

## Brain and Cognitive Evolution: Forms of Modularity and Functions of Mind

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Genetic and neurobiological research is reviewed as related to controversy over the extent to which neocortical organization and associated cognitive functions are genetically constrained or emerge through patterns of developmental experience. An evolutionary framework that accommodates genetic constraint and experiential modification of brain organization and cognitive function is then proposed. The authors argue that 4 forms of modularity and 3 forms of neural and cognitive plasticity define the relation between genetic constraint and the influence of developmental experience. For humans, the result is the ontogenetic emergence of functional modules in the domains of folk psychology, folk biology, and folk physics. The authors present a taxonomy of these modules and review associated research relating to brain and cognitive plasticity in these domains.

For several millennia, scholars have debated whether human traits largely result from our biological nature or are a reflection of nurture, specifically our developmental experiences. The debate continues to this day and has recently pervaded the cognitive neurosciences, at least with respect to theoretical models of brain and cognitive evolution (Elman et al., 1996; Fodor, 1983; Pinker, 1994, 1997; Quartz & Sejnowski, 1997; Tooby & Cosmides, 1995). All serious theorists now agree that there are inherent, gene-driven constraints on and experience-based—especially during the developmental period—modifications of brain organization and cognitive functions. The relation between constraint and the influence of developmental experience can be conceptualized in terms of brain and cognitive plasticity, as shown in Figure 1. The areas above and below the dashed lines in the figure represent theoretical space in which there is little debate; that is, few theorists argue that all features of brain and cognition are due either to gene-driven constraints or to the pattern of developmental experiences. The area within the dashed lines represents the focus of current debate, namely the relative contributions of constraint versus experiences on brain organization and cognitive functions. There are, of course, many nuances within this bounded area and some degree of characterization is necessary to define the range of

theoretical positions. Still, a brief but simplified sketch of the two ends of the theoretical space highlights points of controversy.

One end is represented by the position that brain and mind are a constellation of modular systems with a high degree of inherent constraint (Fodor, 1983; Lenneberg, 1967; Pinker, 1994; Tooby & Cosmides, 1995), although the expression of different features of these systems can be contingent on early experiences (Greenough, Black, & Wallace, 1987). As an example, the brain and cognitive systems involved in processing phonemes (e.g., *ba*, *da*) are conceptualized as inherent, but the phenotypic expression of one phonemic system or another is contingent on early exposure to associated sounds (Cosmides & Tooby, 1994). Gallistel (2000) suggested that inherent navigational systems can include mechanisms that enable the formation of relevant memory patterns, such as star patterns used by migratory birds to guide navigation back to the birth site for breeding. The ability to form such experience-dependent memories is, however, assumed to occur within the constraints of an evolved, modular system. The other end is represented by the position that the anatomical and functional organization of the neocortex emerges through interaction between minimal inherent constraint and developmental experience (Elman et al., 1996; Finlay, Darlington, & Nicastro, 2001; La Cerra & Bingham, 1998; Quartz & Sejnowski, 1997). The ability to process language-specific phonemes, as an example, results from constraints on the range and form of auditory information that can be processed. Within these constraints, regularities in spoken language interact with a largely uncommitted neocortex. The eventual result is the creation of systems that support language-specific processing (Paterson, Brown, Gsödl, Johnson, & Karmiloff-Smith, 1999).

Theorists at both ends of the theoretical space tend to focus on adaptive and functional benefits of inherent constraint on or openness to experiential modification of brain organization and cognitive functions, often without full consideration of attendant costs. Cost–benefit trade-offs are, nonetheless, common to biological systems (Williams, 1957), including the brain (Kaas, 2000), and

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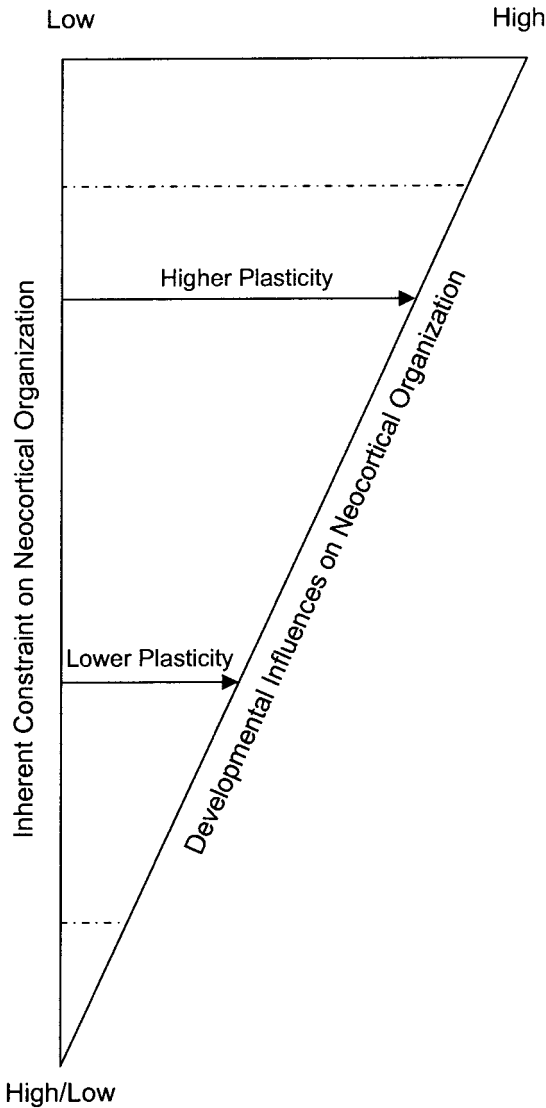


Figure 1. The triangle represents the relation between inherent constraint and the influence of developmental experience on brain organization and cognitive functions. As degree of inherent constraint increases, the potential for experiential modification decreases. The length of the arrows in the center of the triangle represents the corresponding degree of brain and cognitive plasticity. The area above the first dashed line represents the position that the organization of the neocortex is almost completely dependent on developmental experiences, whereas the area below the second dashed line represents the position that the organization of the neocortex is almost completely determined by genetic constraints. Few theorists hold either of these positions.

any potential cost of inherent constraint or openness to experiential modification influences the evolution of brain and cognitive plasticity. The most basic of these cost–benefit trade-offs are illustrated in Figure 2, trade-offs that can only be appreciated in the context of the ecologies in which the species evolved (Dukas, 1998). In this view, the brain is an information-processing organ that provides the interface between the organism and the ecologies in which the organism is situated. The brain functions to guide the

organisms’ behavior so as to achieve outcomes, such as predator avoidance or mate finding, that covary with survival and reproduction in these ecologies. Selection will favor brain and cognitive systems that are open to experiential modification to the degree that associated information patterns—such as those generated by predators—are variant across generations and lifespans. Selection will favor inherent constraint to the degree that information patterns are invariant across generations and lifespans. Of course, different brain and cognitive systems can vary with respect to relative degree of openness and constraint to the extent that associated information patterns are variant or invariant, respectively. From this perspective, plasticity is the result of cost–benefit trade-offs during brain and cognitive evolution.

One of the central goals of this article is to provide some structure to the inner section of the triangle presented in Figure 1 by proposing four forms of modularity and three forms of plasticity. These core features of constraint and openness are described in the third section below. The first and second sections (Evolution and Brain Organization and Experiential Modification of Brain Organization, respectively) provide respective reviews of research related to the issues of inherent constraint on and experiential modification of brain organization and cognitive functions. The

Variant Across Generations and Lifespans	
Low Constraint and High Plasticity	
<p>Slow initial learning of evolutionarily relevant information patterns and poor discrimination of relevant and irrelevant information</p> <p style="text-align: center;"><b>Costs</b></p> <p>Low ability to adjust to change in information pattern</p>	<p>High ability to adjust to change in information pattern</p> <p style="text-align: center;"><b>Benefits</b></p> <p>Fast, efficient processing of evolutionarily relevant information patterns and good discrimination of relevant and irrelevant information</p>
High Constraint and Low Plasticity	
Invariant Across Generations and Lifespans	

Figure 2. Information patterns that covary with survival and reproduction. The rectangle highlights cost–benefit trade-offs that are predicted to influence the evolution of brain and cognitive plasticity.

fourth section (Domains of the Human Mind) presents a taxonomy of functional domains of the human mind and discusses each domain in terms of the forms of phenotypic plasticity introduced in the third section (Soft Modularity).

### Evolution and Brain Organization

Comparative (i.e., across-species) analyses of complex animals have demonstrated similarity in the subdivisions of the central nervous system (CNS) and similarity of functional organization and specialization of these subdivisions (Krubitzer, 1995). These analyses of brain morphology suggest a conservation of CNS subdivisions (constraint), and a conservation of the genes that may regulate the generation of such subdivisions (Krubitzer & Huffman, 2000). The literature in these areas of comparative brain morphology and comparative genetics is large and growing, and thus an exhaustive survey is not possible. A sampling is, however, provided in the respective subsections below. Our goal is to present evidence and the evolutionary logic for some degree of evolved organization of brain and functions of mind. A detailed, step-by-step discussion of these issues is needed to fully appreciate the power of the evolutionary approach for understanding how the brains and minds of different species can be similar and yet different.

The research we describe in the following sections suggests that the basic architecture of the brain and some functions of mind (e.g., sound perception) are conserved across mammalian and perhaps many nonmammalian species. Our goal is to describe what appears to be the basic architecture of the brain, specifically the neocortex, and possible genetic and developmental mechanisms that regulate constraint in the CNS. This, in turn, provides a frame for understanding how evolution can act on conserved brain systems to create species-specific neurocognitive specializations. To achieve this goal, we provide in the first section a brief overview of research comparing various cross-species similarities in CNS subdivisions in an attempt to establish homology (i.e., similarity due to a common ancestor) and evolutionary relationship. A brief survey of the cross-species conservation of genes that code for the prenatal organization of the CNS and a description of theories of neocortical development and evolution are provided in the second and third sections, respectively. At the end of the third section we describe a model that provides a frame for understanding cross-species continuities in brain development and evolution and helps to clarify how the brains of different species can be both similar, different, and modifiable in response to evolutionary pressures.

### Comparative Neurobiology

Comparative neurobiology can be used as a tool to better understand brain evolution. One can examine extant species whose lines branched off the evolutionary tree at different points in evolutionary history. Although extant species have continued to evolve independently, they provide the best example of a history of brain organization and evolution. For example, in mammalian evolution three major lines have emerged: *prototheria* (extant example: duck-billed platypus, *Ornithorhynchus anatinus*); *metatheria* (extant example: eastern gray kangaroo, *Macropus giganteus*); and *eutheria* (i.e., placental mammals; extant example: human being, *Homo sapiens*). Thus, comparative neurobiologists can

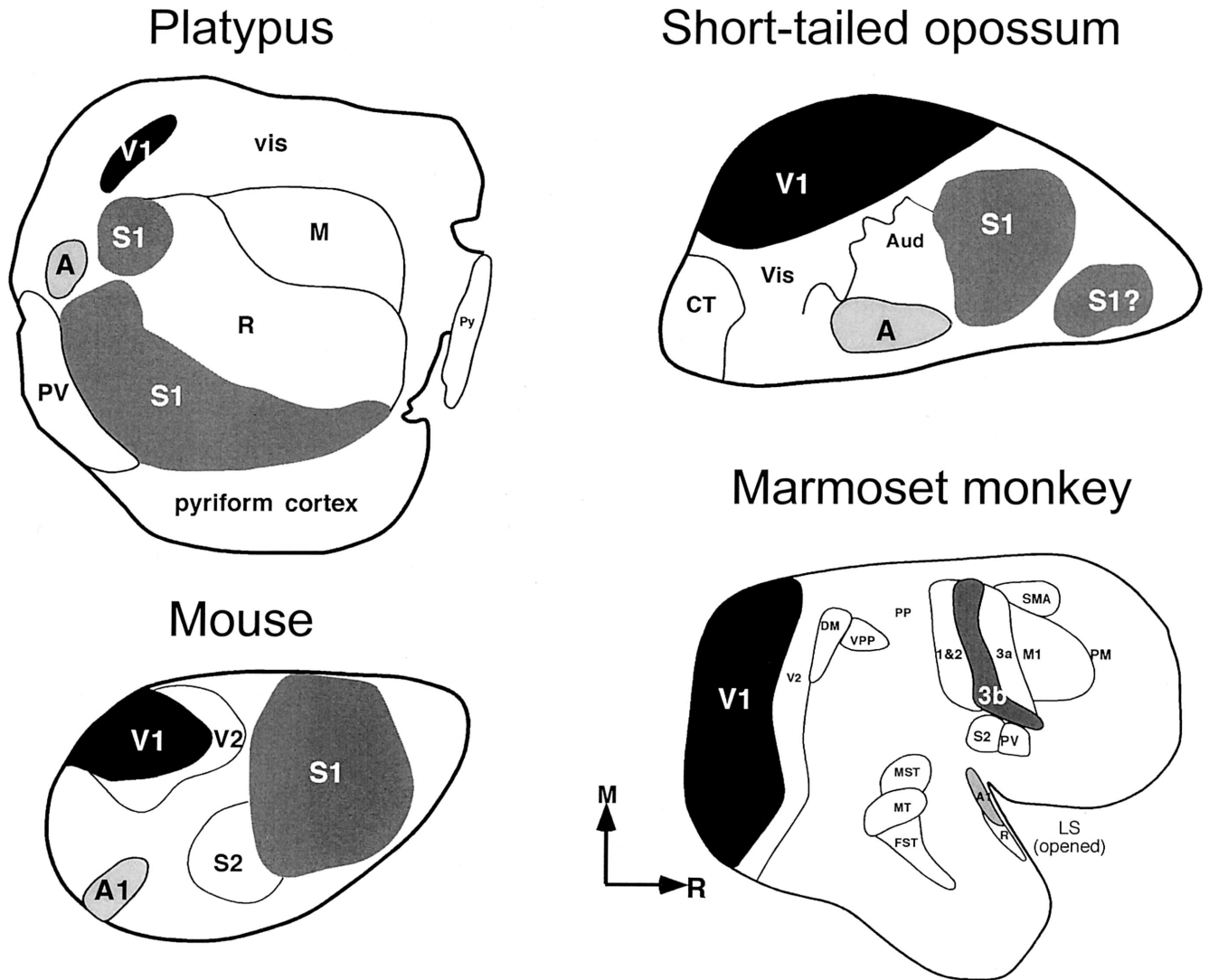
examine the functional morphology of example species from these lines in an attempt to deduce similarities (constraints conserved from a common ancestor) and differences (species-specific adaptations) in the brains of species that share recent to very distant common ancestors.

Analyses of many species have uncovered much constraint or conservation in the nervous system. For example, the diencephalon (including the thalamus and hypothalamus) of all mammals studied, including prototherian, metatherian and eutherian mammals, appears highly similar. The organization of the thalamus, a diencephalic structure that is the relay for sensory information from the periphery to the neocortex, is highly conserved across mammals. Many of the sensory nuclei of the thalamus (e.g., the lateral geniculate nucleus) are not only architectonically alike, they are also functionally similar in terms of cellular physiology and connectivity (Jones, 1985). In even a novice examination of a mouse (*Mus musculus*) and human thalamus, some conserved and apparently homologous nuclei are readily apparent. Similarities such as these exist in other positions along the neural axis as well. For instance, many brainstem nuclei, such as the cuneate, gracile, and trigeminal nuclei have been identified in all mammals studied, including humans (Butler & Hodos, 1996).

Conservation of CNS subdivisions is not limited to subcortical regions. For example, the CA1 and CA3 divisions of the hippocampus are conserved across mammalian lineages (Butler & Hodos, 1996). Regions, or areas in the neocortex are also conserved, particularly primary areas, as illustrated in Figure 3. This figure shows the homologous primary sensory areas (primary visual, somatosensory, and auditory cortex) in prototherian (platypus), metatherian (short-tailed opossum, *Monodelphis domestica*) and eutherian (mouse and marmoset monkey, *Callithrix jacchus*) mammals. The homology of these areas has been established using multiple methods that are both anatomical and functional (see below). All mammals, including humans (Disbrow, Roberts, & Krubitzer, 2000; Engel, Glover, & Wandell, 1997), have basic auditory, visual, and somatosensory neocortical regions (Krubitzer, 1995; Northcutt & Kaas, 1995), and reptiles and birds have analogous (i.e., same function but independent evolution), perhaps homologous, regions in the telencephalon (the analogue to the neocortex; Doupe & Kuhl, 1999; Karten, 1997). In addition, Disbrow et al. (2000), using functional imaging techniques, demonstrated the presence of multiple areas in the somatosensory cortex of humans. They nicely demonstrated these areas to be analogous and likely homologous to areas previously described in the anterior parietal cortex of monkeys. The pattern emerging from current research suggests that some of the specialized functions of the mammalian neocortex and subcortical regions are conserved across species.

