

Evolutionary Psychology: New Perspectives on Cognition and Motivation

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Abstract

Evolutionary psychology is the second wave of the cognitive revolution. The first wave focused on computational processes that generate knowledge about the world: perception, attention, categorization, reasoning, learning, and memory. The second wave views the brain as composed of evolved computational systems, engineered by natural selection to use information to adaptively regulate physiology and behavior. This shift in focus—from knowledge acquisition to the adaptive regulation of behavior—provides new ways of thinking about every topic in psychology. It suggests a mind populated by a large number of adaptive specializations, each equipped with content-rich representations, concepts, inference systems, and regulatory variables, which are functionally organized to solve the complex problems of survival and reproduction encountered by the ancestral hunter-gatherers from whom we are descended. We present recent empirical examples that illustrate how this approach has been used to discover new features of attention, categorization, reasoning, learning, emotion, and motivation.

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INTRODUCTION

Both before and after Darwin, a common view among philosophers and scientists has been that the human mind resembles a blank slate, virtually free of content until written on by the hand of experience. Over the years, the technological metaphor used to describe the structure of the human mind has been consistently updated, from blank slate to switchboard to general-purpose computer, but the deeper assumption remained. The implications are wide ranging. According to this view, the mechanisms that produce learning operate in the same way, whether they are acquiring the grammar of a language, a fear of snakes, or an aversion to sex with siblings. The mechanisms that produce reasoning deploy the same procedures, whether they are making inferences about the trajectory of a billiard ball, the beliefs and desires of another person, or what counts as cheating in social exchange. The same goes for attention, categorization, memory, motivation, and decision making.

This perspective grants that evolution may have equipped the mind with a few primary reinforcers that have hedonic value (food, water, pain avoidance, sex). But it assumes that the neurocomputational systems that collect and process experiences are largely content free and domain general, designed to operate uniformly on information drawn from any stimulus class (cf. Herrnstein 1977, Gallistel 1995).

A very different picture of the human mind is emerging from evolutionary psychology, an approach to the cognitive sciences that integrates evolutionary biology, psychology, information theory, anthropology, cognitive neuroscience, and allied fields (for reviews, see Barkow et al. 1992, Buss 2005). In this view, human nature—the species-typical information-processing architecture of the human brain—is packed with content-rich adaptive problem-solving systems. Like expert systems (in artificial intelligence), each is designed to deploy different concepts, principles, inference procedures, regulatory variables, and decision rules when activated by cues of its proper domain. Why?

From this perspective, the cognitive and evolutionary sciences are connected as follows:

1. Each organ in the body evolved to serve a function: the intestines digest, the heart pumps blood, the liver detoxifies poisons. The brain is also an organ, and its evolved function is to extract information from the environment and use that information to generate behavior and regulate physiology. From this perspective, the brain is a computer, that is, a physical system that was designed to process information. Its programs were designed not by an engineer, but by natural selection, a causal process that retains and discards design features on the basis of how well they solved problems that affect reproduction (Williams 1966, Dawkins 1982).

The fact that the brain processes information is not an accidental side effect of some metabolic process: The brain was designed by natural selection to be a computer. Therefore, if you want to describe its operation in a way that captures its evolved function, you need to think of it as composed of programs that process information. The question then becomes, what programs are to be found in the human brain? What are the reliably developing, species-typical programs that, taken together, constitute the human mind?

2. These programs were sculpted over evolutionary time by the ancestral environments and selection pressures experienced by the hunter-gatherers from whom we are descended. Each evolved program exists because it produced behavior that promoted the survival and reproduction of our ancestors better than alternative programs that arose during human evolutionary history. Evolutionary psychologists emphasize hunter-gatherer life because it takes a long time for natural selection to build a computational adaptation of any complexity. Simple, quantitative traits can change faster, but it takes thousands of

years (i.e., many human generations) for natural selection to assemble a complex program composed of many different, functionally integrated parts (Tooby & Cosmides 1990a).

