as to the location at which they previously saw food, but storsers consistently return to the original location. In combination with the absence of effects of retention interval in studies comparing storsers and nonstorsers in spatial tasks, these results suggest that spatial cues are more readily detected than object-specific cues in storing birds but not in nonstoring birds (MacPhail & Bolhuis, 2001).

The phylogenetic inflection hypothesis is also consistent with the results of a study showing that the posterior hippocampus of London taxi drivers, who have extensive navigational experience, is larger than that of control subjects and that hippocampal volume in this group correlates with number of years spent as a taxi driver (Maguire et al., 2000). It is possible, but unlikely, that London cabbies represent a genetically distinct subpopulation naturally selected for hippocampal growth potential. Therefore, these findings suggest that substantial hippocampal growth can result from experience alone, that is, in the absence of any constructive manipulation of spatial memory by natural selection.

In summary, the phylogenetic construction account of spatial memory in food-storing birds has not been discredited. However, current evidence is equally consistent with the phylogenetic inflection hypothesis, which suggests that spatial memory in food-storing birds depends on domain-general and taxon-general processes of learning and memory that have acquired their adaptive properties through the effects of natural selection on upstream noncognitive processes. The four routes model provides a common evolutionary framework for comparison of these hypothesis and, by highlighting that current data do not distinguish between them, indicates that in spite of confident claims to the contrary, it is not yet known whether spatial memory in food-storing birds has been shaped by phylogenetic construction, phylogenetic inflection, or both of these evolutionary processes.

### Ontogenetic Construction

Ontogenetic construction occurs when developmental selection (interaction between a cognitive system and its environment during ontogeny) generates adaptive change to the mechanism of a cognitive process, that is, to its rules and/or representations. In this section, it is argued that the distinctive cognitive mechanisms underlying face recognition in adulthood and theory of mind are at

least as likely to arise through ontogenetic construction as through phylogenetic construction.

Research on face processing provides evidence of phylogenetic inflection as well as ontogenetic construction. Therefore, face processing adds to imprinting and spatial memory a third example of phylogenetic inflection and provides a clear indication that this kind of cognitive evolution is not confined to nonhuman animals. By contrast, ontogenetic construction may occur only in humans or only under the influence of human culture (Tomasello, 2000; Tomasello, Kruger, & Ratner, 1993).

### Face Recognition

Three observations have encouraged the hypothesis that human face recognition evolved through phylogenetic construction, that is, that it is mediated by a cognitive process that has been shaped by natural selection such that it processes faces via mechanisms distinct from those underlying the recognition of other visual objects: (a) the face inversion effect—whereas most objects are slightly harder to recognize when inverted than when upright, face recognition is severely impaired by stimulus inversion (Yin, 1969); (b) prosopagnosia—some patients with damage to the temporal cortex show selective impairment in face recognition (Farah, Klein, & Levinson, 1995); and (c) neonatal preference—newborn babies, as young as 30 min old, turn their eyes and heads to track a face for longer than they track other visual objects of comparable complexity, contrast, and spatial frequency (Goren, Sarty, & Wu, 1975; M. H. Johnson, Dziurawiec, Ellis, & Morton, 1991).

Closer examination of the evidence supports the hypothesis that natural selection has shaped something that is involved in face recognition and the idea that the cognitive mechanisms used to process faces by adult humans are different from those used to process other visual objects. The phylogenetic construction hypothesis infers from this conjunction that the thing that has been shaped by natural selection is the cognitive mechanism that mediates face processing. However, it is at least equally likely that what natural selection has shaped is a noncognitive process that influences the supply of input to recognition mechanisms (phylogenetic inflection) and that these mechanisms, which are naturally selected to be relatively domain general, acquire distinctive properties in the course of ontogeny through experience with faces (ontogenetic construction).

The evidence of phylogenetic inflection—that natural selection has shaped a noncognitive process—comes from studies showing that the neonatal face preference is elicited by stimuli consisting of three high contrast blobs arranged in an inverted triangle, can be detected reliably only using tracking procedures, and declines sharply between 4 and 6 weeks after birth (M. H. Johnson, 1999; M. H. Johnson et al., 1991). In combination with neurophysiological data (Atkinson, 1984), these findings suggest that the neonatal face preference is mediated by subcortical structures such as the superior colliculus and pulvinar. If this is the case, then the neonatal face preference is based on a noncognitive process that is distinct, neurologically and psychologically, from that which mediates face recognition during later development and adulthood. The shaping by natural selection of the process responsible for the neonatal face preference constitutes phylogenetic inflection because it biases toward face stimuli the input to recognition mechanisms.