### Comparative Genetics

In addition to the observation that many subdivisions of the CNS appear to be conserved across different lineages, it has been suggested that many genes that code for the development of these different subdivisions are also conserved across species, including humans (Cavaillé et al., 2000; Chan & Jan, 1999; Gilbert, Opitz, & Raff, 1996; Holland & Holland, 1999; Katz & Harris-Warrick, 1999; Krubitzer & Huffman, 2000; Manzanares et al., 2000; Reichert & Simeone, 1999). As we noted, many of the basic



**Figure 3.** Four cartoon flattened right hemispheres from representative animals from the three major mammalian lineages: prototherian platypus (*Ornithorhynchus anatinus*), metatherian short-tailed opossum (*Mondelphis domestica*), eutherian mouse (*Mus musculus*), eutherian marmoset monkey (*Callithrix jacchus*). The neocortex was removed from the rest of the brain. The medial ( $\uparrow$  M) surface of the cortex is up, and the rostral ( $\rightarrow$  R) surface is to the right. All of these mammals have a primary somatosensory cortical area (S1; medium gray), a primary auditory area (A/A1; light gray) that are likely to have been present in the common mammalian ancestor. Aud = secondary auditory area; CT = caudal temporal area; DM = dorsal medial area; FST = fundal superior temporal area; LS = lateral sulcus; M = presumptive motor cortex; M1 = primary motor area; MT = medial temporal area; MST = medial superior temporal area; PM = premotor area; PP = posterior parietal area; PV = parietal ventral area; R = rostral somatosensory region; S2 = secondary somatosensory area; SMA = supplementary motor area; V1 = primary visual area; V2 = secondary visual area; vis = visual cortex; VPP = ventroposterior parietal area; 1 & 2, 3a, 3b = regions of the somatosensory cortex.

building blocks and specializations (e.g., for processing sounds) are the same for the human brain and other brains (Karten, 1997). These conserved CNS subdivisions must of course be genetically mediated, and were likely present in the common ancestor.

Recent research suggests that the genes that establish or regulate the generation of these subdivisions are conserved as well. Reichert and Simeone (1999), for instance, reported the existence

of several homologous genes that guide the development of the CNS in the fruit fly (*Drosophila*), laboratory mouse, and human. Abnormalities in the CNS are found in *Drosophila* mutants in which these genes are not expressed, and replacement with homologous human genes "rescue the brain and other defects" (Reichert & Simeone, 1999, p. 591). These same *Drosophila* genes have been shown to influence cortical development in the mouse,

and other studies suggest that other homologous genes may control the development of the basic structure of the CNS in invertebrates and vertebrates (e.g., Holland & Holland, 1999; for a review, see Rubenstein, Shimamura, Martinez, & Puelles, 1998). In addition, there are transcription factors, growth factors, and secreted molecules that appear to be conserved between chick (*Gallus domesticus*) and mouse in the developing telencephalon. These genes, such as BMPs, SHH, WNTs, and FGFs, appear to function as patterning centers in the developing telencephalon and regulate the genesis of subdivisions in both species (see *An intrinsic model*). Some of the genes, such as SHH, are also responsible for a similar function, that is, generation of ventral structures in the developing CNS in nonmammals (Lee, Danielian, Fritsch, & McMahon, 1997). We hypothesize that some or all of these genes are involved in the regionalization of the human forebrain. There are many more examples of genes that seem to be homologous as well as analogous in terms of their function in nervous system development, across species as diverse as the fly, chick, and mouse (Brose & Tessier-Lavigne, 2000; Chan & Jan, 1999), but their description is beyond the scope of the current review.

The conservation of homologous genes for brain development suggests that the functional capabilities of the human brain and mind, including the neocortex, would be similar in some respects to the functional capabilities of the brain and mind of other mammals and probably many nonmammalian species (Karten, 1997). We predict, on the basis of invariant environmental and ecological conditions described in a later section (Soft Modularity), some degree of continuity (and homologous genes) across species. For instance, on the basis of the three-dimensional organization of physical space and the physics of information transmission—such as the conduction of sound through air and water—neural, perceptual, and cognitive systems that are sensitive to these forms of information would be expected to evolve in many species (Shepard, 1994). As an example, portions of the mammalian temporal cortex and its analogue in reptilian and avian species subserved the processing of sounds, including specialized regions for processing conspecific vocalizations (Doupe & Kuhl, 1999; Karten, 1997), although species-specific specializations within these brain systems are also found (Preuss, 2000). At the same time, it remains to be seen if these brain and functional continuities are due to conserved genes.

#### *Development of the Neocortex*

Because evolutionary change often results from changes in developmental processes, it is difficult to separate theories of neocortical evolution and neocortical development. In this section we describe current theories of neocortical development; we relate them in a later section (*Evolution of the neocortex*) to theories of neocortical evolution.

It has been understood for nearly a century that the human neocortex is subdivided into many functionally and architectonically (e.g., cell type and organization) distinct areas (Brodmann, 1909). *Arealization* refers to the formation of these areas (largely prenatally) in the developing neocortex and is best understood in the sensory cortices. A sensory cortical area is defined as being *distinct* if it has a complete electrophysiological representation of the sensory epithelium (e.g., skin), unique stimulus preference, architectonic appearance, and pattern of connections. In the adult,

electrophysiological recording results and histochemistry have been used to define some areas in the neocortex, especially primary sensory areas (Kaas, 1982). How these areas are established, either evolutionarily or within the development of a single brain, has been the subject of much debate (O'Leary, 1989; Rakic, 1988; for a review, see Rubenstein et al., 1999). As we describe below, two opposing schools of thought have emerged.

#### *Neocortical Arealization: Opposing Views*

What was once a very hard-lined distinction between two different theoretical standpoints of prenatal neocortical arealization is transforming into a new theory of neocortical development that accepts the validity of both arguments. One view, first postulated by Rakic (1988, 1995a) and referred to as the protomap hypothesis, states that the development of discrete neocortical areas is dependent on a mechanism or mechanisms intrinsic to the neocortex. Specifically, molecules in the proliferate prespecify the tissue to become a certain cortical area, or at least an area within a particular sensory system (e.g. a visual cortical area), by setting up columns of neurons—that is, radial units—that are later organized into cortical areas. The neurons that compose these neocortical areas receive and generate prespecified inputs and outputs to and from other cortical and subcortical areas and later respond to a restricted class of stimuli, such as features of conspecific vocalizations. The opposing idea, referred to as the protocortex hypothesis, emphasizes the role of thalamic input in the determination of neocortical areal fate (for a review, see O'Leary, Schlaggar, & Tuttle, 1994). This hypothesis rests on the idea that cortical precursor cells are nonspecific, establishing their identity later in development, thus giving the developing cortical neuroepithelium a tabula rasa character. In this view, the thalamic afferents, particularly those from sensory projection nuclei, “assign” neocortical territories.

*An intrinsic model.* Consistent with the general idea of Rakic's (1988) proposal, recent results have shown that the developing neocortex is “patterned” early in development, with differential expression of genes in different cortical areas. These gene expression patterns are unperturbed in mice lacking thalamocortical inputs, suggesting that some degree of arealization may occur without thalamic input (Miyashita-Lin, Hevner, Wassarman, Martinez, & Rubenstein, 1999; Nakagawa, Johnson, & O'Leary, 1999; see also Bishop, Goudreau, & O'Leary, 2000). It has been postulated that patterning centers in the midline of the developing telencephalon (brain tissue that will include the neocortex) have a primary role in regulating neocortical regionalization (Miyashita-Lin et al., 1999; Rubenstein et al., 1999). A dorsal patterning center expresses high levels of BMP and Wnt genes. Mutations that affect Wnt signaling lead to defects in the most medial cortical regions (e.g., the hippocampal complex; Grove, Tole, Limon, Yip, & Ragsdale, 1998). Mutations affecting BMP signaling lead to dorsal-midline patterning defects, such as limited growth of the neuroectoderm, and increased cell death (Furuta, Piston, & Hogan, 1997).

The rostradorsal midline of the telencephalon expresses high levels of FGF8, a gene that is a member of the family of mammalian genes that govern fibroblast growth factors. These factors regulate growth and patterning in multiple embryonic tissues (Crossley & Martin, 1995; Lee et al., 1997; Reifers et al., 1998;

A. S. Tucker, Yamada, Grigoriou, Pachnis, & Sharpe, 1999). This domain has been postulated to regulate rostral patterning of the telencephalon and its constituents, including the neocortex (Crossley, Martinez, Ohkubo, & Rubenstein, 2001; Fukuchi-Shimogori & Grove, 2001; Rubenstein et al., 1999). Furthermore, a new study suggests that FGF8 may play a general role in anterior–posterior patterning of the neocortex (Fukuchi-Shimogori & Grove, 2001). In sum, there is clear evidence that the largely prenatal development of “areas” in the neocortex is at least to some extent dependent on intrinsic, genetically mediated properties of the neocortex.

*An extrinsic model.* If cortical precursor cells are predetermined in terms of their fate (protomap hypothesis), and thalamic afferents do not provide neuronal identity, then transplanting cells, redirecting afferents, or altering the size of the neuroepithelium should not have an effect on areal or regional fate. This is not the case. When cells from the location of visual cortex (presumably destined to be visual cells) are transplanted into the developing somatosensory cortex, barrel cells that are common in the somatosensory cortex are formed (Schlagger & O’Leary, 1991). Also, in an elegant series of experiments, Sur and colleagues demonstrated that if retinal input is rerouted to the auditory cortex so as to maintain normal thalamocortical connectivity, the auditory cortex develops many of the same properties of the visual cortex (Roe, Kwon, & Sur, 1992; Roe, Pallas, Hahm, & Sur, 1990; Sharma, Angelucci, & Sur, 2000). In addition, in early development the removal of all cells destined to be visual cortical cells prior to the thalamic innervation of the neocortex results in a rostral shift (in a position that would normally be occupied by the somatosensory cortex) of lateral geniculate connections (the lateral geniculate nucleus is the primary visual nucleus of the thalamus; Huffman, Molnar, et al., 1999). In other words, neocortical neurons in a rostral location—where the visual cortex would not normally be—respond electrophysiologically to visual stimuli and receive input from the lateral geniculate nucleus. These studies and others (e.g., Catalano & Shatz, 1998) suggest that input from the thalamus and synaptic activity play a major role in the determination of areal fate and thus appear to be very important for regionalization of the neocortex.

*Conclusion.* The above sections highlighted basic issues related to inherent, gene-driven constraints and prenatal experiences (e.g., through input from the thalamus) on the organization of the neocortex, although the sections only provided a brief overview of this very complex and dynamic area of study. On the basis of what is currently known, including the evidence described above, most developmental neurobiologists now agree that normal and (in most species) largely prenatal development of the neocortex appears to depend on both internal (e.g., region specific gene expression) and external (e.g., inputs from the thalamus) influences (Gao & Pallas, 1999; Levitt, 1995; for review, see Pallas, 2001; Ragsdale & Grove, 2001). However, the mechanisms guiding the interaction between internal and external influences to produce the highly complex functional specificity of the neocortex are not yet known.

### *Comparative Ecology and Brain Evolution*

There is clearly some degree of similarity in the inherent organization of the human neocortex and that of other mammals and the telencephalon of many nonmammalian species. There are, however, unique species-specific differences in the organization of

the neocortex. As aptly articulated by Preuss (2000, 2001; Preuss & Kaas, 1999), neurobiological studies of brain organization and development have been based largely on the assumption of cross-species similarities, have been restricted to only a few presumably modal species such as laboratory rats (*Rattus norvegicus*) and rhesus macaques (*Macaca mulatta*), and have not systematically explored cross-species differences from an evolutionary perspective. As a result, more is known about similarities across a few well-studied species than about species-specific specializations. On the basis of what is known, a reasonable conclusion would be that ecological (e.g., navigational) and survival-related demands that are constant across species are associated with conserved organizational (e.g., radial units, auditory cortex) and functional (e.g., sound processing) features of the neocortex and subcortical regions.

At the same time, ecological and survival-related demands that are unique to a specific species would be associated with species-specific adaptations within the constraints of these conserved systems. An example would be the selective attention to and processing conspecific vocalizations within the broader constraints of the auditory system. Niche-specific specializations do not, in and of themselves, imply any particular degree of inherent specification of the associated anatomical or functional systems. Thus, a question that cannot be fully answered at this time is, What is the relative balance of inherent specification and experiential pattern that results in these species-specific specializations?

*Comparative ecology.* Whatever the balance, the clearest evidence for species-specific brain and cognitive specializations comes from studies of the cortical architecture of evolutionarily related species that have different morphological and behavioral specializations (e.g., Barton, 1996; Barton & Dean, 1993; Barton, Purvis, & Harvey, 1995; Catania, 2000; Catania, Lyon, Mock, & Kaas, 1999; Dukas, 1998; Dunbar, 1993; Hof, Glezer, Nimchinsky, & Erwin, 2000; Huffman, Nelson, Clarey, & Krubitzer, 1999; Moss & Shettleworth, 1996; Moss & Simmons, 1996). The comparison of species with a recent common ancestor is important because existing differences cannot be attributed to their distant evolutionary history. Rather, these differences are more likely to reflect current differences in reproductive strategy or adaptations to different social or ecological niches, factors that can be empirically studied and related to brain organization and cognitive functions (e.g., Catania, 2000).

Huffman, Nelson, et al. (1999) provided one example with their comparison of the somatosensory cortex of three species of marsupial. All of these related species have the same basic cortical architecture, but cortical areas associated with morphological or behavioral specializations are enlarged. In the striped possum (*Dactylopsila trivirgata*), the fourth digit is 30% larger than the other digits and is used for prey capture, specifically for locating and extracting insects from the bark of trees. The cortical area corresponding to this digit occupies about 33% of the somatosensory cortex devoted to the forepaw and 10% of the entire somatosensory cortex. There is also an over-representation of the tongue, which is used in a specialized way, similar to the long digit. In contrast, the northern quoll (*Dasyurus hallucatus*) does not have this morphological or behavioral specialization, and only 3% to 5% of the somatosensory cortex is devoted to this digit. The northern quoll uses whiskers on the snout and other parts of the face to locate prey, whereas the striped possum is much less

dependent on whiskers. The cortical representations of these whiskers occupy about 55% more somatosensory cortex in the northern quoll than in the striped possum.

There are many other examples as well, and a few of these are illustrated in Figure 4. Here, it can be seen that the somatosensory cortex is enlarged (referred to as cortical magnification) for the associated morphological specializations involved in foraging and prey capture (see Catania, 2000, for a similar analysis of related species of *insectivora*). Huffman, Nelson, et al. (1999) argued that these species differences are evolved, genetically mediated specializations associated with the different foraging activities of the species. On the basis of Rakic's model (e.g., Rakic, 1988) and the finding of some degree of prenatal organization to the mammalian neocortex (Miyashita-Lin et al., 1999), cross-species differences in

the number of radial units supporting these evolved morphological and behavioral specializations are likely. For this example, the number of prenatally generated radial units and cortical areas within the somatosensory cortex is assumed to differ across the species shown in Figure 4. For the raccoon (*Procyon lotor*), the number of prenatal neocortical areas devoted to the forepaws is expected to be considerably higher than that devoted to the forepaws in the squirrel (*Sciurus carolinensis*), reflecting different foraging specializations. The number of cortical areas devoted to the lower and upper lips is expected to be considerably higher in the squirrel than in the raccoon.