3. Although the behavior our evolved programs generate would, on average, have been adaptive (i.e., reproduction promoting) in the ancestral environments that selected for their design (their environment of evolutionary adaptedness), there is no guarantee that it will be so now (Tooby & Cosmides 1990b, Symons 1992). Modern environments differ importantly from ancestral ones, particularly when it comes to social behavior. We no longer live in small, face-to-face societies, in seminomadic bands of 25–200 men, women, and children, many of whom were close relatives. Yet our cognitive programs were designed for that social world.
4. Perhaps most importantly, the brain must be composed of many different programs, each specialized for solving a different adaptive problem our ancestors faced.

Our hunter-gatherer ancestors were, in effect, on a camping trip that lasted a lifetime, and they had to solve many different kinds of problems well to survive and reproduce under those conditions: hunting, evaluating plant resources, cooperating with others, avoiding predators, dividing resources among kin, selecting fertile mates, deterring sexual rivals, avoiding infectious diseases, detecting alliances, avoiding incest, learning grammar, negotiating dominance hierarchies, and managing aggression, for example. When natural selection was reconceptualized as replicator dynamics and combined with game theory (Williams 1966, Dawkins 1982, Maynard Smith 1982), it became possible to derive powerful (and nonintuitive) inferences about what counts as adaptive behavior in these domains.

Results from evolutionary game theory and data about ancestral environments

Computational adaptations: evolved systems designed (by natural selection) to monitor information and use it to functionally regulate behavior or physiology

Environment of Evolutionary Adaptedness: the series of ancestral environments/selection pressures that sculpted the design of an adaptation

Replicator dynamics: how genes change in frequency in a population

can be used to identify and dissect adaptive information-processing problems, to see what properties programs capable of solving them would need. This exercise often reveals that what counts as a solution differs radically and incommensurably for different adaptive problems. Consider, for example, food choice versus mate choice. The computational structure of programs that are well engineered for choosing nutritious foods will fail to produce adaptive behavior unless they generate different preferences and trade-offs than programs designed for choosing fertile sexual partners. Similarly, machinery that reliably and efficiently learns which local organisms are predators and the best way to respond to each (freeze? run? climb a tree?) lacks properties that will cause the reliable and efficient acquisition of grammar (and vice versa).

Evolutionary psychologists therefore expect (and find) that the human mind contains a large number of information-processing devices that are functionally specialized and therefore domain specific, with different devices activated by different kinds of content (snakes versus smiles, food versus mates, cues of social exchange versus cues of aggression). No one doubts that the mind contains some adaptive specializations that execute (relatively) domain-general computations (e.g., Brase et al. 1998, Rode et al. 1999, Gallistel & Gibbon 2000, Gigerenzer & Selten 2001). But these cannot produce adaptive behavior unless they interact with a large number of expert systems that are domain specialized and content rich (e.g., Pinker 1997, 2010; Cosmides & Tooby 2001; Cosmides et al. 2010). True blank slates—architectures that are content free except for a few hedonic reinforcers—lack the computational properties necessary to produce behavior that tracks fitness (Cosmides & Tooby 1987, Tooby et al. 2005). (For comprehensive introductions to the

conceptual foundations of evolutionary psychology, which include detailed arguments for each point listed above, along with controversies and responses, see Tooby & Cosmides 1992, 2005.)

Knowing that natural selection produces computational systems that solve adaptive problems reliably, quickly, and efficiently allows evolutionary psychologists to approach the study of the mind like an engineer. One starts with a good specification of an adaptive information-processing problem and does a task analysis of that problem. This allows one to see what properties a program would have to have in order to solve that problem well. This approach generates testable hypotheses about the structure of the programs that compose the mind—a point we hope to illustrate in this review.

From the earliest days of the field, evolutionary psychologists have used sexual selection theory to explore the psychology of mating relationships in humans and other animals (Trivers 1972, Symons 1979, Daly & Wilson 1988, Buss 1989). They have already produced a massive literature on this topic, opening up an area of study that had been neglected by the psychological sciences (for recent reviews, see Buss 2005, part III, and Roney 2009).