Turning to face processing in adults, there is evidence that the mechanisms mediating face recognition differ from those underlying recognition of other objects in the degree to which they depend on configural or holistic representations rather than on featural or decompositional analysis (Farah, Wilson, Drain, & Tanaka, 1998). This comes not only from the inversion effect but also from experiments showing that face recognition is impaired substantially more by whole face masking stimuli than by masks consisting of jumbled face features and that the difference in disruption caused by whole- and part-based masking stimuli is much smaller when the stimuli are houses (Farah et al., 1998). Thus, it can be assumed that the cognitive mechanisms of face recognition are distinct from those typically involved in recognition of other visual objects. The question is how have they become distinctive: through natural selection (phylogenetic construction) or developmental selection (ontogenetic construction).

Neural localization of face processing does not provide evidence that natural selection has shaped adult face processing mechanisms. Face processing in adults is localized in the ventral temporal cortex (Farah et al., 1995) and, more specifically, in the posterior lateral fusiform gyrus (Ishai, Ungerleider, Martin, Maisog, & Haxby, 1997; Kanwisher, McDermott, & Chun, 1997), but it cannot be assumed that it was “put there” by natural selection. The inference from neural localization to innateness is appealing in the case of face processing because faces constitute a natural category of stimuli, a category that is likely to have been present and important in the evolutionary history of hominids. However, the inference is undermined by functional magnetic resonance imaging (fMRI) data indicating not only that faces activate the fusiform gyrus more than do houses and chairs but also that houses activate a medial temporal region more than do faces and chairs and that chairs activate a lateral temporal region more than do faces and houses (Ishai et al., 1997). Thus, processing of unnatural stimulus categories is also localized within the temporal cortex, suggesting that localization is a product of developmental, not natural, selection.

Further evidence that mature face processing mechanisms are ontogenetically rather than phylogenetically constructed comes from two sources. First, behavioral data indicate that people with extensive experience breeding and judging specified breeds of dog use the holistic mechanisms typical of adult human face processing to recognize individual dogs of their specialist breed (Diamond & Carey, 1986). Second, extensive training to recognize individual Greebles (a novel category of three-dimensional, configural stimuli) is associated with increased activation in the fusiform gyrus, close to the fusiform face area, on presentation of a novel member of this stimulus class (Gautier, Tarr, Anderson, Skudlarski, & Gore, 1999).

The results of the dog expert and Greeble studies and the finding that unnatural category recognition is localized in the temporal cortex suggest wealth of the stimulus: that is, that experience is enough to produce distinctive face recognition mechanisms and therefore that those mechanisms are products of ontogenetic construction. These findings imply that distinctive face recognition mechanisms are constructed from domain-general recognition mechanisms through experience with faces and that the contribution of natural selection to this process is confined to its role in the provision of domain-general recognition mechanisms and in biasing input via the neonatal face preference.

Data indicating wealth of the stimulus do not logically exclude the possibility of phylogenetic construction. It could be argued that the mechanisms used in early ontogeny to recognize faces and other stimuli were favored by natural selection because they have the potential, given sufficient face input, to yield distinctive face processing mechanisms. This is not impossible, but at present, there is no positive evidence supporting the phylogenetic over the ontogenetic hypothesis, for example, evidence of heritable variation in face processing mechanisms (Grice et al., 2001).

In summary, current evidence is consistent with the hypothesis that face processing has evolved not through phylogenetic construction but through a combination of phylogenetic inflection and ontogenetic construction. Early input to the mechanisms responsible for object recognition has been biased toward faces by the action of natural selection on a noncognitive input process (phylogenetic inflection), and extensive experience of individual face recognition in the course of ontogeny results in faces being processed via more holistic mechanisms than other stimulus classes (ontogenetic construction).