At the same time, a "second factor that can account for the differences we observe in the neocortical organization in mammals is the ability of the neocortex to change its pattern of organization

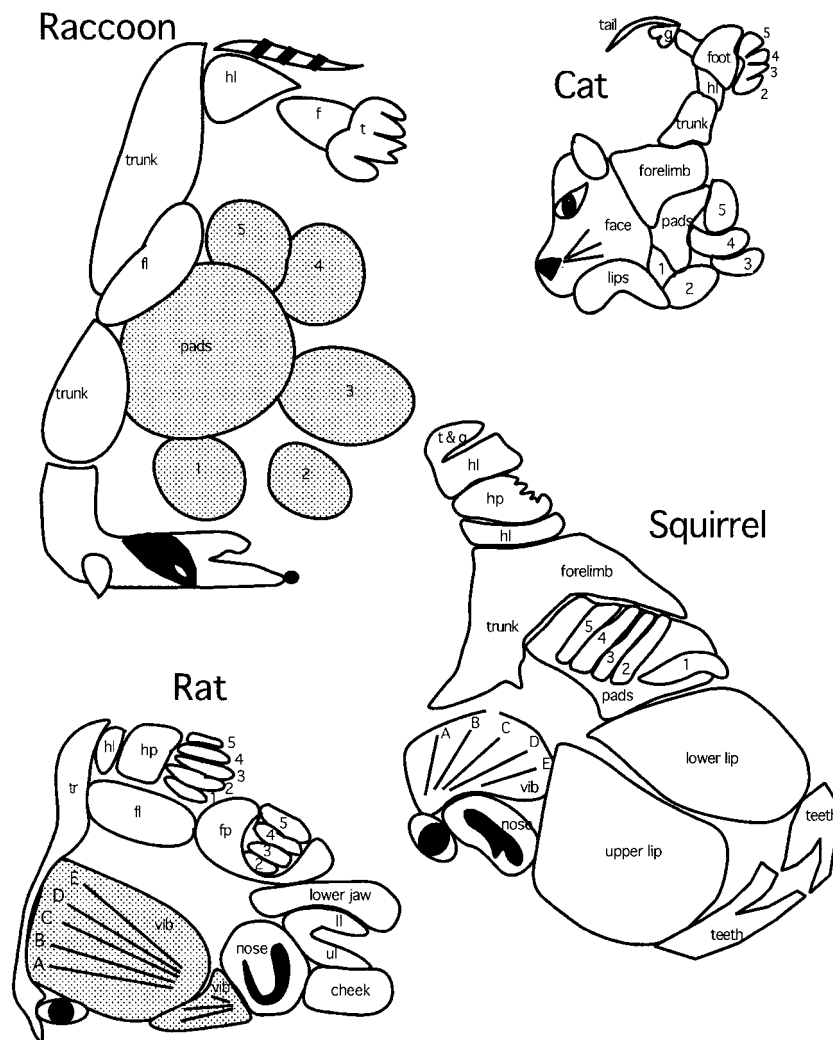


Figure 4. Examples of body representations in the somatosensory cortex, from "Organization of Somatosensory Cortex in Three Species of Marsupials, *Dasyurus hallucatus*, *Dactylopsila trivirgata*, and *Monodelphis domestica*: Neural Correlates of Morphological Specializations," by K. J. Huffman, J. Nelson, J. Clarey, and L. Krubitzer, 1999, *Journal of Comparative Neurology*, 403, p. 29. Copyright 1999 by Wiley-Liss, Inc. Reprinted with permission. f = foot; fl = flank; fp = forepaw; g = glabrous; hl = hindlimb; hp = hindpaw; ll = lower lip; ul = upper lip; t = tail; tr = trunk; vib = vibrissae (whiskers); A-E = individual vibrissae representations; 1-5 = paw digits.

throughout an individual's life" (Huffman, Nelson, et al., 1999, p. 27). In other words, initial, genetically mediated neocortical differences would result in cross-species differences in the sensitivity of the corresponding body regions. When these differences in sensitivity are combined with cross-species differences in the early attentional and behavioral activities associated with the practice of different foraging strategies during play, the result would be the large cross-species differences observed by Huffman, Nelson, and colleagues and by others (e.g., Barton, 1996; Catania, 2000).

*Evolution of the neocortex.* Our goal here is to describe how selection could act on the basic architecture or organization of the neocortex to create species-specific brain and cognitive specializations (see also Preuss, 2000, 2001). With respect to Rakic's (1988) model, sexual reproduction (or mutations) should result in within-species variability in many traits potentially related to brain evolution. Included among these are the number of radial units composing any given neuroanatomical region; the cytoarchitectonic features, or connectivity of radial units or clusters of neurons (e.g., the number and type of interconnections within layers of radial units); and the degree and pattern of connectivity between different neocortical and subcortical regions. Genetic alterations in the code for the prenatal generation of neurons are the most likely mechanism resulting in these individual differences (Caviness, Takahashi, & Nowakowski, 1995). For instance, individual variability in the timing or mode of cell division of the progenitor cells that produce neurons could result in significant individual, as well as species-level, differences in the number of radial units in a given neuroanatomical region (Rakic, 1998). Selection could then act on the resulting variability, across individuals, in the fidelity and sensitivity of the associated sensory, cognitive, and behavioral systems and result in the evolutionary modification of these systems and corresponding differences across species (Kornack, 2000; Krubitzer & Huffman, 2000; Rakic, 1995b).

Indeed, Kornack and Rakic (1998) found that differences in the size of the neocortex of the mouse and rhesus macaque could be explained, at least in part, by "substantially *more* successive rounds of cell division . . . during the neurogenetic period" (p. 1245) in macaques than in mice. These differences resulted in more progenitor cells in macaques than in mice and an accompanying increase in the number of radial units that compose the same area of the visual cortex. Differences were also found in the number of neurons that were produced and migrated to different layers of the visual cortex. Preuss, Qi, and Kaas (1999) found considerable variability across various species of monkey and ape (including humans) in the microcircuitry of regions of the primary visual cortex, although it is not clear (but seems likely) whether these differences arise through the same mechanisms described by Kornack and Rakic. Either way, there also appear to be differences in the dynamics of progenitor cell division and neuron generation for different regions of the neocortex within the same species, which in turn would result in different anatomical and presumably functional capacities of these different cortical regions (see also Barone & Kennedy, 2000).

Changes in genes (e.g., novel genetic interactions that can result from sexual reproduction) that regulate the prenatal dynamics of neurogenesis thus provide one plausible mechanism that could account for evolutionary increases in the number of radial units and thus increases in the size of the neocortex, as well as a mechanism that can accommodate change in the architecture of

radial units and cortical fields. These same mechanisms can also account for cross-species differences in the number of radial units composing distinct cortical regions and within-species differences in the number and specialization of radial units composing different regions (e.g., auditory and visual cortices; Kornack, 2000; Kornack & Rakic, 1998). If any such change in neurogenesis is heritable and if the accompanying change in perceptual, cognitive, or behavioral systems covaries with survival or reproductive outcomes, then the result would be an evolutionary modification of this brain region.

In theory, these mechanisms could also result in the formation of hybrid radial units. These units appear to emerge at the border of preexisting, functionally distinct neocortical areas and consist of neurons that show processing characteristics of both areas (see Krubitzer & Huffman, 2000; Rakic, 1988). One potential result of the emergence of hybrid radial units is the evolution of functionally distinct neurocognitive systems, although this has been debated. For instance, some scientists have suggested that human language is a unique form of conspecific communication and arose from the evolution of distinct, hybrid areas, such as Broca's area (Killackey, 1995; Northcutt & Kaas, 1995; see also Nimchinsky et al., 1999). Other scientists have argued that human language is better conceived as being analogous, albeit more complex, with the communication systems of other primates and that brain regions homologous to Broca's and Wernicke's areas exist in other primates (Cantalupo & Hopkins, 2001; Gannon, Holloway, Broadfield, & Braun, 1998; Preuss, 2000). In any case, selection acting on variability in brain organization and function created by modification of the pattern of gene expression governing early brain development is likely to be the key to understanding brain and cognitive evolution.

#### Experiential Modification of Brain Organization

Even if changes in the dynamics of early brain development are the key to brain and cognitive evolution, the issue of the selection pressures that resulted in any such change has been debated. In the first section herein, we focus on this theoretical issue, specifically whether the evolutionary expansion of the neocortex was the direct result of selection or an incidental effect of selection acting on other traits. An incidental expansion of the neocortex is of considerable theoretical importance, as it would imply that much of the neocortex is unspecialized in terms of past selection pressures. An unspecialized neocortex, in turn, would presumably respond within the limits of the underlying sensory and perceptual systems to a broad range of information and thus evince a high degree of plasticity (Quartz & Sejnowski, 1997). In the second section we focus on empirical research on the degree to which postnatal experience, learning, and injury can actually influence neocortical functioning and organization.

#### *Allometry and Size of the Neocortex*

*Allometry* refers to systematic relations among different features of body morphology, architecture, and development (Harvey, Martin, & Clutton-Brock, 1987), relations that complicate the determination of whether any particular trait is the direct result of evolutionary selection (Larson & Losos, 1996). As an example, body size and brain size are allometrically related across species.



Although this relationship is not perfect, larger bodies are generally associated with larger brains. Selection that favored an increase in body size might also result in an incidental increase in brain size, that is, an increase in brain size in the absence of direct selection for improved perceptual or cognitive competencies. The body–brain allometry is, however, a crude index of any potential incidental expansion of the neocortex. A more central issue is the potential for allometric relationships among different regions of the brain, specifically whether selection that operated to increase the size of one brain area could result in increases in the size of other areas. The question has been vigorously debated (Barton, 1999, 2002; Barton & Harvey, 2000; Clark, Mitra, & Wang, 2001; de Winter & Oxnard, 2001; Finlay & Darlington, 1995; Finlay et al., 2001; Sultan, 2002; S. S.-H. Wang, Mitra, & Clark, 2002) and, as we noted, is highly relevant to the broader issue of brain plasticity.

Finlay and Darlington (1995) factor-analyzed the covariances among the absolute size of 12 brain regions across 131 species of mammal and found that a single factor accounted for 96% of the variance. Results for this factor suggest a single mechanism may account for the absolute size of many different brain regions and thus provide evidence inconsistent with the position that these are evolved and specific brain adaptations to specific features of social or ecological niche. Finlay and Darlington conceded that specific brain and cognitive adaptations are found but argued that they appear to be less important than a more general mechanism that influenced the evolution of the absolute size of all brain regions. Their proposed mechanism involves the genes regulating prenatal neocortical development. As we noted, a several-fold increase in the size of the neocortex could occur as a result of genetic changes that prolonged the division of the progenitor cells that give birth to neurons (Rakic, 1988, 1995b), which according to Finlay and Darlington could significantly increase the size of the neocortex in the absence of ecological selection pressures. More precisely, selection that favored an increase in the size of one brain region could result in a corresponding increase in the size of all other brain regions, if change in the number of progenitor cell divisions was general. The implication is that much of the neocortex is underspecified with respect to past selection pressures and thus highly open to modification through developmental experience.

The analytic techniques used by Finlay and Darlington (1995), as well as their basic conclusion, have been questioned by several research teams that have analyzed the same data set (Barton & Harvey, 2000; Clark et al., 2001; de Winter & Oxnard, 2001). In contrast to Finlay and Darlington, who focused on absolute volume of different brain regions, these other scientists have focused on relative volume of different brain regions, or each region's volume as a percentage of total brain volume. In addition, Clark et al. (2001) analyzed systems of brain regions that often operate together—cerebrotypes—to determine if these integrated systems were related to identifiable social or ecological pressures. These techniques controlled for the allometric relation between brain size and body size and among different brain regions and allowed inferences to be drawn about the selection pressures that may have influenced the evolution of integrated systems of brain regions.

Using this approach, Clark et al. (2001) found that distinct cerebrotypes emerged for species of insectivore, shrew, and primate and were consistent with adaptations to specific ecological and social niches (see also de Winter & Oxnard, 2001). For

example, complex social dynamics are associated with larger neocortical volumes across species of primate (Barton, 1996; Dunbar, 1993; Sawaguchi, 1997) and carnivore (Dunbar & Bever, 1998). The critical social variable is not simply aggregating in large groups, as in herding, but rather dynamics that involve developing and maintaining long-term relationships with conspecifics and competition that involves, for instance, social deception (e.g., furtive mating). Most species of Old World monkey (Africa and Asia) tend to live in large social groups that encompass this form of social dynamic, whereas most species of New World monkey (South America) do not. Clark et al. found that Old World monkeys have a proportionally larger neocortex than do New World monkeys. A more rigorous test of the adaptation hypothesis was provided by a comparison of New World monkeys, such as one species of spider monkey (*Ateles geoffroyi*), that live in social groups similar to those found in Old World monkeys. These New World species have higher neocortical volumes (69% of total brain volume) than less-social New World species (62%) and volumes similar to that of Old World species (70%). Although the assumptions of de Winter and Oxnard differ in some respects from those of Clark et al., both sets of analyses provided examples of convergent evolution. In other words, species without a recent common ancestor but that occupy similar ecological and social niches “converge in their brain proportions” (de Winter & Oxnard, 2001, p. 711).

The potential for allometric expansion of the neocortex must also be evaluated in terms of cost–benefit trade-offs. Not only does expansion of brain size result in higher basal metabolic costs (consuming about 20% of calories in the average human; Armstrong, 1990), it results in a number of trade-offs regarding neuronal size and organization (Kaas, 2000). Doubling the size of a neocortical region cannot be achieved by doubling the size of neurons. To maintain the same conduction properties (e.g., speed of transmission), dendrites that are doubled in length must be quadrupled in diameter (Kaas, 2000). The costs associated with proportional increases in the size of neurons may account for the most common pattern of larger cortical areas being associated with more neurons, although there are some neuronal size differences across cortical regions and species. Because cortical expansions result in an increase in the number of neurons, each neuron must communicate with proportionally fewer neurons than before the expansion. The result appears to be increased specialization of interconnected clusters of neurons; the microarchitecture necessarily becomes more modularized and specialized for processing finer grained pieces of information as cortical areas expand (Kaas, 2000).

The metabolic and developmental costs of maintaining and constructing expanded neocortical areas create pressures that should result in an evolutionary reduction—to the smallest size necessary—of allometrically expanded regions. Nonetheless, specializations associated with cortical expansion confer benefits such as increased specialization of neuronal circuits and a corresponding increase in the fidelity of information the region can process. These benefits could maintain an allometric expansion or result in an area-specific expansion—if they outweighed costs. One result, in theory, would be the evolution of differences in the microarchitecture of analogous (due to convergent evolution) or homologous (due to a common ancestor) regions of the same general cortical area (Kaas, 2000). In other words, niche-related expansion

sions in the proportional size of specific brain regions, such as areas of the neocortex, might also be accompanied by niche-related modifications in the microarchitecture of these regions. Preuss et al. (1999) found differences in the microarchitecture of at least one area of the primary visual cortex when they compared monkeys with apes and humans with other apes, as noted earlier. The functional and evolutionary significance of these results are not yet clear (see Preuss, 2000, for a related discussion), but they do suggest that the primary visual cortex of different species of primate is differentially sensitive to different forms of visual information.

Despite these intriguing differences in microarchitecture and the finding of apparently niche-related differences in cerebrotypes across mammalian species (Clark et al., 2001; de Winter & Oxnard, 2001), the issue of whether, and if so to what degree, there has been a nonselected allometric expansion of the neocortex is far from resolved. It is very likely that there are considerably more niche-related brain and cognitive specializations than suggested by Finlay and Darlington's (1995; Finlay et al., 2001) analyses, but some proportion of unspecialized neocortex cannot be ruled out (Barton, 1999).

### *Experience and Brain Organization*

There is now considerable evidence that many neocortical and subcortical regions show molecular, neuronal, and organizational changes in response to postnatal experience, learning, or injury (Buonomano & Merzenich, 1998; Kaas, 1991; Ramachandran, 1993) and that such changes are more readily achieved during development than in adulthood (Stiles, 2000; Wiesel, 1982). The potential for dynamic change in brain functioning and organization is evident across a wide range of species, suggesting that the underlying mechanisms may be evolutionarily old. At the same time, limits on the extent to which dynamic organization is possible and whether the potential for reorganization varies from one brain region to the next are not fully understood and, as a consequence, are areas of intense theoretical interest (for a discussion, see La Cerra & Bingham, 1998; Stiles, 2000).

### *Injury*

Evidence regarding these issues, obtained from adults of human and nonhuman species, comes in part from research on the relation among injury, experimental manipulations (e.g., anesthetization of skin areas), and subsequent changes in brain functioning and organization (Buchner, Kauert, & Radermacher, 1995; Fox, Glazewski, & Schulze, 2000; Jain, Catania, & Kaas, 1997; Moore et al., 2000; Ramachandran, 1993; Rörich, Meyer, Niehaus, & Brandt, 1999; Witte, 1998). For instance, therapeutic amputation of a digit or limb in monkeys results in an immediate suppression of activity of the corresponding somatosensory cortex, but regained functioning of many of these cells sometimes occurs within a few hours (Kaas, 1991). The functional reorganization of these cells is typically associated with stimulation of adjacent digits, nearby body regions, or body regions represented in adjacent neocortical areas and may reflect the disinhibition of preexisting neuronal connections into these cortical regions (Buchner et al., 1995; Buonomano & Merzenich, 1998). There are also longer term reorganizations of disrupted cortical areas, whereby adjacent cor-

tical regions expand into the area associated with an injury or into more remote cortical areas that are horizontally connected to the disrupted region (e.g., Florence & Kaas, 1995; Witte, 1998). These results demonstrate injury-related modifications of the organization of the adult brain but also suggest that these organizational changes are restricted to circumscribed neural regions.