It is less obvious how knowledge and principles from evolutionary biology can guide research in more traditional areas of the cognitive sciences. So we have chosen examples from visual attention, spatial cognition, categorization, reasoning, learning, and motivation. In each case, the theoretical framework provided by evolutionary psychology led to new questions and surprising results—ones suggesting the existence of content-specialized procedures. Through these cases, we hope to illustrate key features of evolutionary psychology: the importance of considering ancestral environments; how hunter-gatherer studies and models from behavioral ecology, such as optimal foraging theory, can lead research in strange new directions; the role of evolutionary game theory in generating specific hypotheses about cognitive design; how adaptationist

hypotheses are tested against alternatives; the importance of content-specificity; and the need to be computational, even when researching motivation and emotion.

VISUAL ATTENTION

Visual attention is an umbrella term for a suite of operations that select some portions of a scene, rather than others, for more extensive processing. Most research in this area has explored how attention is deployed in response to either (a) low-level visual features (color, intensity, orientation, contrast) or (b) information that is personally or task relevant, given a volitionally chosen goal. This reflects a usually implicit assumption of the field: that the function of attention is to enhance the processing of features necessary for building accurate knowledge of what exists in the world and the performance of goals chosen by the individual.

Very few studies have considered the possibility that there are evolved systems designed to deploy attention in response to particular categories of information, in a way that is independent of volitional goals. Volitional attention is important for a tool-using species, but focusing too exclusively on a single task can be very costly. An evolutionary perspective suggests there should be systems that incidentally scan the environment for opportunities and dangers; when there are sufficient cues that a more pressing adaptive problem is at hand—an angry antagonist, a stalking predator, a mating opportunity—this should trigger an interrupt circuit on volitional attention and activate programs specialized for processing information about the new problem in an adaptive manner. According to this view, attention is a complex system with interacting components, some serving object perception, some deployed volitionally, and some monitoring the environment in an ongoing manner for adaptively important situations. These monitoring systems are likely to be category driven because their function is to detect the presence of situations defined over high-level objects (e.g., people, animals, antagonists,

cooperators), which can rarely be identified on the basis of low-level features alone.

Faces regulate social interaction, so initial attempts to look for category-specific attentional systems started with the human face. In short order, systems were found that preferentially attend to human faces (Ro et al. 2001) and that snap attention to the location at which a pair of eyes is gazing (Friesen & Kingstone 2003). But is this caused by an adaptive specialization that evolved for attending to faces—one with design features that were functionally organized by natural selection for that purpose? Because faces are important now, as well as ancestrally, a skeptic could argue that preferential attention to faces is caused by a domain-general expertise system—an evolved system to be sure, but one that will cause preferential attention to any perceptual cue that, if attended, would enhance performance on current tasks.

In principle, evidence from developmental disorders could rule out this expertise hypothesis, just as it did in the debate about face recognition (Duchaine et al. 2006). Autism, for example, may selectively disrupt attention to faces (Chawarska et al. 2010, Remington et al. 2012). But a different way of approaching the question is to compare attention to faces with attention to stimulus classes with which people have much less experience, but that were important ancestrally. Could there be a category-specific attentional system analogous to the appendix: there because it was adaptive in our evolutionary past, but relatively useless now?

Animal Monitoring: An Appendix in Visual Attention?

The survival of the typical undergraduate research subject might depend on how vigilantly she monitors cars and trucks as she drives or crosses the street, but not on her ability to spot edible turtles, avoid an ornery warthog, or judge whether the lion laying sated in the grass has just started attending to potential prey. The opposite is true of the hunter-gatherers from whom she is descended. For our foraging ancestors, nonhuman animals presented either dangers

(e.g., predators) or opportunities for hunting (e.g., prey). Snakes and spiders—ancestral dangers of little consequence in modern cities and suburbs—do capture attention in what appears to be a parallel search process (Öhman et al. 2001). But what about other animals, including ones that may not be fear relevant? And what about attentional monitoring, as distinct from attentional capture? Because animals can change their behavior and location quickly, the lives and livelihoods of our ancestors turned on their ability to monitor them for changes in their state and location. Does our visual attention system harbor a mechanism that monitors animals in an ongoing fashion?