### *Theory of Mind*

Like other phylogenetic construction hypotheses, the hypothesis that theory of mind is an innate module (e.g., Leslie & Thaiss, 1992) has two parts. First, it claims that to process input from complex social interactions, humans use cognitive mechanisms that generate and manipulate distinctive kinds of representations. They are distinctive in being representations of mental representations (e.g., beliefs). This claim, which is based primarily on logical analysis of what people say about mental states, is relatively uncontroversial and will not be challenged here. Second, and crucially, the phylogenetic construction hypothesis claims that the capacity to represent mental representations has been specifically shaped by natural selection for its adaptive role in complex social interactions.

By contrast, the ontogenetic construction hypothesis suggests that the potential to conceive of, or represent, mental states arises in the course of development through experience of one's own behavior and that of others, including and in conjunction with the mentalistic language of those who have already developed mature theory of mind. As part of a suite of mechanisms for language, natural selection may have provided humans with a general capacity for metarepresentation—the ability to represent representations—but according to the ontogenetic construction hypothesis, the evidence does not indicate that it has primed the development of mental state concepts in particular.

Support for the phylogenetic construction view has been adduced from evidence that representation of mental states (i.e., theory of mind or mentalizing) (a) is impaired by brain injury, (b) develops in an invariant sequence, and (c) is present in nonhuman primates. These three sources will be considered before turning to the principal source of support for the phylogenetic construction hypothesis: the heritability of autism.

Several studies have provided evidence of specific deficits in mentalizing following brain injury (e.g., Fine, Lumsden, & Blair, 2001; Happe, Brownell, & Winner, 1999; Stone, Baron-Cohen, & Knight, 1998). For example, Happe et al. (1999) showed that relative to age-matched controls, patients with right-hemisphere damage following stroke had greater difficulty in comprehending

stories and cartoons necessitating the attribution of mental states than in understanding similar stories that did not require inferences about beliefs and desires. The neural localization of theory of mind is a topic of interest in its own right, but as was seen in the case of face processing, it cannot answer the question of whether mentalizing evolves phylogenetically or ontogenetically. Neural, and specifically cortical, localization of function can be highly dependent on experience (M. H. Johnson, 1999; Schlagger & O'Leary, 1993).

If the theory of mind normally develops in a standard sequence, in spite of variability in relevant experience, this would support the phylogenetic construction view by implying poverty of the stimulus. However, research on normal development of theory of mind does not indicate an invariant sequence of development because success on false-belief tasks is the only widely recognized milestone and these tests are far from "factor pure" (Jacoby & Kelley, 1992). In addition to requiring apprehension that beliefs can be true or false, false-belief tasks make substantial demands on language comprehension and working memory (Bloom & German, 2000). Different research groups have proposed a variety of earlier signs of theory of mind (e.g., use of communicative gestures, joint attention, and pretense), but in each case, it has been argued that the capacity in question is not specifically related to the representation of mental states (see S. C. Johnson, 2000, for a review). It has been shown that Baka children, like children in western cultures, tend to begin passing false-belief tests between 3 and 5 years of age (Avis & Harris, 1991), but even if one disregards the factor impurity of these tests, this degree of concordance with respect to a single threshold does not constitute an invariant sequence of development. Furthermore, and crucially, neither the within- nor the between-culture studies that are thought to support phylogenetic construction have demonstrated that children's success on false-belief tasks is not experience dependent. These studies do not assess potentially relevant experience or explicitly compare groups that differ in this respect (Gopnik & Meltzoff, 1997).

Research that does examine the social environment of theory of mind development undermines the poverty of the stimulus argument. For example, research shows that between 30 and 36 months of age, just before children begin to pass false-belief tests, there is a sharp increase in the frequency with which mothers refer to their own mental states when talking to infants (Brown & Dunn, 1991) and that development of theory of mind is substantially delayed in deaf children (Peterson & Siegel, 1995), with whom parents rarely communicate about imaginary or unobservable phenomena (Marschark, 1993). These findings imply the kind of correlation between experience and development anticipated by the ontogenetic construction hypothesis, not the developmental invariance claimed as evidence of phylogenetic construction.