The effects of injury on brain functioning and organization, as well as on associated functional competencies, are more difficult to study in developing organisms than in adults (Stiles, 2000). One complication is that different brain systems may support the same functional competency at different points in development. For instance, early injury may result in little initial functional loss, suggesting compensatory changes in brain functioning and organization, but functional deficits or a failure to show normal developmental change may be evident at a later age, suggesting less compensatory change (e.g., Goldman, 1971). Moreover, the research of Stiles and her colleagues (see Stiles, 2000, for a review) suggests that different competencies may show different degrees of compensatory change in brain functioning and organization following early brain injury. In this longitudinal study, children who experienced neocortical injury prenatally or prior to 6 months of age were assessed on measures of language competence, spatial cognition, and ability to express affect (e.g., based on facial expressions). Through early childhood, these children tended to show less severe deficits than corresponding lesions would produce in adulthood, suggesting partial but incomplete compensatory changes. Some of the improvements in functional competency appeared to reflect change in behavioral strategies used during task performance, whereas other improvements may have resulted from compensatory change in brain functioning and organization (Stiles, 2000).

For the spatial and affective measures, the relation between lesion site and functional deficits was similar to that associated with brain injury in adulthood, suggesting that other cortical systems did not assume the functions normally supported by the injured tissues. The relation between lesion site and language deficits was more complicated, however. During the early stages of language acquisition, pervasive delays and deficits were evident regardless of lesion site, but as these children matured some lesion-deficit relations (e.g., poor vocabulary associated with left-temporal lesions) were similar to those associated with lesions in adulthood. Although in need of replication, the results suggest that "there is no simple or uniform pattern of deficit and recovery that can be captured by the traditional models" (Stiles, 2000, p. 264) of compensatory change in brain functioning and organization following early injury.

### *Experience*

Repeated sensory stimulation and other types of experience and learning are associated with a variety of molecular and other cortical changes in the somatosensory, auditory, and visual cortices in adulthood (Bao, Chan, & Merzenich, 2001; Buonomano & Merzenich, 1998; Kaas, 1991; Recanzone, Merzenich, Jenkins, Grajski, & Dinse, 1992). Most generally, it appears that experience, that is, repetitive stimulation, results in cortical and subcortical modifications, within limits, of preexisting systems. Specifically, alterations in physiological topographic organization were observed; for instance, repeated sensory stimulation can result in a

several-fold increase in the size of the corresponding somatosensory cortex and simultaneous stimulation of adjacent body regions can result in overlapping cortical fields, that is, cortical areas that respond to stimulation of both body regions (Jenkins, Merzenich, & Recanzone, 1990; X. Wang, Merzenich, Sameshima, & Jenkins, 1995). These changes appear to reflect, at least in part, changes in the efficiency of preexisting synapses or the generation of new synaptic connections among preexisting neurons (Witte, 1998), although experience can also maintain newly generated neurons in the hippocampus (Kempermann, Kuhn, & Gage, 1997).

Experience-based change in brain functioning and topographic organization has also been demonstrated in normally developing brains, beginning with the seminal studies of Rosenzweig and colleagues (e.g., Rosenzweig & Bennett, 1972; Rosenzweig, Krech, Bennett, & Diamond, 1962; Rosenzweig, Krech, Bennett, & Zolman, 1962) and Greenough and colleagues (see Greenough et al., 1987). In the former studies, newly weaned rats were exposed to varying degrees of social and environmental enrichment or impoverishment. Many of the enrichment conditions included spending as much as 23 hr/day in an environment with other rats and many objects to explore, whereas impoverishment involved social isolation and no objects to explore. Enrichment conditions were associated with higher cortical and subcortical weights and changes in some enzymatic activity. The changes in brain weight were, however, modest. Animals experiencing enriched environments had cortices that were about 4% heavier and subcortical weights that were 2% heavier than littermates experiencing impoverished conditions. In one manipulation, Rosenzweig and Bennett (1972) found that active exploration of an enriched environment, without social contact, led to similar changes in brain weight and enzymatic activity and, in fact, resulted in a 10% increase in the weight of the occipital cortex. Follow-up research suggested that the change in cortical weight was due to increased dendritic branching (Holloway, 1966). It was also found that brain-weight differences across genetic strain of rat were two to four times larger than the brain-weight differences when comparing rats that experienced enriched versus impoverished conditions (Rosenzweig, Krech, Bennett, & Diamond, 1962); individual differences in human brain weight, volume, and organization also appear to be strongly influenced by genetic differences (Baaré et al., 2001; Thompson et al., 2001).

More recent studies have focused on experience-independent and experience-dependent influences on the architecture of specific brain regions (e.g., Crowley & Katz, 2000; White, Coppola, & Fitzpatrick, 2001), following the early work of Wiesel and Hubel (see Wiesel, 1982; Wiesel & Hubel, 1965) and Rakic (1976). As an example, White et al. (2001) assessed the response patterns and microarchitecture of circuits of visual cortex neurons, specifically neurons that respond to the angular orientation of presented objects. Here, the development of orientation selectivity was compared across groups of normally reared, dark-reared, and lid-sutured ferrets (*Mustela putorius furo*). The dark-reared group was deprived of normal experiences during the time when these neural circuits show a rapid increase in sensitivity to object orientation, and the lid-sutured group experienced an abnormal pattern of visual experiences (some light passes through the lid). The dark-reared group responded to angular orientation, and the microarchitecture of the associated neural circuits was near normal. However, fine-grain behavioral, electrophysiological, and anatom-

ical assessments indicate that the dark-reared group showed less specificity in orientation responses (e.g., distinguishing between objects of similar orientation) and smaller neuronal circuits with fewer within-circuit interconnections than did the normal-experience group. The lid-sutured group showed the poorest levels of specificity in behavioral and electrophysiological orientation responses and the least complex circuits.

The results are consistent with findings of earlier studies of the visual cortex in other species, namely that the basic organization of this area of cortex is achieved without sensory experience but that normal experiences—in terms of species' evolutionary history (Greenough, 1991)—are needed to achieve optimal organizational and functional specificity (Wiesel, 1982) and that abnormal experiences, especially during the critical period of development, can result in abnormal or muted neuronal responses (e.g., Wiesel & Hubel, 1965). The mechanisms underlying the interaction between experience-independent architecture and experience-dependent modifications are not fully understood. One view is that over-generation of synaptic connections in the neocortex of some mammals results in an increased sensitivity to early experiences (Huttenlocher, 1990) and that actual experience patterns result in the selective maintenance (active connections) or degeneration (inactive connections) of synaptic connections (Greenough et al., 1987). Some recent work suggests that the mechanism may be more complex, whereby experiential patterns dynamically influence the organization of cortical fields rather than simply maintaining pre-organized fields (White et al., 2001). Either way, the maintained or generated pattern of connections appears to result in a more optimal sensitivity to the specifics of the organisms' ecology than would presumably be achieved in the absence of experience-dependent change. These studies of the visual cortex are consistent with the combination of intrinsic and extrinsic influences on neocortical arealization we described earlier and suggest that postnatal experiences influence, within constraints, the organization and functioning of some neocortical areas.

### Soft Modularity

The research we have just described suggests there are gene-driven and experience-driven influences on brain and presumably cognitive organization and functioning, although it may be many decades before the interaction between genetic and experiential influences are fully understood. Our goal for the current review is to suggest a framework for conceptualizing the associated issue of brain and cognitive plasticity (see Figure 1). Specifically, we propose three forms of plasticity, each representing evolved responses to different types of social and ecological variability. On the basis of the cost–benefit trade-offs described in Figure 2, our basic assumption is that information patterns that covary with survival and reproductive outcomes and that are invariant across generations favor the evolution of inherent, gene-driven constraints on brain organization and cognitive functions. Variable information patterns, in contrast, favor the evolution of brain and cognitive systems that are open to experience-driven modifications in these domains. For an illustration of this concept, consider Figure 5. The distributions represent evolutionarily significant domains that contain both invariant and variant information patterns, with the means representing invariant patterns and the tails representing variant patterns. As an example, the mean of the top

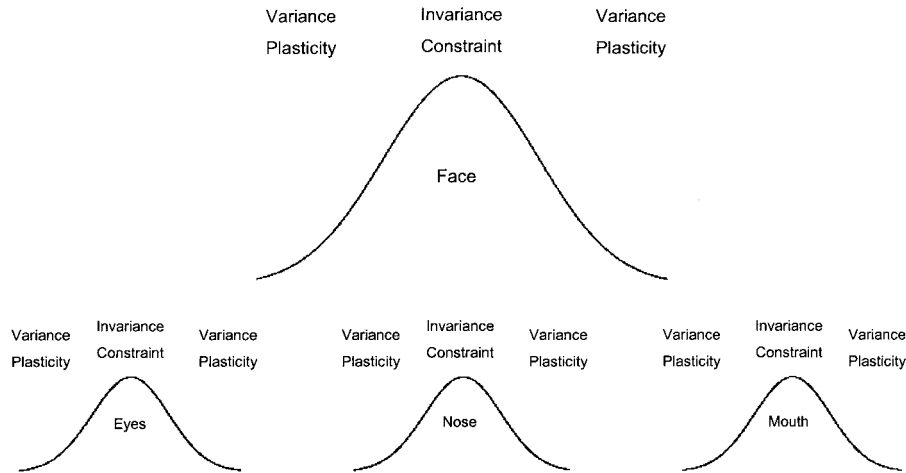


Figure 5. Conceptual representation of invariance and variance for an evolutionarily significant form of information. Invariant information, such as basic shape of the human face, is represented by the mean of the distributions and variations (i.e., individual differences) by the tails.

distribution represents the basic structure of the human face, including shape, eyes, nose, and mouth. The tails represent variation, or individual differences, in this basic structure. The smaller distributions represent the same concept, but for more discrete pieces of information.

In other words, the basic pattern of the human face is invariant, and thus inherent constraints on the brain and cognitive systems that are sensitive to these patterns are predicted to evolve, as these constraints would enable the fast, efficient identification of conspecifics (e.g., parents). Sexual reproduction, mutations, and development perturbations (e.g., poor nutrition) result in variability around this basic pattern. Brain and cognitive systems that are sensitive to this variability, and thus support the identification of specific individuals, are predicted to evolve to the extent that the ability to discriminate one individual from another results in a selective advantage. Systems associated with sensitivity to variation must per force be plastic, as a new cohort of individuals is produced each generation. The combination of inherent constraint and openness to experience-driven modification is captured by the concept of soft modularity, as described in the *Forms of Modularity* section below. The *Ecological Variability* section provides discussion of the relation between developmental experiences and soft modularity.

### Model of Soft Modularity

#### Forms of Modularity

Neurobiologists, evolutionary and cognitive psychologists, and philosophers use the term *module* differently (Cosmides & Tooby, 1994; Fodor, 1983; Krubitzer & Huffman, 2000). Definitions range from circumscribed cortical or subcortical areas that process distinct and limited forms of sensory information (Krubitzer & Huffman, 2000) to complex systems that involve cognitive, affective, and social components (Cosmides, 1989). To provide structure, four general forms of modularity are defined in the Appendix, although a finer grain analysis would produce more than four distinct categories. In any case, the different forms are assumed to

represent information processing at different levels of abstraction and complexity, with systems at successive levels (e.g., face recognition, at the cognitive level) integrating patterns of information processed at lower levels (e.g., perceptual mechanisms for processing distinct facial features). The result is assumed to be a functional module that creates an analogue representation of the environment. These analogues are represented in working memory, possibly in Baddeley's (2000) episodic buffer, which may engage the right prefrontal cortex (Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000). The buffer holds perceptual and cognitive information generated by current ecological circumstances, integrates this information with memories of related situations, and enables the organism to behaviorally respond to the situation.

#### Ecological Variability

As we stated, our basic assumption is that degree of plasticity covaries with relative variance or invariance of evolutionarily significant information patterns. Invariant patterns are a common focus in evolutionary psychology and are defined in terms of stable problems that have recurred during the species' evolutionary history (Tooby & Cosmides, 1992, 1995). Stable and recurrent problems are assumed to result in the evolution of inherently constrained modular systems that process the associated information patterns and support a suite of possible solutions. One pattern of information can result in the facultative expression of one pre-specified solution and another pattern in the expression of an alternative solution (Cosmides, 1989; Tooby & Cosmides, 1995).

The three-dimensional structure of the physical world is the most stable feature of most evolutionarily significant ecologies (Shepard, 1994). As described by Gallistel (1990, 2000) and Dyer (1998), the evolved function of associated brain and cognitive systems should be to support navigation and accompanying activities, such as finding prey or migrating seasonally (e.g., Alerstam, Gudmundsson, Green, & Hedenström, 2001). Invariant features of physical space should favor the evolution of inherent, gene-driven brain and cognitive systems that are sensitive to the associated

information, as well as mechanisms for accommodating feature variations within physical space. These variations include, as examples, the specific configuration of landmarks in which the organism is born or the position of celestial bodies (e.g., the sun) at various latitudes. These featural variations cannot be prespecified but sensitivity to associated information patterns (e.g., star pattern) can, as can mechanisms that enable the organism to remember these configurations and navigate in this specific ecology.

The other primary class of evolutionarily significant information is generated by the dynamic relations among biological organisms (Darwin, 1859; Geary, 1998). When survival and reproductive outcomes are dependent on the relationships among biological organisms, some degree of unpredictability should, in theory, confer survival or reproductive advantage (Maynard Smith & Price, 1973). Important classes include host–parasite (Hamilton & Zuk, 1982) and predator–prey (Dawkins & Krebs, 1979) relationships, as well as social competition (Alexander, 1989). Host–parasite relationships involve a never-ending and coevolving interplay between the hosts' immune-system defenses and the parasites' defense-evasion mechanisms (Van Valen, 1973). Variability in immune-system defenses—achieved through sexual reproduction and mutation—is needed to avoid the rapidly evolving evasion mechanisms in the parasite. Variable defenses, in turn, create pressures for the coevolution of the parasites' evasion mechanisms (e.g., Hamilton, Axelrod, & Tanese, 1990). For coevolving features of predator–prey relationships and social competition, variability is more likely to be at the behavioral level and at the level of supporting brain and cognitive systems. Behavioral and immune-system variability must, however, occur in the context of stable forms of information, such as specific immune-system molecules or the morphology and movement patterns of prey or predator species.

### Architecture

The point in the *Ecological Variability* section is that most evolutionarily significant information patterns (e.g., prey evasion behavior) will show some degree of variance and invariance, and thus we predict some degree of experience-driven and gene-driven influences on the organization and functions of supporting brain and cognitive systems. The extent of invariance (e.g., three-dimensional structure of proximate physical space) or variance (e.g., social dynamics) will differ from one domain to the next, and thus a frame for capturing potential differences in the relative degree of inherent constraint and openness to experiential modification should be useful. The three forms of plasticity that define the concept of soft modularity provide the beginnings of such a frame. As described in Table 1, the first form is conceived as supporting the processing of stable classes of information and accommodating variability within these classes. The second form involves cognitive mechanisms for demarcating, expanding, or even constructing new categories of information (e.g., different species), but within broader constraints (e.g., animate beings). The final form enables the expansion and contraction of neural modules on the basis of patterns of experience and use.

For the first form of plasticity, our analogy is a perceptual or cognitive module with a hard exoskeleton and soft internal structures. The exoskeleton defines the range and forms of domain-

specific information that is processed by neural and perceptual modules and any constraints within this range. For example, perception of human speech sounds falls in the range of roughly 200 Hz to 6,500 Hz (Hirsh, 1988), the range that allows for maximal communication of acoustical information (Kiang & Peake, 1988), as noted in Table 1. The bandwidth for perception of speech sounds creates boundaries—that is, an exoskeleton—that result in constraints on the form of communication system that can evolve. Presumably, the exoskeleton would also include mechanisms that are specific to the acoustical patterns that can be produced by the human vocal apparatus (Liberman & Mattingly, 1989). The soft internal structures are mechanisms that operate within these constraints and accommodate within-category variability, if within-category discriminations result in survival or reproductive advantages. In this example, soft structures refer to mechanisms that enable the discrimination of the speech patterns of different people.

The exoskeleton analogy differs in some respects from the model proposed by R. Gelman (1990; R. Gelman & Williams, 1998), who also argued for inherent constraints that are skeletal in nature, but her analogy is more akin to a vertebrate than an invertebrate skeleton. Perhaps the differences between our proposal and that of R. Gelman are more apparent than real. Still, the different analogies—exoskeleton versus a vertebrate skeleton—lead to somewhat different conceptualizations of evolved modularity and plasticity. The exoskeleton form of soft modularity also differs in some respects from the developmental model proposed by Karmiloff-Smith (1992). For instance, the soft internal structures are assumed to differ from one domain to the next, as contrasted with Karmiloff-Smith's focus on more general representational systems.