It does. New et al. (2007a) addressed this question using the change detection protocol, in which subjects are asked to spot the difference between two rapidly alternating photos that are almost identical, but include one difference. This paradigm is famous for eliciting change blindness—a condition in which observers are unaware that an element of the scene is changing (e.g., whole buildings can repeatedly appear and disappear without the subject noticing). In this protocol, the only task subjects are given is to detect changes, so they are free to follow their own inclinations in attending to different entities in photos of complex natural scenes. This allows one to see whether the attentional system monitors animals more than other objects.

It turns out that change blindness is limited largely to inanimate objects. Changes to nonhuman animals (and to people) are detected faster and more accurately than changes to plants, buildings, tools, and even vehicles. For example, changes to a small bird at the periphery of a complex natural scene were detected faster and more accurately than changes to a large building at a scene's center. The time course of responses revealed that animals not only capture attention, but they are monitored in an ongoing manner for changes in their state and location.

A series of control tasks showed that the attentional advantage found for animals was not due to lower-level visual features, expectation of motion, task demands, properties of the back-

ground scene, or how interesting the targets were judged to be. The monitoring system responsible appears to be category driven, that is, it is automatically activated by any target the visual recognition system has categorized as an animal.

What is the origin of this animal-monitoring system? It could have been built into visual attention because of its benefits over evolutionary time, regardless of its current utility. Another possibility is that the visual system does not start out biased to monitor some categories of information over others; but it might be designed to create category-specific monitoring systems as an expertise, for any class of stimuli that are frequently encountered and important to monitor. New et al. (2007a) tested between these phylogenetic and ontogenetic accounts by comparing change detection for nonhuman animals to that for vehicles and humans.

Vehicles versus animals. Ontogenetically, monitoring vehicles for sudden changes in their states and locations is a highly trained skill of life-and-death importance to car-driving, street-crossing research subjects, but it was of no importance phylogenetically. In contrast, monitoring animals was important phylogenetically, but having your attention drawn to pigeons and squirrels is merely a distraction in modern cities and suburbs. If the ontogenetic expertise hypothesis were true, one would expect people to develop a category-specialized system for monitoring vehicles, such that changes to vehicles are detected as well as—or, indeed, better than—changes to nonhuman animals. But the reverse was true: Speed and accuracy at noticing changes were far greater for nonhuman animals than for vehicles. This is what one would expect if animal monitoring arises from an animal-specific evolved system rather than content-free learning.

People are an interesting stimulus class because they were important and frequently encountered phylogenetically and ontogenetically. As such, they represent an upper boundary on the effects that expertise can create, over and above any evolved bias. How well

are nonhuman animals monitored, compared to people?

People versus nonhuman animals. If preferential attention to a given category is acquired by domain-general learning processes alone, then category-driven differences in expertise would have to arise from differences in the frequency of experience with a stimulus class and differences in the current utility of monitoring it. This would predict that preferential attention to people should be much stronger than preferential attention to nonhuman animals.

From infancy, we are immersed in immense numbers of important transactions with other humans, which could have driven the acquisition of human-oriented attentional expertise without invoking any evolved bias toward humans. Moreover, the amount of experience subjects living in American cities and suburbs have with the human species is greater, by many orders of magnitude, than their experience with taxa such as birds, turtles, fish, insects, or African mammals. Do these vast differences in exposure rates and current utility translate into vast differences in the extent to which people are monitored compared to nonhuman animals?

No. New and his associates found that the differences between attention to humans and to other species were marginal at best; indeed, changes to nonhuman animals were detected just as well as changes to people in some of their experiments. Finding similar performance when exposure rates differ by orders of magnitude is inconsistent with any acquisition theory that invokes domain-general expertise with no evolved biases.

People are more important and more frequently seen than virtually any other category of stimuli, yet they recruit little more attention than nonhuman animals. This suggests that domain-general expertise systems, if they exist, do little more than fine tune an evolved system for monitoring people. At the same time, the fact that nonhuman animals were monitored about as well as people—and much bet-

ter than vehicles and other objects—implies the existence of a content-specialized system that was shaped by ancestral selection pressures, not general learning processes.