Representation of mental states by nonhuman primates is not directly predicted by the phylogenetic construction hypothesis—theory of mind mechanisms could be innate and species specific—but it would provide a much-needed boost for the poverty of the stimulus argument. Even when they are reared among humans, nonhuman primates are unable to understand or participate in conversation about mental states. If, in spite of this, they develop theory of mind, it would indicate, contrary to the ontogenetic construction view, that the capacity to represent mental states does not depend on this linguistic experience. However, there is a growing consensus that nonhuman primates do not represent men-

tal states. In the 20-year period following the publication of Premack and Woodruff's (1978) seminal paper "Does the Chimpanzee Have a Theory of Mind?," numerous studies reported primate behavior that could have been based on mentalizing, but in each case, the data were equivocal (see Heyes, 1998, for a review). The reported behavior could have arisen from mental state attribution, but it could also have occurred by chance, as a consequence of associative learning, or through reasoning not about mental states but about observable properties of the environment in which the behavior occurred. The major experimental studies published since 1998 have either stated that their results are equally explicable in mentalistic and nonmentalistic terms (Hare, Call, Agnetta, & Tomasello, 2000) or reported negative findings (Call & Tomasello, 1999; Povinelli & Bierschwale, 1999; Reaux, Theall, & Povinelli, 1999; Theall & Povinelli, 1999).

Research on autism is thought by some researchers to provide decisive support for the phylogenetic construction account of theory of mind. Numerous, carefully controlled studies have reported that the performance of autistic children and adults is specifically impaired on tasks that are likely to involve representation of mental states (e.g., Baron-Cohen, 1989; Baron-Cohen, Spitz, & Cross, 1993; Happe, 1993; Leslie & Thaiss, 1992), and autism is known to be a genetically heritable disorder; the phenotype has a 36%–91% concordance rate in monozygotic twins and zero concordance in dizygotic twins (Bailey et al., 1995).

There are two reasons why this combination of facts does not imply that the mechanism mediating representation of mental states is heritable. First, it remains uncertain whether the profile of impairment shown by autistic children and adults is best characterized at the cognitive level as a deficit in the capacity to represent mental states (Frith & Happe, 1994). There is empirical support for alternative theories proposing that autism is characterized by weak central coherence (Frith, 1989) or by a deficit in executive functioning (Pennington & Ozonoff, 1996). Each of these theories suggests that what are disturbed in autistic development are domain-general cognitive mechanisms, which process both social and asocial stimuli, and that this disturbance is conspicuous in tasks involving mentalizing because they typically make heavy demands on the general mechanisms. The "theory theory" has been supported against these alternatives by reports that the performance of autistic children is impaired on false-belief tasks, which require representation of mental representations, but not on false-photograph tasks, which require representation of physical representations (Leekam & Perner, 1991; Leslie & Thaiss, 1992). However, more recent evidence indicates that when the two types of task require inhibition of equally strong prepotent responses, autistic children are impaired in the performance of both, implying that their problems are not specific to the representation of mental representations (Russell, Saltmarsh, & Hill, 1999).

Second, even if it were true that the cognitive profiles of children and adults with autism are best characterized in terms of a mentalizing deficit, it would not follow that autistic individuals inherit an abnormality at gene loci that normally code for the development of a distinctive mechanism for the representation of mental states (Karmiloff-Smith, 1998; Paterson, Brown, Gsodl, Johnson, & Karmiloff-Smith, 1999). This inference would be supported by evidence that autistic infants who have not had the opportunity for ontogenetic construction are specifically impaired on tasks requiring mental state attribution, but there is no such

evidence available. None of the tests that can be given to infants clearly require representation of mental states (S. C. Johnson, 2000). Instead, there is evidence that autistic infants show early impairments in joint attention (e.g., Baron-Cohen et al., 1996), a behavior that does not require representation of mental states but that is likely to have a major effect on rate of cultural learning, including cultural learning of theory of mind. Therefore, at most, research on autistic infants would support the inference that natural selection has shaped a behavior-control process underlying joint attention, which influences the type and extent of interpersonal information received by infants. This process may contribute to the ontogenetic development of mechanisms for the representation of mental states, but there is no positive evidence that such a role has been specifically favored by natural selection.

In summary, whereas research on theory of mind has not demonstrated poverty of the stimulus or heritability of a mechanism for the representation of mental representations, it has identified variables in the social environment that correlate with development of the capacity to represent mental states. Therefore, rather than supporting phylogenetic construction, the evidence is also consistent with an ontogenetic construction hypothesis, which proposes that the capacity to represent mental states is learned through exposure to a social, linguistic environment in which theory of mind is used to explain behavior.