In any event, we predict an exoskeleton form of modularity would evolve when survival or reproductive outcomes are dependent on the fast, efficient processing of stable (across generations) information patterns in a restricted domain and on the discrimination of variation within this domain. The clearest example is for species in which long-term social relationships are related to survival and reproductive outcomes, which includes nearly all species of primate (Foley, 1996). For these species, selection should favor the evolution of some degree of inherent constraint in the neural and perceptual and, in some species, cognitive modules involved in recognizing conspecifics, as well as plastic mechanisms for learning about specific individuals. Within-category plasticity would support the recognition of individuals or discriminations between individuals within the category of conspecifics and provide a mechanism for remembering past social episodes with specific individuals. Another example is provided by a contrast of fruit-eating versus leaf-eating primates. Both classes of species must focus on specific categories of food, but the former must deal with greater variation within these categories. In particular, fruit-eating primates must discriminate between ripe and unripe fruit, must remember the location of spatially dispersed food sources, and must adjust foraging strategies to seasonal variations in the availability of these foods (Barton, 1996).

For at least some domains, the exoskeleton (i.e., inherent constraints) may also result in perceptual and cognitive biases that functionally result in abstract rules. These rules then guide the organism's interactions with other biological organisms or the physical world. One example comes from the dynamics of social

Table 1  
*Soft Modularity and Three Forms of Plasticity*

Exoskeleton
<p>Predicted and defining features</p> <ol style="list-style-type: none"> <li>1. Exoskeleton refers to inherent constraints on the types of information the organism attends to and processes. The absolute boundaries are determined by the basic physics of information conduction, with the constraints for individual species falling within this range (Shepard, 1994). An example is the bandwidth for human speech perception, 200 Hz to 6,500 Hz, which is in the range that allows for maximal communication of acoustical information within the physiological constraints of the auditory system (Kiang &amp; Peake, 1988).</li> <li>2. Plasticity would occur within the constraints of the exoskeleton, and the associated "soft" mechanisms would evolve for species and domains in which within-category discriminations result in survival or reproductive advantage. An example is the ability to discriminate different acoustical patterns generated by different speakers.</li> <li>3. For some domains, the exoskeleton may include mechanisms that result in information-processing and behavioral constraints within the domain but enable a degree of functional plasticity. Examples include the rules of grammatical language (Pinker, 1999) and the rules of engagement for competition with conspecifics (Jackendoff, 1992). At the cognitive level, these constraints can be conceptualized as abstract rules.</li> </ol>
Rule-based category formation
<p>Predicted and defining features</p> <ol style="list-style-type: none"> <li>1. Features of the exoskeleton would include inherent biases that result in the creation of evolutionarily significant classes of living and nonliving things, including conspecifics, prey species, and tools (Barton &amp; Dean, 1993; Blake, 1993; Dennett, 1990).</li> <li>2. For some species, the exoskeleton may include additional mechanisms that result in the creation of subcategories within these broader classes. The resulting abstract rules (at the cognitive level) would enable finer grained social and behavioral discriminations within broad categories. One example is in-group-out-group formation in humans.</li> </ol>
Resource distribution
<p>Predicted and defining features</p> <ol style="list-style-type: none"> <li>1. For many species, the brain is one of the most expensive organs to maintain (Armstrong, 1990) and thus mechanisms for energy conservation and redistribution are expected to evolve.</li> <li>2. These mechanisms would be fast acting and respond to learning, behavioral activities, and peripheral injury. The result would be the redistribution of calories and other resources from infrequently used neural modules to more frequently used modules. Example would include increases in the size of the somatosensory and other cortices that result from repeated sensory stimulation (Buonomano &amp; Merzenich, 1998).</li> <li>3. Such mechanisms would result in more efficient perceptual, cognitive, and behavioral competencies through experience-driven expansions of the supporting brain regions and reductions in the size of brain regions supporting less frequently used cognitions and behaviors. These changes, however, would occur within the limits imposed by any inherent, species-specific brain morphologies (Huffman, Nelson, et al., 1999).</li> </ol>

competition, as in male–male competition for mates. The dynamics of such competition tend to be structured by “rules of engagement” or a form of social grammar (e.g., Andersson, 1994). A common sequence would involve coordinated vocal threats and physical displays. If one male does not retreat, then the competition escalates to minor physical bouts and from there to more serious physical bouts. The rules of engagement allow individuals to make judgments about the abilities of would-be competitors. These rules, along with memories for previous bouts with the same individual or similar individuals, provide an advantage in that they enable less competitive individuals to retreat before suffering real injury and allow more competitive individuals to defend resources with minimal effort. At the same time, a competitive advantage can be achieved by behavioral unpredictability within the constraints of these rules. Unpredictability would, for instance, partially negate advantages that experienced competitors will have as a result of the large repertoire of memories and strategies accrued during previous competitions.

The second form of plasticity is assumed to occur within the context of the exoskeleton and involves perceptual and cognitive biases that result in the creation of categories and mechanisms for acquiring information about the characteristics of objects or organisms in these new categories. The specific rules are likely to differ from one domain or species to the next, but the basic principles may be the same. Consider, for instance, the survival demands of herbivores and carnivores. Both herbivores and carnivores likely show some inherent specializations for detecting meaningful species, such as the motion patterns of conspecifics or prey species (Blake, 1993). At the same time, herbivores are likely to show perceptual and cognitive specializations for processing information about flora, especially species used as food sources, whereas carnivores should, and apparently do, show adaptations for processing information about fauna, especially prey species (Barton & Dean, 1993). For highly specialized species, the systems for detecting and obtaining food are likely to show a high degree of inherent specification and comparatively little plasticity. For

species in which food sources change across seasons, years, or even generations, selection should favor a different form of adaptation. Rather than specific modules for the detection and capture of specific prey, more general, but still inherent, constraints that bias attention to and the processing of a wider category of biological information is predicted (e.g., small mammals; R. Gelman, 1990). In addition to these constraints, mechanisms—conceptualized as the rules for category formation—for creating categories of prey species or edible species of flora are expected. Categorization would include perceptual and cognitive systems for discriminating, for example, related prey species, as well as for acquiring knowledge about the behavior, growth patterns, and so forth of these species.

Although the evidence is only suggestive, a recent study by D. J. Freedman, Riesenhuber, Poggio, and Miller (2001) provides preliminary support for the existence of neural systems that create cognitive categories on the basis of experience, systems that appear to be distinct from those that enable discrimination of individuals within each category. Here, D. J. Freedman and his colleagues recently demonstrated that monkeys (species was unspecified, but presumably macaques) are able to form categories of never-before-seen dogs and cats; that is, these animals developed two distinct categories (dogs vs. cats) on the basis of repeated exposure to examples within each category. Groups of cells in the lateral prefrontal cortex were active during the categorization of exemplars into one category or the other but were not active in discriminating one dog (or cat) from another.

The final form of plasticity would involve changes in the distribution of glucose and other resources within the very expensive brain (Armstrong, 1990). As mentioned above, brain tissue is costly and mechanisms that reduce these costs and divert resources to those areas that subserve critical survival and reproductive functions as needed would be adaptive. A clear example is the seasonal change in the behaviors, cognitions, and size of the underlying brain regions that facilitate mating, as in seasonal changes in the complexity of bird song (Ball & Hulse, 1998) or spatial competencies associated with finding mates (Gaulin, 1992; Gaulin & Fitzgerald, 1989). With this form of plasticity, expensive brain tissue is not maintained during times of the year when the associated social and cognitive competencies do not provide a selective advantage. The previously described research on the relation between experience and changes in the size of the somatosensory cortex provides other examples (e.g., Buonomano & Merzenich, 1998). Here, experience results in increases in the size of brain regions supporting frequently engaged behaviors and decreases in the size of brain regions that are less frequently used. This form of plasticity enables fast changes in neural modules—and presumably in the corresponding perceptual, cognitive, and functional systems—in response to short-term fluctuations in the local ecology. It is likely that this form of plasticity could be found even for systems subject to the first two forms of plasticity, as well as for highly constrained modules of the type described by Tooby and Cosmides (e.g., Tooby & Cosmides, 1995) and by others (e.g., Gallistel, 2000).

#### *Development and Plasticity*

As noted in Figures 1 and 2, plasticity implies brain and cognitive systems that are open to experiential modification, espe-

cially during the developmental period. The benefits of developmental plasticity are, of course, balanced by costs associated with delayed maturation, specifically the risk of death before having the opportunity to reproduce. The benefits associated with a long developmental period and the corresponding increase in plasticity must therefore be significant. On the basis of the model described above, we would predict the primary benefit of developmental plasticity to be the ability to accommodate information patterns that have been variable during the species' evolutionary history and that this variability largely results from dynamic interactions among biological organisms. For many species of primate, and especially for humans, these dynamics result primarily from the complexity of social living (Alexander, 1989; Geary, in press; Geary & Flinn, 2001). Primate species that occupy complex social niches have a longer developmental period and a larger neocortex than do their cousins who occupy less complex niches (Dunbar, 1993; Joffe, 1997; Kudo & Dunbar, 2001; Sawaguchi, 1997), although foraging demands are also related to size of the neocortex (Barton, 1996).

For these domains, we predict that prenatal brain organization results in an exoskeleton that comprises neural and perceptual modules that process stable forms of information in these domains (e.g., the general shape of the human face). The result is biases in early postnatal attentional, affective, and information-processing capacities (R. Gelman, 1990) as well as biases in self-initiated behavioral engagement of the environment. The latter generate evolutionarily expectant experiences, that is, experiences that provide the environmental feedback needed to adjust modular architecture (the soft internal structures) to variation in information patterns in these domains (Greenough, 1991; Greenough et al., 1987). These behavioral biases are expressed as common juvenile activities, such as social play and exploration of the ecology (Geary, 1995). We propose here that these experience-expectant processes are features of the first two forms of plasticity described in Table 1.

As an illustration, consider that the strong bias of human infants to attend to human faces, movement patterns, and speech reflects, in theory, the initial and inherent organizational and motivational structure of the associated modules (D. G. Freedman, 1974). Such biases reflect the evolutionary significance of social relationships (Baumeister & Leary, 1995) and in effect recreate the microconditions (e.g., parent-child interactions) associated with the evolution of the supporting modules (Caporael, 1997). Attention to and processing of this information provides the exposure to within-category variation that is needed to adapt the architecture of these modules to variation in parental faces, behavior, and so forth (R. Gelman & Williams, 1998).

#### *Domains of the Human Mind*

Although much has been learned about the brain systems that support many cognitive functions (e.g., Cabeza & Nyberg, 1997, 2000), there remains a substantive divide between neurobiological research on the organizational and functional properties of the brain (e.g., types of information to which neurons respond) and cognitive research on the organizational and functional properties of the mind (e.g., working memory and representational systems). The divide results, in part, from different levels of analysis, ranging from the mechanisms guiding the physical development of the

brain to cognitions (e.g., attributional biases) that influence social dynamics. The former are tightly wedded to observable physical changes in brain organization and physiological functioning, and the latter are more abstract models of complex cognitive and behavioral systems. Our goal here is to provide a framework for bridging this divide, that is, to propose a taxonomy of the fundamental information-processing domains of the human mind (see Geary, 1998). We constructed the taxonomy on the basis of the assumption that the human brain and mind, and that of other species, is adapted to process and respond to three general classes of information: social, biological, and physical.

As shown in Figure 6, these classes coalesce around the areas of folk psychology, folk biology, and folk physics (Baron-Cohen, 1995; Baron-Cohen, Wheelwright, Stone, & Rutherford, 1999; Medin & Atran, 1999a; Pinker, 1997; Spelke, Breinlinger, Macomber, & Jacobson, 1992). The second level of the figure reflects the motivational and affective salience of conspecifics and their behavior. Specifically, for any sexually reproducing species and especially for highly social species, much of the mind and brain is predicted to function to process and respond to social information (Barton, 1996; Brothers & Ring, 1992; Dunbar, 1998; Geary & Flinn, 2001; Humphrey, 1976). The third level represents functional modules as defined in the Appendix, whereas the fourth level represents cognitive modules, which in turn would be supported by perceptual and neural modules (not shown in Figure 6). Functional modules are goal related and represent the dynamic engagement of an array of neural, perceptual, and cognitive modules and an integration of the associated processing with affective and motivational systems. As an example, the individual-level functional module represented in Figure 6 is instantiated during one-on-one social discourse and engages systems for processing and responding to nonverbal behavioral cues, language, and so forth. These cognitive systems are integrated with affective and motivational systems and function to direct behavioral strategies toward the achievement of social goals.

The first two sections focus on functional social and ecological systems, respectively. The sections include subsections on predicted forms of cognitive modules, potential neural correlates, and potential pressures associated with their evolution. The sections end with discussion of the relation between these functional systems and soft modularity. We address the relation between developmental experiences and soft modularity in the final section.

### Functional Social Systems

On the basis of differences across individual- and group-based social behavior, distinct cognitive and functional modules are predicted to support these different forms of social dynamic and are discussed in the first and second subsections, respectively (Bugental, 2000; Caporael, 1997; Dunbar, 1998). The taxonomy of sociocognitive modules shown in Figure 6 was developed to accommodate both forms of social dynamic and was derived from comparative studies of the forms of information used in social communication and that govern patterns of group dynamics as well as of social competencies that are more uniquely human (e.g., Altmann et al., 1996; Hauser, 1996; Leavens & Hopkins, 1998; Pinker, 1994).

### Individual-Level Systems

*Cognitive modules.* Caporael (1997) and Bugental (2000) described patterns of recurrent and universal one-on-one relationships in humans, including parent-child attachments and friendships. Although there are motivational and affective differences associated with different forms of one-on-one relationship, they all appear to be supported by the same suite of sociocognitive competencies, including the ability to read nonverbal communication signals, facial expressions, language, and theory of mind (e.g., Adolphs, 1999; Brothers & Ring, 1992; Dennett, 1987; Humphrey, 1976; Leslie, 1987; Moscovitch, Winocur, & Behrmann, 1997; Pinker, 1994). Theory of mind is especially salient in humans and represents the ability to make inferences about the intentions, beliefs, emotional states, and likely future behavior of other individuals (Baron-Cohen, 1995; Gopnik & Wellman, 1994). The integration of sociocognitive information processed by these proposed modules with motivational and affective systems provides the basis for the development and maintenance of long-term relationships. These modules (e.g., processing facial expressions) are also engaged during the dynamics of one-on-one social interactions, providing cues to the on-line emotional states and intentions of other people. These sociocognitive competencies may also be used to manipulate and deceive other people.

*Neural correlates and potential modules.* There is a substantive body of research on biases in the forms of social information that humans and many other species process and some indications

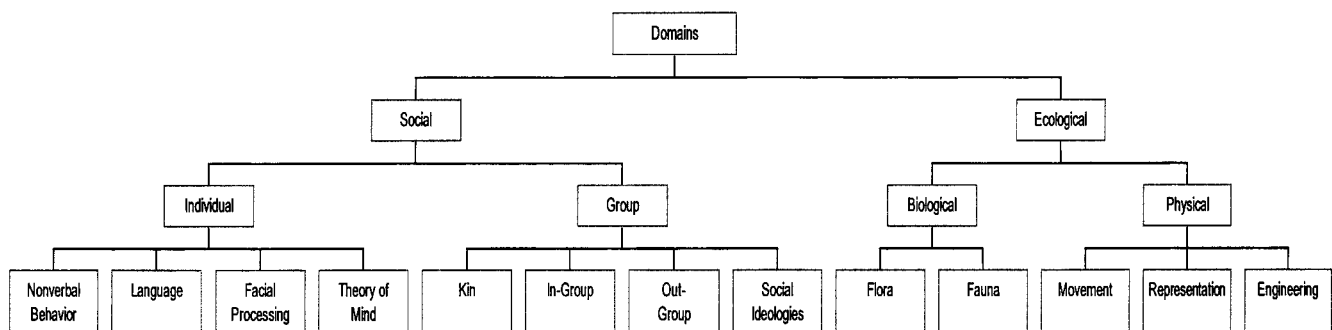


Figure 6. Proposed domains of the human mind. From *Male, Female: The Evolution of Human Sex Differences* (p. 180), by D. C. Geary, 1998, Washington, DC: American Psychological Association. Copyright 1998 by the American Psychological Association.



that these biases may be the result of modular neural, perceptual, and cognitive systems. Whether any such modularity results from inherent constraints, developmental experiences, or some combination of the two is not entirely clear because much of this work has been conducted with adults.