Automatic Regulation of Attention by High-Level Social Cues

Paleoanthropology and studies of modern hunter-gatherers show that our ancestors evolved as a group-living species, in small, face-to-face bands consisting of 25–200 men, women, and children. Because most of one's interactions will be with ingroup members in this social ecology, a default setting that allocates more attention to ingroup than outgroup members would be functional. Not surprisingly, people find it easier to visually distinguish and recall individuating information about ingroup members than outgroup members. This phenomenon—ingroup heterogeneity paired with outgroup homogeneity—is well-established in social psychology (Anthony et al. 1992, Ostrom & Sedikides 1992). It is often mentioned in conjunction with the cross-race recognition deficit: For some perceivers, people of a different race “all look alike”—another case of outgroup homogeneity (for an interesting discussion, see Levin 2000). Are there circumstances that modulate attention in a way that reverses this bias?

It may be safe to ignore outgroup members in most circumstances, but not when there are cues that they might intend to harm you. This line of reasoning led Ackerman et al. (2006) to propose a system that automatically upregulates attention to outgroup faces in response to cues of aggressive intent. To test this hypothesis, the researchers used race as a proxy for group membership, and tested recognition memory for ingroup and outgroup faces when their expression was neutral versus angry. The faces of black and white men were briefly shown to white subjects, who were then given an old/new recognition test. When expressions on the faces were neutral, subjects were better at recognizing the faces of white than black men, replicating the well-known outgroup homogeneity effect. But

when the faces were angry, subjects were just as good—and sometimes better—at recognizing the faces of black men. Not only did outgroup homogeneity disappear for angry faces, but it was reversed when subjects were operating under processing constraints. When exposure times were brief and distractor photos were present, the subjects were better at recognizing the faces of angry black men than angry white men, demonstrating outgroup heterogeneity.

This striking result reverses well-established effects from two large literatures: outgroup homogeneity and the cross-race recognition deficit. Yet it is precisely what one would expect on an evolutionary-functional account. The anger of an ingroup member is less likely to erupt into aggression because ingroup members participate in a network of cooperative relationships that afford other opportunities for resolving disagreements (see below). Because outgroup members are outside this network, aggression may be the only bargaining tool open to them, making their anger more dangerous. Importantly, angry expressions increased attention to the individuating features of outgroup members only; ingroup faces were recognized just as well when they were neutral as when they were angry.

Activating evolutionarily important goals, such as self-protection and mating, can modulate attention and other cognitive processes in functional ways (Maner et al. 2005, Becker et al. 2010, Kenrick et al. 2010). But the upregulation of attention to angry outgroup faces found by Ackerman et al. was not in response to any instruction or explicitly represented goal state. It occurred spontaneously in response to an ancestrally relevant threat cue: the species-typical facial expression associated with anger. More interestingly, attention was upregulated only when this species-typical threat expression was on the face of an outgroup member. Ingroup members elicited attention regardless of their emotional state; but when processing limitations forced a trade-off between angry ingroup and outgroup members, the system preferentially attended to angry outgroup members. This pattern suggests a system that is func-

tionally specialized for adaptively regulating attention in response to high-level social cues.

SPATIAL COGNITION AND NAVIGATION

Evolutionary psychology is concerned with the evolved architecture of the mind. Many computational mechanisms within this architecture will be the same in males and females (i.e., sexually monomorphic), and others will be different (i.e., sexually dimorphic). Sex differences in behavior can arise in either case. When boys and men encounter different social feedback, environments, and experiences than girls and women, sexually monomorphic mechanisms can generate sex differences in behavior. Sexually dimorphic mechanisms can also generate sex differences in behavior. The design of a computational system in women might differ from the design of the homologous system in men: different inferences, decision rules, signal detection thresholds, preferences, and motivational systems can cause women and men to make different decisions based on the same information. But a sexually dimorphic design could also lead men and women to seek out and remember different kinds of information, social feedback, environments, and experiences. For this reason, the mere discovery that men and women have different experiences is not sufficient to support the hypothesis that sex differences in their behavior were generated by a sexually monomorphic psychology.