### Ontogenetic Inflection

A cognitive process evolves through ontogenetic inflection when developmental selection, interaction between the cognitive system and its environment during ontogeny, adaptively biases input to a cognitive mechanism without resulting in qualitative change to the mechanism itself. Unlike the earlier discussions of phylogenetic inflection and ontogenetic construction, this section examines a single example, imitation, in some detail. This is appropriate because to argue that a cognitive process evolves through ontogenetic inflection rather than phylogenetic construction, one must show both that the locus of adaptive modification is the input to a cognitive mechanism not the mechanism itself (as for phylogenetic inflection) and that the source is developmental selection rather than natural selection (as for ontogenetic construction). In addition, imitation is an interesting example because research in this area not only shows that developmental selection can change cognitive processes but also includes a model of how such change occurs.

### Imitation

Imitation consists of learning a new motor pattern or configural body movement (e.g., a facial gesture or dance movement) by observing another individual, a model, performing that motor pattern. It subsumes some phenomena described as *observational learning* but excludes, among others, cases in which model observation results in nonspecific behavioral activation (*social facilitation*) or in learning about the properties of inanimate objects rather than about body movement (*observational conditioning*, *emulation learning*, and *stimulus enhancement*; Heyes, 2001; Whiten & Ham, 1992). Two theories of imitation, one suggesting that it evolved through phylogenetic construction and the other that it is a product of ontogenetic inflection, are outlined, and then the evidence for each is evaluated.

Active intermodal matching theory (AIM; Meltzoff & Moore, 1997) is the most clearly elaborated of those that suggest that imitation is based on a distinct cognitive mechanism shaped by natural selection to mediate cultural transmission: that is, that imitation evolved through phylogenetic construction. AIM was formulated to explain copying of adult facial gestures by human infants but has been applied to imitation generally (e.g., Decety, Chaminade, Grezes, & Meltzoff, 2002). It suggests that there is an innate imitation mechanism that, compared with other mechanisms of motor learning, represents body movements in a distinctive way.<sup>7</sup> When an individual observes another's body movement, the imitation mechanism forms a supramodal (neither sensory nor motor) representation of the movement's "organ relations." Then, in a goal-directed selection process, this supramodal representation is compared with proprioceptive feedback from the observer's motor output, also encoded supramodally, and motor variants that match the representation of the modeled movement are favored for future production.

By contrast, associative sequence learning theory (ASL; Heyes, 2001; Heyes & Ray, 2000) suggests that imitation arises through ontogenetic inflection. It assumes that the same mechanisms mediate imitation and practice-based motor learning: Body movement is represented in the same way when individuals are learning a new movement by observing its performance as when they are learning a new movement with any other kind of guidance. However, in the case of imitation, these domain-general mechanisms of motor learning are processing atypical input, that is, observed, rather than executed, body movements. According to ASL, processing of this atypical input is made possible by a set of bidirectional excitatory links or vertical associations, each of which connects sensory (usually visual) and motor representations of the same movement. Consequently, when such a link has been established, movement observation activates not only a sensory representation but also a representation of the kind that can be processed by mechanisms of motor learning.

The ASL hypothesis casts imitation as an example of inflection rather than construction because it suggests that imitation occurs through the same mechanisms as practice-based motor learning but has distinctive input. It casts the inflection, the input alteration, as having an ontogenetic rather than phylogenetic source because it proposes that the vast majority of vertical associations are formed through experience in which a movement is concurrently observed and executed.<sup>8</sup> Experience of this kind is obtained when individuals watch themselves performing an action, directly or using a device such as a mirror, and when an individual watches another as the two engage in synchronous action in response to a common stimulus, because the second individual is imitating the first, or in the context of explicit training.

<sup>7</sup> Meltzoff and Moore (1997) pointed out that rather than being innate, the mechanism that creates supramodal representations of organ relations from visual input may be experiential in origin. However, they did not identify prenatal experience of a kind that might be sufficient to support this process of ontogenetic construction.

<sup>8</sup> A few vertical links appear to be innate (e.g., those connecting sensory and motor representations of yawning and smiling in humans), and insofar as they are adaptive, these would be classified as products of phylogenetic inflection.

Three lines of evidence are frequently cited in support of AIM, the phylogenetic construction theory of imitation: (a) activation of Broca's area, in the left inferior frontal cortex, during imitation (Iacoboni et al., 1999); (b) facial gesture imitation in neonates (e.g., Meltzoff & Moore, 1977); and (c) comparative data suggesting that apes, but not other animals, are capable of imitation (Thorndike, 1898; Whiten & Ham, 1992). The first of these is thought to imply that there is a distinctive imitation mechanism, and the other two are cited as evidence that this mechanism is innate.