In any case, cognitive studies suggest distinct and potentially modular systems for the processing of facial and nonverbal communication cues (Rosenthal, Hall, DiMatteo, Rogers, & Archer, 1979), language, (Pinker, 1994), and theory of mind (Adolphs, 1999; Baron-Cohen, 1995; Frith & Frith, 1999). The processing of this information engages an integrated and distributed system of neocortical and subcortical systems, and the parallel operation of these systems results in functional social competencies. Included among these are regions of the fusiform gyrus and portions of the prefrontal cortex for processing facial features (George et al., 1999; Halgren, Rajj, Marinkovic, Jousmäki, & Hari, 2000; Nakamura et al., 2000; Ó Scalaidhe, Wilson, & Goldman-Rakic, 1997), portions of the left temporal and frontal cortices for processing aspects of human language (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000), the right lateral occipitotemporal cortex for processing information patterns associated with the human body (e.g., shape; Downing, Jiang, Shuman, & Kanwisher, 2001), portions of the right posterior superior temporal sulcus for processing human biological motion (Grossman et al., 2000), and the amygdala and other subcortical regions, as well as cortical regions, for the parallel processing of the emotional valence of these cues (Adolphs, Damasio, Tranel, & Damasio, 1996; Buchanan et al., 2000).

To illustrate, it appears that portions of the left superior temporal sulcus (STS) selectively respond to the phonetic aspects of human voice patterns (Belin et al., 2000) and that the right temporal cortex is engaged during the processing of the prosody aspects of speech (Buchanan et al., 2000; Morris, Scott, & Dolan, 1999). Speech processing, especially socially and emotionally salient speech, engages areas in the prefrontal and frontal cortices as well as several subcortical areas, including the amygdala (D. M. Tucker, Luu, & Pribram, 1995). Among other things, the amygdala appears to process aspects of human speech that signal threats and other human vocalizations that convey negative affective states, especially fear (Isenberg et al., 1999; Morris et al., 1999). The results of many of these studies are, however, open to interpretation, given that a single brain region may process different forms of information (Cabeza & Nyberg, 2000). Nonetheless, one interpretation is that different elements of human speech convey different types of information and that specialized and distributed submodules support the processing of this information. Other prefrontal and limbic systems appear to subservise motivational features of social information processing, with threat cues, for instance, prompting a fight-or-flight response or increased social affiliation (Taylor et al., 2000).

The integration across these neural, perceptual, and cognitive modules appears to engage portions of the right prefrontal cortex and limbic system, with current on-line content and affective social information being integrated with memories for related situations (Damasio, 1995; Prabhakaran et al., 2000; D. M. Tucker et al., 1995). It is far from certain, but the integration of this information may be instantiated as Baddeley's (2000) episodic buffer, that is, a working-memory representation of the social discourse. In theory, the working-memory representation enables functional social

competencies, such as responding to a question or planning a social tactic. In short, the parallel processing of various forms of social information and the integration and representation of these information patterns in episodic working memory results in a functional module, as defined in the Appendix.

*Evolutionary considerations.* As we noted earlier, the complexity of social relationships covaries with brain size, especially volume of the neocortex (e.g., Clark et al., 2001; Kudo & Dunbar, 2001), and for many species the nature of these relationships often influences survival and reproductive prospects (e.g., Goodall, 1986). From a comparative perspective, language and theory of mind are the most highly developed sociocognitive competencies in humans (Frith & Frith, 1999; Pinker, 1994) and are hypothesized to be the evolutionary result of the complexity of human social dynamics (Humphrey, 1976). Other primates use and respond to conspecific facial expressions, vocalizations, and body language (Hauser, 1996; Leavens & Hopkins, 1998; Nahm, Perret, Amaral, & Albright, 1997), but none of these primates has a grammatical language. There is little evidence to suggest that monkeys have a theory of mind, although other great apes—but this is debated (Parker & McKinney, 1999; Povinelli & Preuss, 1995; Premack & Woodruff, 1978)—may have a proto theory of mind. These competencies include the ability to make inferences about the behavior of conspecifics that exceeds the competencies of monkeys but not the specific ability to make inferences about the inferences of conspecifics.

In any event, it follows from the previously described relation between neocortical volume and social complexity (e.g., Clark et al., 2001; Kudo & Dunbar, 2001) that the neocortical areas that support the unique aspects of human language and theory of mind will be larger in absolute size and (or) evince more complex microcircuitry than homologous areas in other primates, just as the previously described cross-species differences in foraging strategies are associated with differences in the size and organization of the somatosensory cortex (Huffman, Nelson, et al., 1999). Indeed, Rilling and Insel's (1999) neuroimaging study of individuals from 11 primate species suggests that the human neocortex has more surface area than expected, based on overall body and brain size, in areas that support aspects of human language (i.e., the left temporal cortex) and theory of mind (i.e., portions of the prefrontal cortex; see Adolphs, 1999; Baron-Cohen et al., 1994; Frith & Frith, 1999).

Although in need of replication, Rilling and Insel's (1999) findings converge with related comparative studies. For instance, Rauschecker, Tian, and Hauser (1995) reported that cells in the same area (i.e., the STS) that are activated during the processing of phonetic features of human voice patterns selectively respond to conspecific vocalizations in the rhesus macaque (see also Belin et al., 2000). Gannon et al. (1998) found that the planum temporale—associated with speech comprehension in humans—shows the same hemispheric asymmetry in chimpanzees as in humans (Geschwind & Levitsky, 1968), although it is not known if this area subserves the processing of conspecific vocalizations in chimpanzees (see also Cantalupo & Hopkins, 2001). Whether these portions of the STS or other areas of the left temporal cortex are homologous areas for the processing of conspecific vocalizations is not currently known, but it is a possibility (Preuss & Kaas, 1999). On the basis of Rakic's (1988) model, a gradual evolutionary expansion or modification of these areas could readily accom-

modate both the similarities in human speech and vocal communication in other primates (and mammals; Doupe & Kuhl, 1999), as well as the differences. For instance, the evolution of the unique features of human language could have entailed, at least in part, an increase in the number of radial units in the STS and changes in the microcircuitry of these units to accommodate the greater complexity of human vocalizations. In short, the comparative data are not definitive but do suggest continuities in the brain and cognitive systems that support social dynamics across primate species and are in line with an evolutionary expansion of the systems that are most unique to humans (e.g., Cantalupo & Hopkins, 2001).

### *Group-Level Systems*

*Cognitive modules.* A universal aspect of human social dynamics involves the parsing of the social world into groups (Alexander, 1989; Geary & Flinn, 2001; Premack & Premack, 1995). The most consistent of these groupings are shown in Figure 6 and reflect the categorical significance of kin, the formation of in-groups and out-groups, and ideologically based social identification. The categorical significance of kin is evident in a wide range of species (Hamilton, 1964) and is most strongly reflected in the motivational disposition for humans to form families and wider kinship networks of one form or another in all cultures (D. E. Brown, 1991; Caporael, 1997). For humans and some other species (e.g., chimpanzees; de Waal, 1982), social parsing also involves the formation of in-groups and out-groups. In traditional societies, in-group members are kin and social allies and share beliefs, such as origin myths, that distinguish them from other groups and assign special significance to their own group (D. E. Brown, 1991). In all societies, in-groups and out-groups are defined by differing social and moral ideologies that favor in-group members and, under extreme conditions, devalue and even dehumanize out-group members (Stephan, 1985). It is also clear that the dynamics of in-group–out-group formation are influenced by social ideologies, such as religion (Horowitz, 2001), that support a larger in-group.

*Neural correlates and potential modules.* In some species, kin recognition mechanisms involve olfactory cues (e.g., Pfennig & Collins, 1993), and there is some evidence for similar mechanisms in humans. For instance, many human mothers recognize the odor of their infant within 24 hr of giving birth (Fleming, Steiner, & Corter, 1997). These findings suggest that the human olfactory bulb is specialized for the detection of human pheromones and other odor-carrying molecules and may quickly form memories of infant odors after the mother has given birth. However, little is known about other brain or cognitive systems that support kin biases, although it is likely that these engage basic motivational and affective systems. Similarly, little is known about the brain systems underlying in-group–out-group social psychology, the associated social categorizations, and the tendency to rally around ideologies.

*Evolutionary considerations.* As we stated, kin-biased relationships are found across many species, ranging from invertebrates to primates, and are readily understandable in terms of inclusive fitness (e.g., Altmann et al., 1996; Hamilton, 1964). Inclusive fitness refers to the effect that an individual's behavior has on their own reproduction outcomes and those of their kin. Selection would strongly favor individuals who facilitated the survival and reproductive prospects of kin because the reproduc-

tive success of kin would per force increase the altruist's genetic contributions to the next generation (Hamilton, 1975). The selective advantages of a kin bias would favor cognitive and affective mechanisms that enabled the parsing of conspecifics into kin and nonkin and the preferential treatment of the former.

The evolutionary function of in-group–out-group formation and the associated tendency (for humans) to form in-groups on the basis of ideologies is predicted to be related to coalitional competition (Alexander, 1989; Geary & Flinn, 2001; Wrangham, 1999). In nonhuman species, these social coalitions compete with other coalitions to gain access to or control of the resources that covary with survival (e.g., food; Silk, 1987) or reproductive outcomes (i.e., mates; Packer, Gilbert, Pusey, & O'Brien, 1991). In many species of primate, for instance, coalitions of female kin cooperate to compete with other kin-based coalitions to secure and retain access to the resources, such as fruit trees, that will improve survival prospects. Offspring born in coalitions that gain control of these resources are healthier and survive in greater numbers than do offspring born in other networks (Silk, 1987). When such coalitional behavior covaries with survival or reproductive prospects (e.g., Goodall, 1986), any affective, motivational, or cognitive system, such as in in-group–out-group social psychology, that supported coalitional behavior would evolve.

When applied to humans, it is plausible that the general dynamics of in-group–out-group formation are the evolutionary result of coalitional competition and function to enable the formation of large competition-related in-groups. Stephan's (1985) review of the social psychology of intergroup relations supports this position, as do numerous studies on the social identification processes underlying group formation, categorization, and competition (e.g., Macrae & Bodenhausen, 2000; Sherif, Harvey, White, Hood, & Sherif, 1961). Humans readily form in-groups and out-groups and process information about members of these groups in ways that are favorably biased toward the in-group, particularly when the comparisons are made between competing groups. Moreover, Stephan (1985) found that "anticipated competition caused in-group members to feel more hostility toward the out-group than did anticipated cooperation" (p. 615). Considerable evidence for coalitional competition can be found outside of the social psychology laboratory, and in many instances the outcomes of this competition covary with survival and reproductive outcomes (Chagnon, 1988; Horowitz, 2001; Keeley, 1996).

An in-group–out-group social psychology, which likely evolved in the context of competition between relatively small kin-based groups, more likely than not provided the foundation for the evolution of social ideologies (Alexander, 1989). The evolutionary root of these ideologies is likely the shared belief systems that helped to define in-groups in traditional societies. The function and ultimate selection pressure, however, is likely to have been the resulting ability to increase group size and the accompanying competitive advantage (Wrangham, 1999). These ideologies are important because they appear to be the basis for the formation of large nation-states, that is, the social organization of individuals who have never met, and never will, and thus are unable to develop one-on-one reciprocal relationships. Such ideologies define the perceived mutual self-interest of individuals who compose these groups and are the basis for the cultural evolution of large-scale societies and large-scale levels of group conflict.

### Soft Modularity

*Individual-level modules.* If one function of the proposed individual-level modules is to enable the formation and maintenance of social relationships, then these modules should show the first form of soft modularity described in Table 1, the exoskeleton. We predict that, with respect to humans, the exoskeleton is composed of neural, perceptual, and cognitive modules that are sensitive to the basic and universal features (e.g., general shape of the human face) that define the structure of human communication and the dynamics of one-on-one relationships. The latter would include inherent motivational biases to form relationships with other people (Baumeister & Leary, 1995), affective mechanisms (e.g., warmth, guilt) needed to maintain these relationships (Trivers, 1971), and inferential and attributional biases that guide social dynamics (e.g., Cosmides, 1989). We conceive of the exoskeleton of the modules as including features that are sensitive to invariant information patterns conveyed in each of the individual-level areas shown in Figure 6: nonverbal behavior (e.g., gestures and body language), language, facial processing, and theory of mind. At the same time, some degree of plasticity (soft internal structures) within the exoskeleton constraints would be needed to enable the identification of specific individuals and to maintain relationships with specific individuals.

For instance, gestures appear to be a universal and apparently inherent mode of human communication (Rosenthal et al., 1979) but show a regional “dialect” (McNeill, 2000). McNeill demonstrated that both English and Spanish children use gestures to communicate but by 3 years of age adopt the movement styles of the region. Regional and individual variation in gesture patterns expressed in the context of a universal communication system is analogous to the pattern found for human language (Doupe & Kuhl, 1999) and is consistent with both inherent constraints and plasticity within these constraints. Specifically, constraint in the form of an exoskeleton (e.g., resulting in implicit knowledge that gestures convey social information; Iverson & Goldin-Meadow, 1998) and plasticity in the form of soft internal structures can accommodate the universal communicative features of gestures and body language as well as of regional dialects and the unique gestural styles and body language (e.g., walking gait) of specific individuals.

Although not definitive, results from several recent neuroimaging studies are consistent with the exoskeleton form of modularity (George et al., 1999; Nakamura et al., 2000). The studies indicate that the left and right fusiform gyri, as well as other areas of the temporal cortex, are selectively activated when people process features of conspecific faces. George and colleagues (1999) found that only portions of the right fusiform gyrus were activated when processing highly familiar faces, and Nakamura and colleagues (2000) found that the right fusiform gyrus was activated during the processing of faces and that the right temporal pole was activated during the discrimination of familiar and unfamiliar faces. Thus, there appear to be specific areas of the temporal cortex that are highly sensitive to invariant forms of information conveyed by human faces (e.g., eye position)—the exoskeleton (including the bilateral fusiform gyrus)—and subareas within and (or) adjacent to this region that change in response to repeated exposure to the same face—the soft internal structures (including the right fusiform gyrus).

A general-learning interpretation of face processing in these regions has been offered, however. Gauthier, Tarr, Anderson, Skudlarski, and Gore (1999) trained adults to discriminate between different novel objects, called *greebles*. After extensive training, the right fusiform gyrus was activated while discriminating different greebles. Gauthier et al. concluded that “the face-selective area in the middle fusiform gyrus may be most appropriately described as a general substrate for subordinate-level discrimination that can be fine-tuned by experience with any object category” (p. 572). The difficulty with this interpretation is that the greebles had several facelike attributes, including a round facelike shape on top of a more slender (necklike) base, a projection in the center that was noselike, and so forth. If the bilateral fusiform gyrus is the exoskeleton for processing facelike information and portions of the right fusiform gyrus are the soft internal structures that encode memories of the distinct features of familiar faces, then the Gauthier et al. results are not unexpected. In support of this interpretation, these same areas do not generally respond to other types of objects or environmental scenes that do not have facelike features, except for individuals with inherent sociocognitive deficits, such as autism (Nakamura et al., 2000; Schultz et al., 2000).

Theory of mind is also predicted to show general constraints on the types of information processed (e.g., a mismatch between vocal intonation and facial expression) and on the types of inferences drawn from this information (e.g., deception). Plasticity in the form of memory mechanisms for representing characteristics of familiar minds are expected as well, as these representations are a necessary feature of long-term relationships. Just as one recognizes the face and voice of familiar people, one also comes to understand how each individual “thinks.” In addition, theory of mind may show a form of functional plasticity analogous to the rules of grammar (see Jackendoff, 1992). A grammar-like feature to theory of mind would result in an exponential increase in the complexity and flexibility of social behavior, but the link to more basic motivational and affective systems would be preserved (as mediated, in part, by the amygdala; Humphrey, 1976; D. M. Tucker et al., 1995). In this view, theory of mind is used to achieve many of the same social goals, such as mating or dominance, as are found in other primates. The means to achieve these goals are highly adaptive but constrained by a “social grammar” in much the same way as was described earlier for the rules of engagement for male–male competition.

*Group-level modules.* As stated, the parsing of the social world into favored and disfavored groups is a universal dynamic in humans (e.g., Horowitz, 2001) and many other species (Altmann et al., 1996; de Waal, 1982; Packer et al., 1991). The flexibility of parsing might be understood in terms of the second form of plasticity described in Table 1, rule-based category formation. The mechanisms that underlie the operation of such rules are not currently known but are predicted to act on specific forms of information, such as groups of conspecifics, with different rules for forming different types of categories (e.g., Bugental, 2000). As an example, the attributions regarding in-group members and out-group members clearly differ, as do the rules that define relationships among friends, spouses, and family members.