Evolutionary psychology provides a framework for predicting the presence and absence of sex differences in the design of computational systems. No sex differences are expected in mechanisms that evolved to solve problems that were the same for ancestral men and women. The evolved architecture of mechanisms should differ between the sexes only when the adaptive problems faced by ancestral males and females were systematically different over long periods of evolutionary time. This principle can slice domains very finely indeed, as we illustrate using research on the presence—and absence—of sex differences in spatial cognition.

Spatial Specializations for Foraging

In cognitive tests tapping spatial cognition and navigation, men often outperform women (Voyer et al. 1995). Psychologists have long assumed that this male advantage is general, holding across spatial problems and domains. It is not. Evolutionary psychologists have discovered that women outperform men in certain spatial tasks. This female advantage was predicted in advance of any data, based on a careful analysis of how the spatial and navigational problems associated with foraging for plant foods differ from those associated with hunting.

There is a sexual division of labor in hunter-gatherer societies, with men specializing in hunting and women specializing in gathering sessile resources, such as plant foods (Marlowe 2007). These tasks place different demands on spatial cognition. Animals move from place to place, and they do their best to evade their predators. Tracking an animal can take a hunter into unknown territory, requiring a certain amount of dead reckoning to return to camp in an energy-efficient way (spatial tasks showing a male advantage, such as mental rotation, are thought to tap this navigational skill; Silverman et al. 2000). Plants, by contrast, stay in one place. But when a forager encounters a plant, the berries may need another week to ripen, the twining vine may be too young to have produced a mature tuber, and it may be a month before mature nuts appear on the mongongo tree. A hunter who is opportunistically harvesting plants as he tracks animals does not need to remember the location of plants that are of no immediate use. But being able to relocate a plant at a later time, when it has become harvestable, is important for a forager who specializes in gathering edible plant foods. And, although foraging women occasionally hunt small animals when the opportunity arises, they typically specialize in gathering plants and other sessile resources.

To return to these sessile resources when they are harvestable, a forager needs to remember their location at two scales. The first scale is within a patch: this requires encoding an

edible plant's position relative to other plants and landmarks in a tangled bank of vegetation. Based on this adaptive problem, Silverman & Eals (1992) had looked for and found a female advantage in object-location memory, which was content-general—as it should be, given the need to encode the position of edible plants relative to rocks, trees, and other objects. The second scale is one that supports navigation back to the resource patch at a later time. Navigation at this scale requires encoding the resource's absolute location within a represented environment—a quite different task, more similar to dead reckoning. Reasoning that navigational specializations in women at this larger scale should be triggered by the presence of plant resources, New et al. (2007b) conducted their first study at a farmers' market.

After taking people around and having them taste and rate foods at different stands, the researchers brought subjects back to a place where they could not see any of the stands and asked them to point to where each of the foods had been—a task that taps both spatial memory and the kind of vector integration necessary for efficient navigation. Women outperformed men—an advantage that held even when the researchers controlled for a variety of experimental variables, including visits to the farmer's market and particular stalls, and how often each food is eaten and liked (none of which predicted any variance in pointing accuracy). This is not because the researchers happened to find a particularly gifted sample of women: Men scored higher than the women did on a general not-plant-related sense-of-direction test (one that also predicted unique variance in pointing accuracy across sexes). Consistent with the idea that pointing accuracy taps navigation between patches, women succeeded without the relational cues that Silverman & Eals (1992) identified as important for finding a resource within a tangled bank. Follow-up studies by Krasnow and colleagues (2011) showed that this female spatial advantage is not caused by differences in women's ability to remember the identity of food resources they have

seen; it reflects better spatial memory for the absolute location of plant foods within a spatial frame. This female spatial memory advantage was highly domain specific: It was elicited only by fruiting trees. No spatial sex differences were found for other categories tested, including buildings, animals, tools, or gender-stereotyped objects, including jewelry and electronics.