Research using fMRI (Iacoboni et al., 1999) and magnetoencephalography (Nishitani & Hari, 2000) has found more activity in the left inferior frontal cortex when people are performing finger movements cued by movement observation than when their movements are self-paced or cued by inanimate stimuli. This has been interpreted as indicating that the left inferior frontal area (IFA) is the site where imitation-specific, supramodal representations of body movement are implemented. However, more carefully controlled positron emission tomography experiments suggest that the left IFA mediates body movement recognition (e.g., naming) rather than imitation. These experiments show that the left IFA is more active when people are passively watching meaningful arm movements (e.g., mime of opening a bottle) than when they are passively watching static hands and that, in comparison with the same control, the left IFA is not active during passive observation of meaningless arm movements or of meaningful or meaningless arm movements under instructions to imitate (Decety et al., 1997; Grezes, Costes, & Decety, 1998). Thus, research on the left IFA does not support the claim that imitation is mediated by distinctive, supramodal representations of body movement (see Heyes, *in press*, for further discussion).

The primary, developmental evidence in support of the phylogenetic construction hypothesis has been questioned by reanalysis of the entire corpus of neonatal imitation data (Anisfeld, 1991, 1996). This reanalysis found that (a) tongue protrusion is the only gesture for which there is reliable evidence that observation increases the frequency of subsequent performance in neonates and (b) the absence of reliable effects for other facial gestures is not due to test insensitivity. Many infancy researchers continue to believe that neonates can imitate a range of facial expressions via a cognitive process (Meltzoff & Moore, 1998), but new data published since Anisfeld's (1991, 1996) critique favor his view. These empirical studies report further evidence that neonatal imitation is confined to tongue protrusion (Anisfeld et al., 2001), a failure to find imitation of tongue protrusion (Ullstadius, 1998), and results suggesting that even the tongue-protrusion effect, when present, is not sufficiently specific to constitute imitation (Jones, 1996). The last study shows that exposure to a variety of interesting stimuli (e.g., a nonsocial light display) causes an increase in the frequency of tongue protrusion in very young infants.

The comparative evidence of an innate cognitive mechanism for imitation is also less than compelling. Contrary to the findings of earlier surveys (Thorndike, 1898; Whiten & Ham, 1992), recent experiments suggest that the capacity to imitate body movements is present not only in our closest primate relatives but also in birds (Akins, Klein, & Zentall, 2002; F. M. Campbell, Heyes, & Goldsmith, 1999; Dorrance & Zentall, 2001; Heyes & Saggerson, 2002). In addition, there is evidence that chimpanzees can imitate only to the extent that they have had prior experience of interacting

with humans (Tomasello, 1996, 2000) or explicit training to imitate (Custance, Whiten, & Bard, 1995). Although incompatible with AIM, these data are consistent with the ASL, ontogenetic inflection, model of imitation because human contact provides chimpanzees with the opportunity to form a relatively rich repertoire of vertical associations. It gives them extensive experience of reflecting surfaces and, because humans tend to treat chimpanzees like children, experience both of being rewarded for matching behavior and of being imitated by their caregivers.

Further evidence in support of ASL comes from research demonstrating neurological and functional equivalence between imitation and other motor learning. For example, most of the areas that show greater regional cerebral blood flow when participants are observing arm movements to imitate than during passive observation are cortical and subcortical regions known to be active during verbally instructed motor preparation and mental practice (Decety et al., 1994, 1997; Stephan, Fink, Passingham, & Silbersweig, 1995). These include the premotor cortex, the supplementary motor area, the inferior parietal gyrus, the superior parietal lobule, the anterior cingulate gyrus, the posterior caudate nucleus, the dorsal frontal gyrus, the cerebellum, the cuneus, and the left precuneus (Grezes et al., 1998). Like studies using electromyography and transcranial magnetic stimulation (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Strafella & Paus, 2000), which show that passive observation of body movements is associated with specific innervation in the corresponding muscles, activation of these areas during observation for imitation suggests that there are direct links, vertical associations, between movement perception and matching movement execution.