For highly social and political species such as humans, category formation should show a high degree of functional plasticity. For instance, the nature of in-group–out-group relationships varies widely. These relationships range from endemic conflict with the

goal of exterminating the out-group to relatively low levels of conflict combined with tolerance and social exchange (Alexander, 1989; Chagnon, 1988; Macrae & Bodenhausen, 2000). If an in-group–out-group social psychology did in fact evolve in the context of coalition-based competition, then the patterns of in-group–out-group relationships—especially the degree of hostility and conflict—should, and do, have some relation to resource availability in the local ecology (e.g., Sherif et al., 1961; Stephan, 1985). Moreover, the rules for category formation should reflect perceived self-interest and perceived sources of threat to that interest. When resources are plentiful and coalitions are not needed, then the contextual pull for in-group–out-group formation is weak and group-level conflict is low in frequency and intensity (Alexander, 1989). When resources are limited and coalitions help to obtain access to and control of such resources, then an in-group–out-group social psychology is invoked and these groups are formed on the basis of a categorical rule: “Those who assist me in achieving the desired goal are members of the in-group and those who cooperate to thwart the achievement of this goal are members of the out-group.”

Just as the rules of grammar can be supplemented by knowledge of individual words in the lexicon (e.g., irregular verbs such as *went* instead of *goed*; Pinker, 1999), human coalitional politics can be supplemented by knowledge of individual people. There can be hostility toward members of a defined out-group, but more friendly relationships can develop with specific individuals who might otherwise be defined as a member of this out-group (Stephan, 1985). These individual relationships are defined by the rules of friendship and thus are predicted to have little or no effect on more general out-group dynamics or attributions. Just as irregular verbs stored in a separate lexicon have no influence on the rules of grammar, as aptly described by Pinker (1999), friendly relationships with individual members of an out-group will have no influence on the rules of in-group–out-group formation or accompanying patterns of attributions or conflict (Macrae & Bodenhausen, 2000).

### *Functional Ecological Systems*

Most species require behavioral systems for negotiating relationships with other species and movement in physical space. These evolved behavioral systems require supporting neural, perceptual, and cognitive modules that are sensitive to the accompanying forms of information. The constellation of modular systems is captured by the notions of folk biology and folk physics (e.g., Gallistel, 1990; R. Gelman, 1990). The first and second subsections provide discussion of these respective classes of module (see Figure 6), and the third provides related discussion of soft modularity.

### *Biological Systems*

*Cognitive modules.* As noted by Medin and Atran (1999b), in “subsistence cultures, survival depends on a detailed appreciation of the habits, affordances, and interactions linked to the biological world” (p. 1). As described for other species (*Comparative Ecology and Brain Evolution* section), humans living in traditional societies are highly dependent on cognitive and behavioral specializations that support foraging and other forms of interaction

with the natural world. Although the source of these specializations is currently debated (e.g., Keil, Levin, Richman, & Gutheil, 1999), the accompanying functional competencies are manifest as hunting, gathering, and horticulture. At the most basic level, the supporting cognitive and functional modules are predicted to result in the ability to categorize and process information in the general domains of flora and fauna and to develop a supporting knowledge base that can be used in the service of obtaining foods and medicines (Atran, 1998; Malt, 1995).

Consistent with the view that these are universal features of folk biology, humans throughout the world are able to categorize the flora and fauna in their local ecologies (Atran, 1998; Berlin, Breedlove, & Raven, 1966; Carey & Spelke, 1994). In fact, humans living in natural environments develop very elaborate and complex classification systems of the flora and fauna in the local ecology and develop mental models of the behavior (e.g., growth patterns) of these plants and animals (for examples, see Medin & Atran, 1999a). Through ethnobiological studies, “it has become apparent that, while individual societies may differ considerably in their conceptualization of plants and animals, there are a number of strikingly regular structural principles of folk biological classification which are quite general” (Berlin, Breedlove, & Raven, 1973, p. 214). Peoples’ classification of plants and animals in traditional societies is similar to the scientific classification of these same organisms (Atran, 1994; Diamond, 1966), although the degree to which particular aspects (e.g., for a specific species) of the classification system are more or less elaborated is contingent on the social and biological significance of the plants or animals to people in the culture (Atran, 1998; Malt, 1995).

People in traditional societies classify flora and fauna on the basis of common features of morphology, behavior, growth patterns, and ecological niche (e.g., arboreal vs. terrestrial). The combination of these cues and inferential biases (e.g., self-initiated movement implies a living organism; R. Gelman, 1990) help to define the *essence* of the species (Atran, 1994; Malt, 1995). The essence is a mental model of the salient characteristics of the species and appears to be analogous to peoples’ theory of mind. This is because mental models of flora and fauna would be well suited for representing and predicting the likely behavior of these organisms (e.g., seasonal growth in plants), just as theory of mind enables the formation of representations of the intentions of other people and thus an improved ability to predict their behavior. Knowledge of the essence of familiar species also allows people to make inferences about the essence of unfamiliar species (Berlin, 1999). For example, knowledge of one species of frog can be used to make predictions about the characteristics of a novel species of frog but not a novel species of bird (Atran, 1994). These mental models and other aspects of folk biological knowledge presumably manifest as working-memory representations that enable the integration of this knowledge and related memories with perceptions and cognitions generated during functional activities, such as hunting. It is possible that this information is integrated with related memories in the episodic buffer (Baddeley, 2000). In any case, the working-memory representations support a functional module, as defined in the Appendix.

*Neural correlates and potential modules.* Some research in the cognitive neurosciences is consistent with the prediction of neural, perceptual, and cognitive modules for processing distinct information patterns generated by plants and animals, although there is not

a consensus on the meaning of these studies (Farah, Meyer, McMullen, 1996; Gaffan & Heywood, 1993; Hart & Gordon, 1992; Laws & Neve, 1999; Warrington & Shallice, 1984). Some of the studies suggest distinct cognitive and brain mechanisms for the categorization of living and nonliving things. As an example, it is often found that damage to the posterior portions of the neocortex results in disruptions in the ability to name living things but not nonliving things (Farah et al., 1996; Warrington & Shallice, 1984). However, occasionally the reverse is found; Sacchett and Humphreys (1992) reported a case study of an individual with a brain injury who could name living things but not man-made nonliving things. The double dissociation across individuals is important because it strengthens the argument for distinct brain and cognitive systems for the categorization of living and nonliving things. Hart and Gordon (1992) reported another injury-related dissociation, but for this individual the distinction was between the categorization of fruits and vegetables versus animals, consistent with the argument for different brain and cognitive systems for representing flora and fauna.

However, a recent series of brain imaging studies did not reveal distinct brain regions associated with decisions during the categorization of names of animals, fruits, tools, and vehicles (Devlin et al., 2001). Moreover, nearly all of these studies were conducted with adults and thus do not directly address the issue of whether any such modularity results from inherent constraint or patterns of developmental experience. Thus, the debate continues as to whether such results are consistent with inherent, modular systems or stem from more general-learning mechanisms operating on environmental regularities (Farah et al., 1996; Gaffan & Heywood, 1993).

*Evolutionary considerations.* Neural, perceptual, cognitive, and inferential systems for processing information about other species should evolve to the extent that the resulting functional and behavioral biases covary with survival outcomes (e.g., predator avoidance). As described earlier, there is evidence for related specializations across a wide range of species (Barton & Dean, 1993; Huffman, Nelson, et al., 1999). As with these nonhuman species, folk biological knowledge covaries with survival prospects for humans living in traditional societies. As an example, Atran's (1994) finding of a highly differentiated taxonomy of fauna for Itza-Maya (Guatemala) hunters is in keeping with the view that the function of this folk biological knowledge is, at least in part, survival related. This taxonomy was "related to features of behavior, habitat, diet, and functional relationships to people" (p. 331), which very likely facilitate the hunting of these animals. The same pattern has been found for plants that serve as foods and medicines in other traditional societies (Clement, 1995; Figueiredo, Leitão-Filho, & Begossi, 1993, 1997).

Research on Western children's formation of biological taxonomies is also consistent with the existence of inherent, and thus presumably evolved, biases that guide the development of folk biological modules (Keil, 1992). For instance, preschool children appear to have an implicit understanding of some differences comparing living and nonliving things, implicitly understand the difference between plants and animals, and readily develop mental models of the essence of plants and animals (Coley, 2000). The former is reflected in the implicit understanding that living things and nonliving things have different types of innards and that living things are capable of self-initiated movement (R. Gelman, 1990;

Hickling & Gelman, 1995). Later, children understand that animals must eat to survive and that they reproduce offspring that share characteristics with their parents (Carey & Spelke, 1994; Coley, 1995). Children of this age also exhibit a similar level of knowledge about plants (Coley, 2000). As with the brain-injury and imaging studies described above, there is no consensus regarding the meaning of this research (e.g., Au & Romo, 1999), that is, whether it is best understood in terms of inherent modular constraints or as the result of general-learning mechanisms.

### *Physical Systems*

*Cognitive modules.* Neural, perceptual, and cognitive systems that enable organisms to act on, respond to, and in some cases, mentally represent the physical world are evident across a wide range of species—from invertebrates to humans—and are likely to show some degree of inherent modularity (Gallistel, 1990; Shepard, 1994). These systems appear to be sensitive to many invariant features of physical space and can accommodate variation (e.g., movement of trajectories, shading—in terms of color perception; Shepard, 1994) within these constraints. For humans and a few other species, one additional aspect of folk physics includes the ability to mentally represent physical objects and mentally manipulate these representations as they relate to the practice of tool use (Baron-Cohen et al., 1999; Lockman, 2000). A useful conceptualization of the most general classes of functional physical module is in terms of movement (Andersen, Snyder, Bradley, & Xing, 1997), representation (Shepard, 1994), and engineering (e.g., tool use; Pinker, 1997), as shown in Figure 6.

The distinction between movement and representation is based on Milner and Goodale's (1995) framework for the functional and anatomical organization of the visual system, although analogous mechanisms are evident in other systems, as exemplified by the bat's use of echolocation to guide prey capture (Dukas, 1998; Moss & Simmons, 1996). Neural and perceptual modules that process movement-related information allow the organism to track and behaviorally respond to current information in the external world. Among other things, the associated perceptual and cognitive systems enable the generation of three-dimensional analogue maps of the environment (Gallistel, 1990), support the tracking of the movement of objects in space (Shepard, 1994), and enable adjustments for the influence of gravity on the trajectory of falling objects, as when these objects are tracked behaviorally (e.g., caught; McIntyre, Zago, Berthoz, & Lacquaniti, 2001). There is also some evidence for distinct visuomotor systems involved in distinct activities that require movement in physical space, such as prey location and capture versus predator avoidance, in keeping with a modular perspective (see Barton, 1996).

In addition to systems for supporting movement, many species also appear to have systems that support the representation of features of the physical environment when they are not directly engaging the environment. Studies in human cognition indicate that performance on tasks that involve the judgment of movement in physical space (e.g., visually tracking a moving object) is only weakly related to performance on tasks that involve generating a mental representation of physical space (e.g., a map; Schiff & Oldak, 1990; Watson & Kimura, 1991), in keeping with our taxonomy of distinct movement and representational systems. The representational systems include, among others no doubt, the abil-

ity to generate a mental model of the physical layout of the habitat (i.e., the geometric coordinates) and for remembering the relative location of landmarks within this habitat. In this case, the map is generated mentally after navigation rather than during the act of navigating (Matthews, 1992).

Tool use is found in one form or another in all human cultures, and it enables people to more fully exploit biological and physical resources in the local ecology (Murdock, 1981). The neural, perceptual, and cognitive systems that enable tool use have not been as systematically studied as the systems supporting movement and representation. Current evidence suggests that these systems involve the ability to mentally represent a nonliving object, to manipulate this representation to explore ways in which the object might be used as a tool, and finally to integrate such representations with active tool-use behavior (Lockman, 2000).

As with folk psychology and folk biology, it is possible that the functional modules associated with folk physics engage Baddeley's (2000) episodic buffer, along with other working-memory systems, such as those that support visuospatial processing and representations. In other words, the actual use of tools, navigation from one place to another, or capturing prey all involve the integration of implicit (potentially inherent) knowledge and memories for related past experiences with information patterns in the current environment. Such integration is necessary for functional and behavioral competence and would seem to require a form of episodic working memory.

*Neural correlates and potential modules.* The processing of information patterns associated with physical space and mental representations of this space appear to engage the parietal cortex, the hippocampus, and several other brain regions (Andersen et al., 1997; Maguire, Frackowiak, & Frith, 1997), and different patterns of information or representation appear to engage relatively distinct systems of brain regions. As an example, memory for the relative location of landmarks is dependent on a spatial-memory system that appears to be distinct, in some respects, from the system that generates an abstract representation of three-dimensional space. In a neuroimaging study, Maguire et al. (1997) contrasted the brain regions involved in navigating a complex route through London—taxi drivers imagined and described these routes during brain imaging—with the brain regions associated with imagining highly salient landmarks. The route and landmark tasks engaged many of the same brain regions, such as parts of the parietal cortex, but the route task also engaged the hippocampus, whereas the landmark task did not (see also Maguire, Frackowiak, & Frith, 1996). Maguire et al. (1998) also provided evidence for distinct brain systems involved in representing physical space (especially the right hippocampus and right inferior parietal cortex) and for speed of movement in this space (especially the right caudate nucleus).

Nakamura et al. (2000) found that regions of the left and right parietal-occipital junctions and portions of the left and right hippocampi were engaged during the processing of scenes and that these regions differed from those engaged during the processing of faces or objects. Recent demonstrations of injury-related functional dissociations between knowledge about tools (e.g., name, description of their use) and the actual use of tools suggests that distinct systems of brain regions support these distinct competencies (Hodges, Spatt, & Patterson, 1999; see also Lockman, 2000). Hodges et al. (1999) concluded that

there are clearly more sophisticated [than object location] processes that facilitate the plausible—if not always correct—manipulation and usage of objects. It seems likely that parietal lobe areas are responsible for the transformation of spatial representations of attended objects into the motor coordinate frame for action, which entails an element of mechanical problem solving. (p. 9447)

The results of Hodges et al.'s (1999) research suggest that distinct systems of brain regions in the parietal cortex and hippocampus and other regions are engaged during the processing of information patterns associated with different aspects of folk physics. However, it is not known if these specialized functions are the result of inherent constraint, developmental experiences, or, more likely, some combination.

*Evolutionary considerations.* Dyer (1998) wrote:

On the most general level, the adaptive significance of spatial orientation is obvious: It is easy to imagine why natural selection has equipped animals with mechanisms that enable them to (1) acquire information about their position and orientation relative to fitness-enhancing resources, such as food or mates; and (2) guide movements in search of better conditions. (p. 201)

In other words, the neural, perceptual, and cognitive systems that enable movement in physical space and that in many species enable the mental representation of physical space, necessarily covary with survival and reproductive outcomes and thus evolve. The ability to use tools to manipulate and to better control the environment is evident in a few species, but is most notable in humans (Pinker, 1997). Hominid tools that are more sophisticated than the tools used by chimpanzees, such as stone flakes used in cutting, have been found in archeological sites that are more than 2 million years old, and more sophisticated tools, such as handaxes, are evident from about 1.5 millions years ago (Gowlett, 1992). These patterns indicate that in comparison to extant nonhuman primates, complex tool use emerged with the genus *Homo*, evolved further with *H. erectus*, and further still with modern humans (see Gowlett, 1992, for an overview).

Accompanying the long history of tool use in humans is a host of supporting anatomical changes (e.g., the human thumb) and a selective advantage (Trinkaus, 1992). The advantages associated with tool use include an increase in the range of foods available to the individual, such as with the use of stone hammers to extract marrow from bone, and an enhanced ability to control some physical resources, as with tools used to start fires. Stated otherwise, tool use enables humans to more fully exploit biological and physical resources, and thus their use covaries with survival prospects in all human cultures.

### *Soft Modularity*

*Biological modules.* The pattern of cross-cultural similarities and differences in folk biological knowledge—as well as the nature of the task itself (i.e., to categorize and learn about other living things)—appears to be most readily understandable in terms of the rule-based categorical plasticity described in Table 1. Inherent and modular constraints (the exoskeleton) can be predicted in terms of neural and perceptual systems that are sensitive to invariant forms of information regularly produced by other living things, such as self-initiated biological motion and basic morphological prototype (e.g., the basic body plan for mammals is the

same across species; R. Gelman, 1990). Plasticity may occur at the level of cognitive modules, specifically as a form of categorical rule that acts on these forms of information. Categorical plasticity would be a necessary feature of any folk biological functional module, at least for humans. Biological categorization would be a reflection of the operation of rules that, for instance, resulted in the broad clustering of objects in the world into animate and inanimate sets (R. Gelman, 1990). One associated categorical rule might be, "If the object shows a basic morphology associated with animals or plants and self-generated growth or movement, then it is animate." Other categorical distinctions would be generated by different rules. For example, animals can be distinguished from plants on the basis of morphology and ease of self-initiated movement (Atran, 1998; Coley, 2000).