An adaptationist approach to sex differences can slice a domain with remarkable precision, a point nicely illustrated by a second finding from the farmer's market study. Although the sexual division of labor among hunter-gatherers suggested the hypothesis that women will have an advantage in remembering the location of gatherable resources, other factors can affect spatial memory as well. Some of these—such as the nutritional quality of the resource—should be relevant to both sexes.

Optimal foraging theory was developed by behavioral ecologists to predict and explain which species foragers will harvest (Schoener 1971). Not surprisingly, its formal models have identified a food's caloric density as one important predictor of whether foragers will spend time searching for it. This led the farmer's market researchers to ask what would otherwise be a very strange question for a traditional cognitive psychologist: All else equal, are people more accurate at pointing to the location of foods of higher caloric density? Is their spatial/navigational performance better for, say, almonds and avocados than for cucumbers and lettuce?

The answer is yes: Calories count for both sexes. There was a robust correlation between a food's caloric density and accuracy at pointing to its location. This was not because people preferred the taste of high-calorie foods: Subjects had rated how much they liked each food during the initial tasting-and-rating phase of the experiment, but there was no correlation whatsoever between how much they liked each food and their pointing accuracy. Moreover, the extent to which calories improved spatial memory was independent of sex and had a similar effect size for women and men.

Content matters. A psychologist expecting to find spatial and navigational processes that operate independently of content would never think to look for any of these effects. Nor were they stumbled upon during more than 50 years of intuition-driven research in spatial cognition.

That calories count for navigation—that high-caloric-density foods activate better spatial memory and processes for returning to their location—is a result undreamt of in the philosophy of most cognitive scientists. So is the discovery that women have a spatial advantage that is not found for most objects, but emerges when the task involves gatherable plant resources. These surprising results imply that content matters deeply: Embedded within the computational systems that govern spatial memory and navigation are elements that respond differentially to plant resources and to the caloric density of foods.

EVOLUTIONARY GAME THEORY AND THE ANALYSIS OF SOCIAL BEHAVIOR

Game theory is a tool for analyzing strategic social behavior—how agents will behave when they are interacting with others who can anticipate and respond to their behavior. Economists use it to analyze how people will respond to incentives present in the immediate situation. Their models typically assume rational actors, who calculate the payoffs of alternative options (anticipating that other players will do likewise) and choose the one most likely to maximize their short-term profits (but see Hoffman et al. 1998).

Evolutionary biologists also adopted game theory as an analytic tool (Maynard Smith 1982), because the behavior of other people can be as relentless a selection pressure as predators and foraging. In contrast to economics, evolutionary game theory requires no assumptions about rationality; indeed, it can be usefully applied to cooperation among bacteria or fighting in spiders. It is used to model interactions among agents endowed with well-defined decision rules that produce

situationally contingent behavior. Although these decision rules are sometimes called strategies by evolutionary biologists, no conscious deliberation by bacteria (or humans) is implied (or ruled out) by this term. Whether the decision rules being analyzed are designed to regulate foraging, fighting, or cooperating, the immediate payoffs of these decisions, in food or resources, are translated into the currency of offspring produced by the decision-making agent, and these offspring inherit their parents' decision rule. In evolutionary game theory, a decision rule or strategy that garners higher payoffs leaves more copies of itself in the next generation than alternatives that garner lower payoffs. By analyzing the reproductive consequences of alternative decision rules over generations, evolutionary biologists can determine which strategies natural selection is likely to favor and which are likely to be selected out.

The evolution of cooperation has been vigorously investigated using game theory. We illustrate the method below and then show how it has led to the discovery of domain-specialized concepts and reasoning procedures.

The Evolution of Two-Party Cooperation: Constraints from Game Theory

The evolution of adaptations for cooperation is tricky, even when only two individuals are involved and they can interact repeatedly. Two-party cooperation, also known as reciprocal altruism, reciprocation, or social exchange, is often modeled as a repeated Prisoner's dilemma game. In each round of the game, the player must decide whether to cooperate or defect—to provide a benefit of magnitude B to the other player (at cost C to oneself) or refrain from doing so. In these games, $B - C > 0$ for both players. In these environments, strategies that always cooperate—no matter how their partners respond—are outcompeted by strategies that always defect, and eventually disappear from the population (see sidebar Unconditional Cooperation Is Not Evolutionarily Stable).