In the area of functional equivalence, many studies show not only that practice and observation are equally effective in promoting skill learning (Blandin, Lhuisset, & Proteau, 1999; Blandin, Proteau, & Alain, 1994) but also that variables such as training schedule (Blandin & Proteau, 2000; Blandin et al., 1994) and stimulus-response compatibility (Heyes & Ray, 2003; Ishikura & Inomata, 1995; Sturmer, Aschersleben, & Prinz, 2000) have the same effects on imitation and practice-based motor learning. In one study using the serial-reaction time task, participants learned a sequential finger movement skill through practice or by observing skilled performance and were then required to demonstrate their sequence knowledge using arm rather than finger movements (Heyes & Foster, 2002). Both groups showed poor transfer, indicating that their sequence knowledge was effector-specific. This result was predicted by ASL, which assumes that movement observation directly activates motor representations and that subsequent reconfiguration of these representations is mediated by domain-general mechanisms of motor learning, but is incompatible with AIM. If observed movements are supramodally represented, it should be possible to express knowledge gained through movement observation using different muscle groups.

In conclusion, the evidence suggests that imitation is based on domain-general mechanisms of motor learning to which social input, observed body movements, becomes accessible through experience. ASL suggests that the developmental selection process that produced this input alteration, or inflection, consists of the formation of vertical associations between sensory and motor representations, through experience of simultaneous observation and execution of movements. Experience of this kind is available to humans and other animals whenever they behave synchronously

with a conspecific, but the human capacity for imitation is also fostered by cultural artifacts and practices such as mirrors and training. Thus, whereas phylogenetic construction accounts typically cast cultural transmission of information as a product of imitation, ASL theory suggests that the human capacity for imitation is, in part, a product of enculturation. This is not to deny, however, that imitation also has important cultural consequences. For example, as suggested by Meltzoff and his colleagues (Gopnik & Meltzoff, 1997; Meltzoff & Moore, 1997), imitation may contribute to the ontogenetic construction of theory of mind.

### Concluding Comments

It has been argued in this article that two distinctions are particularly important in the evolutionary analysis of cognition: between phylogenetic and ontogenetic sources of adaptive change to a cognitive process and between changes to the input of a cognitive mechanism and changes to the cognitive mechanism itself. Acknowledging and combining these distinctions suggest that phylogenetic construction is just one of four routes to the adaptive modification of cognitive processes. A range of cognitive phenomena that are commonly claimed to have evolved by phylogenetic construction have been examined, and it has been argued in each case that the evidence is as consistent or more consistent with the phenomena having evolved via phylogenetic inflection (imprinting, spatial memory in food-storing birds, and the neonatal face preference), ontogenetic construction (face processing and theory of mind), or ontogenetic inflection (imitation).

As a framework rather than a theory, the four routes taxonomy does not, in isolation, make testable predictions. To yield such predictions, it could be readily combined with hypotheses about the types of environment favoring different kinds of adaptive specialization (e.g., Plotkin & Odling-Smee, 1981; Sober, 1994). However, its primary function is to enable the formulation of certain kinds of research questions—questions probing the source and locus of adaptive change rather than asking simply whether adaptive specialization has occurred—and the organization of data in a way that enables trends to be detected. The former effect is appropriate because although evolutionary psychology is immature relative to evolutionary biology, it is well past the point of needing to demonstrate to its practitioners or to a wider audience of psychologists that behavior-control processes can be adaptive. That point was clear even to some of the founders of the psychological tradition that HNEP regards as antithetical to evolutionary analysis—to figures such as Edward Thorndike, B. F. Skinner, and Clark Hull, who were all influenced by Darwinian theory (Smith, 1986).

The task of evolutionary psychology is not to show that natural selection can influence cognitive processes but to establish exactly what kind of effects natural selection, and developmental selection, do and do not tend to have. Just as natural selection tends to be conservative with respect to respiratory pigments (e.g., hemoglobin) and revisionist with respect to respiratory structures (e.g., skin, gills, and lungs), it is likely that some properties of behavior-control systems are more susceptible than others to phylogenetic change and therefore that they show greater variation across species and in the course of development. Organizing existing data on cognitive evolution using the four routes framework, this article found that most putative examples of phylogenetic construction

are more likely to be products of phylogenetic inflection, ontogenetic construction, or ontogenetic inflection. If this is correct, it implies that phylogenetic construction is rare and that natural selection is generally conservative with respect to cognitive mechanisms.

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