Inherent information-processing biases in the form of an exoskeleton and categorization rules, including mechanisms for developing knowledge systems about individual species, would result in similarities in the folk biology of people in different cultures, as well as differences. As an illustration, consider that even though American college students and Itza-Maya hunters produce highly similar taxonomies for common mammalian species on the basis of morphology and behavior, they often differ in some of their more functional categorizations (Atran, 1994, 1998). For example, "Itzaj form a group of arboreal animals, including monkeys as well as tree-dwelling procyonids (kinkajou, cacomistle, raccoon) and squirrels (a rodent)" (Atran, 1998, p. 558). The clustering of these species is based on their occupation of a similar ecological niche rather than morphological similarities, which in turn is functional for these hunters because it aids them in locating these animals. There are also differences in the inferences drawn by Itzaj hunters and American college students. For instance, the former consider large predatory mammals (e.g., jaguars) as the standard prototype for mammals, whereas the latter consider smaller mammals (e.g., raccoons) as the standard prototype (Atran, 1998). The standard prototype, or primary exemplar, then provides the ideal against which inferences about other animals are drawn and provides a functional anchor for making decisions that are useful for the particular ecology. For Itzaj, the exemplar of large and potentially dangerous mammals (e.g., jaguars) likely speeds the identification of these animals and allows fast inferences to be drawn about similar species (e.g., cougars).

*Physical modules.* As we stated, some aspects of the physical environment, especially its three-dimensional structure, are invariant across time and place, and thus genetically prespecified information-processing biases that are sensitive to these forms of information should evolve (Gallistel, 1990; Shepard, 1994; Tooby & Cosmides, 1992). However, other aspects of the physical ecology can be highly variable across locations, as in mountainous terrain versus arctic tundra. For species that occupy a wide range of physical ecologies, some degree of plasticity of the associate neural, perceptual, and cognitive systems is predicted (Potts, 1998). More precisely, mechanisms of the exoskeleton form that support the formation of memories for the specific features of the local ecology would be highly adaptive for such a species (Gallistel, 2000). This form of soft modularity would include constraints (i.e., an exoskeleton) on the type of information processed (e.g., landscapes) but enable the formation of memories for and the development of a knowledge base of the physical ecologies within which the individual lives. Ecologies that are subject to fluctua-

tions in weather patterns and climate, as in seasonal changes, would also create pressures that would favor the same form of soft modularity.

Cognitive and brain research on tool use is less abundant than research on other systems that process folk physical information. Nonetheless, it is clear that tool use is highly plastic in humans (Murdock, 1981) but may have modular constraints (Hodges et al., 1999). Modular constraints would include attentional and neural and perceptual systems that result in an orientation toward inanimate objects, as well as brain and cognitive systems that support the generation of mental representations of these objects as related to tool use. The latter might involve the episodic buffer that guides the mental manipulation of tool-related representations and integrates these within an action frame, that is, a behavioral system (functional module) for using the objects as tools (Hodges et al., 1999; Lockman, 2000). At the same time, the wide range of tools used by humans suggests that the categorization of objects as potential tools is not highly constrained. In fact, the finding that people are able to readily create functional categories of tools, such as those used in domestic activities versus those used in hunting or warfare (Lockman, 2000; Murdock, 1981), suggests the rule-based categorical form of plasticity described in Table 1 may apply to tool use. The fundamental rule governing the categorization of tools and other artifacts appears to be the intent of the creator of the tool; that is, children and adults categorize man-made artifacts on the basis of their intended function (e.g., sitting as in chairs) rather than other attributes, such as shape (Bloom, 1996; Dennett, 1990; S. A. Gelman & Bloom, 2000).

There is also evidence for the third type of plasticity described in Table 1, resource distribution. In a neuroimaging study, Maguire et al. (2000) found that the posterior hippocampus, which appears to support large-scale navigation, was larger in taxi drivers than in age-matched men who were not taxi drivers. Moreover, hippocampal volume "correlated with the amount of time spent as a taxi driver (positively in the posterior and negatively in the anterior hippocampus)" (Maguire et al., 2000, p. 4398). The authors suggested that the right posterior hippocampus is one of the brain structures involved in storing and using complex spatial maps of familiar environments, whereas the anterior hippocampus is involved in encoding the spatial configuration of novel environments. The implication is that the repeated and often times complex navigation of taxi drivers resulted in adaptive changes in the relative size of these different areas of the hippocampus. However, the study is not in itself conclusive, but it is consistent with the predictions of the resource distribution form of plasticity and with the earlier described research on brain plasticity in other species (Buchner et al., 1995; Buonomano & Merzenich, 1998).

### *Development and Soft Modularity*

As noted in the *Development and Plasticity* section, juvenility appears to be an evolved adaptation that functions to allow organisms to practice and refine complex social, foraging, and other competencies needed for survival and reproduction in adulthood. The accompanying evolutionarily expectant experiences are accrued through the organism's natural play, exploration, and social experiences and are predicted to adapt evolved modular systems to local conditions, such as the local language (Bjorklund & Pellegrini, 2000; D. G. Freedman, 1974; Geary, in press; Geary &

Bjorklund, 2000; Gray & Feldman, 1997; Greenough et al., 1987; MacDonald, 1992; Scarr, 1992). Our proposal in this review is that the adaptation of these systems to local conditions occurs, at least in part, by means of the exoskeleton and the rule-based category formation forms of soft modularity. Furthermore, we predict these forms of plasticity to be most evident in those domains that support relationships between biological organisms, that is, the social and biological modules shown in Figure 6, although a lesser degree of soft modularity should also be evident for physical modules. This is because relationships among biological organisms necessarily result in more variability in information patterns than do activities that engage the physical world.

Language is one well-known example whereby the features of individual languages (e.g., phonemes) are accommodated within what appear to be inherent neural, perceptual, and cognitive constraints such that individuals develop the language to which they are exposed (R. Brown, 1973; Kuhl, 1994; Kuhl et al., 1997; Pinker, 1994). Aspects of this accommodation appear to involve the exoskeleton form of plasticity (e.g., for phoneme recognition) and occur as an experience-expectant feature of language development (Doupe & Kuhl, 1999). Similar processes are predicted to occur for the other social domains, as reflected for example, in the recognition of one's parents—the exoskeleton ensures that infants attend to human faces and the soft internal structures are modified to allow recognition of frequently processed faces. Developmental experiences also appear to facilitate later category formation for things such as social activities. Boys' group-level competition (e.g., team sports) provides one example of the early formation of competition-based in-groups and out-groups and the coordination of social activities that provide the practice for primitive group-level warfare in adulthood (Geary, 1998). Of course, the formation of in-groups and out-groups occurs throughout the life span; our point is that these natural games provide the practice needed for the skilled formation and maintenance of coalitions in adulthood and result in the accumulation of memories for associated activities and social strategies.

Experiences during development also appear to result in the fleshing out of many other features of folk psychological, biological, and physical knowledge. Children's implicit folk biological knowledge and inherent interest in living things result, in theory, in the motivation to engage in experiences that automatically create taxonomies of local flora and fauna and in the accrual of an extensive knowledge base of these species. In traditional societies, these experiences include assisting with foraging and play hunting (e.g., Blurton Jones, Hawkes, & O'Connell, 1997). Anthropological research indicates that it takes many years of engaging in these forms of play and early work to learn the skills and knowledge (e.g., how to shoot a bow and arrow) needed for successful hunting and foraging (Hill & Hurtado, 1996; Kaplan, Hill, Lancaster, & Hurtado, 2000). As another example, the development of maplike representations of the large-scale environment occurs more or less automatically as organisms explore this environment (Gallistel, 1990; Poucet, 1993).

For humans, the development of these representations occurs gradually from early childhood through adolescence and requires extensive exploration and exposure to the local environment (Matthews, 1992). More precisely, the research of Matthews (1992) clearly shows that children automatically attend to features of the large-scale environment and landmarks within this environment

and are able to generate a cognitive representation of landmarks and their geometric relations at a later time. Children's skill at generating these representations increases with repeated explorations of the physical environment (see also Landau, Gleitman, Spelke, 1981; Mandler, 1992). Thus, learning about the physical world is a complex endeavor for humans and requires an extended developmental period, in comparison with the more rapid learning that occurs in species that occupy a more narrow range of physical ecologies (Gallistel, 2000). A recent study by Chen and Siegler (2000) suggests that similar processes occur for tool use. Here, it was demonstrated that 18-month-olds have an implicit understanding of how to use simple tools (e.g., a hooked stick to retrieve a desired toy) and with experience learn to use these tools in increasingly effective ways.

In sum, a long developmental period is an evolved feature of human life history and functions to enable the fleshing out of folk psychological, biological, and physical knowledge (Geary, in press). The necessity of a long developmental period results from the complexity and variability of social relationships and social competition (Alexander, 1989; Geary & Flinn, 2001; Gray & Feldman, 1997) and the wide range of biological and physical-ecological (e.g., mountainous vs. desert) niches occupied by humans. In each domain, there is evidence for both inherent and presumably gene-driven constraints that guide attention to and the early processing of invariant information patterns, such as human biological motion or the shape of a human face (D. G. Freedman, 1974; R. Gelman, 1990; Grossman et al., 2000), as well as experience-based modifications of the associated systems to accommodate variation within broader constraints (e.g., recognition of individual faces). The concept of soft modularity seems to capture the basic pattern of invariant and variant information patterns, with developmental experiences functioning to accommodate variant information patterns in the domains of folk knowledge.

### Summary and Conclusion

The function of brain and mind is to process socially and ecologically salient information and to guide the organisms' behavior in ways that result in survival (e.g., prey capture) or reproductive (e.g., mate detection) advantages. When viewed in this light and in terms of the cost-benefit trade-offs that are common to evolved systems (Williams, 1957), debate over the relative contributions of nature and nurture to the anatomical and functional organization of brain and mind center on two questions. What are the information patterns that have covaried with survival and reproductive outcomes during the species' evolutionary history? To what degree are these patterns invariant or variant across generations and lifespans? Invariant patterns are those that provide reliable and consistent information about conditions that have covaried with survival or reproductive outcomes during the species' evolutionary history. Examples include motion patterns generated by conspecifics (e.g., Blake, 1993; Grossman et al., 2000), shape and coloration of fruit for fruit-eating species (Barton et al., 1995), and acoustical patterns generated by human vocalizations (Doupe & Kuhl, 1999), among many others. We predict that an evolved sensitivity to variant information patterns occurs when discriminations within broader, invariant categories result in survival or reproductive advantages. Examples include the ability to



discriminate one human face from another (George et al., 1999) or one species of related plant from another (e.g., edible vs. poisonous mushrooms; Atran, 1998).

The benefits of fast and efficient processing of invariant information patterns and the potential cost of failing to attend to this information or discriminate it from related patterns should favor the evolution of inherently constrained and modular neural, perceptual, and cognitive systems (Cosmides & Tooby, 1994; Gallistel, 2000). We predict that these modular systems process three classes of information: social, biological, and physical. The associated domains for humans, and many other species, are captured by research in the areas of folk psychology (Baron-Cohen, 1995; Premack & Woodruff, 1978), folk biology (Atran, 1998), and folk physics (Shepard, 1994). Associated neuropsychological and brain imaging research is not definitive, but some of this research is consistent with modular systems for processing invariant information patterns in each of these domains, including systems for detecting and processing human motion (Downing et al., 2001), discriminating flora from fauna (Hart & Gordon, 1992), and representing physical space in the service of navigation (Maguire et al., 1998), among others. The prediction of inherent constraint is also supported by research in comparative neurobiology, comparative genetics, and developmental neurobiology. Included among these findings are cross-species similarities in the organization and physiological functioning of many neocortical and subcortical regions (Jones, 1985; Krubitzer, 1995), the possibility that some of these similarities and associated differences across regions may reflect the operation of conserved genes (Krubitzer & Huffman, 2000), and recent findings suggesting that aspects of neocortical arealization may be driven by region-specific gene expression (Miyashita-Lin et al., 1999). However, the relation between these neurobiological and genetic findings and cognitive research on folk knowledge remains to be explored.

Variability in patterns of social, biological, and physical information are common, and in fact, behavioral variability is a predicted feature of relationships among biological organisms (Maynard Smith & Price, 1973). Variability, in turn, would favor the evolution of neural, perceptual, and cognitive systems that are open to experiential modification, to the extent that sensitivity to this variability results in survival or reproductive advantages. For instance, the dynamics of social relationships (i.e., cooperation and competition) can result in a selective advantage for the ability to discriminate one individual from another—if the behavior of individuals differs and has potential survival or reproductive consequences (Cosmides, 1989; Trivers, 1971), as it does in many species (e.g., Goodall, 1986). For humans, our prediction is that modular, folk psychological systems are complemented by systems that can accommodate variability within these domains. These more plastic mechanisms would enable, among other things, the discrimination of one individual from the next based on movement patterns, voice, and how they think.

Again, the research to date is not conclusive, but neural and perceptual systems that accommodate these and other forms of variability (e.g., dialect differences) within broader constraints are evident for speech (Doupe & Kuhl, 1999), face recognition (Nakamura et al., 2000), and gesture (McNeill, 2000). Social and cognitive research suggests plasticity in the ability to form categories related to tool use (Bloom, 1996) and social competition (Stephan, 1985), among other things. An openness to organiza-

tional and functional modification related to experience, learning, and injury has also been demonstrated for the developing (Stiles, 2000) and mature brain (Bao et al., 2001), but again, the relation between this neurobiological research and cognitive research associated with folk knowledge is unclear.

We propose that at all levels—neural, perceptual, cognitive, and functional—the degree of inherent constraint and openness to experiential modification are the evolutionary result of the degree to which the associated information patterns have been invariant or variant during the species' evolutionary history. The combination of constraint and openness is captured by two forms of soft modularity described herein, the exoskeleton and rule-based category formation. For both, we predict that constraint is primarily for invariant information patterns in the domains of folk psychology, biology, and physics, and for openness to experiential modification to capture variability at the level of the individual (soft internal structures) or category (e.g., in-group–out-group, rule-based) within these broad domains. Information variability also results in pressures for an extended developmental period, which in turn enables neural, perceptual, cognitive, and functional (e.g., social behaviors) adaptations to variation across social (e.g., local language) and ecological (e.g., food sources) conditions (Geary, in press). In other words, we predict that brain and cognitive plasticity during the developmental period is an adaptation to accommodate variability in social and ecological conditions, but within the broader constraints of folk knowledge. From an evolutionary perspective, brain and cognitive systems would also be modifiable to some degree in adulthood, a concept captured by the resource-distribution form of soft modularity.

In closing, an evolutionary perspective provides a framework for linking research on brain and cognitive organization and functions from the level of conserved genes that guide the organization of the CNS to folk biological knowledge that guides hunting in traditional societies. More precisely, our prediction is that conserved brain and cognitive systems in complex animals serve similar functions across species, such as to negotiate relationships with conspecifics, other species (e.g., prey or predators), and the physical world. Species-specific adaptations within these broad domains of folk psychological, biological, and physical knowledge are expected as well, as are mechanisms to accommodate variation within each of these domains. The gist is that constraint and plasticity are the evolutionary result of invariant and variant information patterns, respectively, that covaried with survival or reproductive outcomes during the species' evolutionary history.

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## Appendix

### Forms of Modularity

1. *Neural module.* At this lowest level, modularity describes the relation between circumscribed sensory regions and the corresponding radial unit or units. As an example, consider the raccoon paw in Figure 4. Each of the forepaw pads, 1–5, and the supporting regions of somatosensory cortex represent one neural module. Each module provides limited information regarding the environment.

2. *Perceptual module.* Perceptual modules arise from the dynamic integration of activity patterns across individual neural modules and provide a more complex and abstracted representation of the environment and the organism's relation to the environment. Integration across the individual neural modules defining the raccoon forepaws results in the perception of a manipulated object, such as a food item.

3. *Cognitive module.* The next level of abstraction represents the ability to generate and mentally manipulate perceptual representations in the absence of sensory input and enables top-down manipulation of

organism–environment relations. If raccoons had such modules, they could generate a mental representation of a food item in the absence of manipulating it and mentally test various means of manipulating the item to, for instance, better extract food.

4. *Functional module.* These represent the integration of neural and perceptual (and cognitive in some species) modules with affective and motivational systems and direct the behavior of the organism toward evolutionarily significant goals. Affective and motivational systems lead raccoons to approach food sources or mates, for instance, and avoid predators.

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