UNCONDITIONAL COOPERATION IS NOT EVOLUTIONARILY STABLE

Imagine a population of agents participating in a series of prisoners' dilemma games. Each agent is equipped with one of two possible decision rules: "always cooperate" or "always defect." "Always cooperate" causes unconditional cooperation: agents with this design incur cost C to provide their partner with benefit B , regardless of how their partner behaves in return. The other decision rule, "always defect," accepts benefits from others but never provides them, so it never suffers cost C . When two unconditional cooperators interact, their payoff is positive, because $B - C > 0$. When two defectors interact, they get nothing—they are no better or worse off than if they had not interacted at all. But every time a cooperator interacts with a defector, the cooperator suffers a net loss (because it pays cost C with no compensating benefit) and the defector gets B (the benefit provided by the cooperator) while incurring no cost.

Now imagine that the agents are randomly sorted into pairs for each new round, there are n rounds during a generation, and the probability of being paired with a cooperator versus a defector is p versus $(1 - p)$, a function of their relative proportions in the population. The "always defect" rule never suffers a cost, but it earns B every time it is paired with an agent who always cooperates, which is n^*p times; thus np^*B is the total payoff earned by each defector that generation. In contrast, the "always cooperate" rule suffers cost C in every round, for a total cost of n^*C . It earns B only from the n^*p rounds in which it meets another cooperator, for a total benefit of np^*B . Hence, $n(pB - C)$ is the total payoff earned by each cooperator that generation. These payoffs determine the relative number of offspring each design produces. Because $npB > npB - nC$, the "always defect" design will leave more copies of itself in the next generation than the "always cooperate" design. As this continues over generations, unconditional cooperators will eventually disappear from the population, and only defectors will remain. "Always defect" is an evolutionarily stable strategy in an environment where the only alternative is a design that always cooperates. "Always cooperate" is not an evolutionarily stable strategy—a population of unconditional cooperators can be invaded and displaced by designs that always defect.

Although unconditional cooperation fails, agent-based simulations show that decision rules that cause cooperation can evolve and be maintained by natural selection if they implement a strategy for cooperation that is

Adaptation:

phenotypic mechanism designed by natural selection; its features are functionally organized to solve ancestral problems of survival and reproduction

Tit-for-Tat:

a strategy that cooperates on round n of a repeated PD game, unless its partner defected on round $n-1$

conditional—a strategy that not only recognizes and remembers its history of interaction with other agents, but also uses that information to cooperate with other cooperators and defect on defectors (Tit-for-Tat is an example; Axelrod & Hamilton 1981, Axelrod 1984). Conditional cooperators remember acts of cooperation and cooperate in response, so they provide benefits to one another, earning a payoff of $(B - C)$ every time they interact. Because the cooperation of one elicits future cooperation from the other, they cooperate repeatedly, and these positive payoffs accumulate over rounds. In this, they are like unconditional cooperators. The difference is that conditional cooperators limit their losses to defectors. The first time a conditional cooperator interacts with a particular defector, it suffers a one-time loss, C , and the defector earns a one-time benefit, B . But the next time these two individuals meet, the conditional cooperator defects, and it does not resume cooperation unless its partner responds by cooperating. As a result, designs that defect cannot continue to prosper at the expense of designs that cooperate conditionally. Nor can they harvest gains in trade from interacting with one another. Over generations, conditional cooperators outproduce defectors because they harvest gains in trade from interacting repeatedly with one another.

Defectors are often referred to as “cheaters” in two-party reciprocation or social exchange. The results of evolutionary game theory tell us that cognitive adaptations for participating in social exchange can be favored and maintained by natural selection, but only if they implement some form of conditional cooperation. To do so, they require design features that detect and respond to cheaters (see Reasoning section, below).

Collective Action

A similar analysis applies to collective actions: situations in which three or more individuals cooperate to achieve a common goal and then share the resulting benefits. Defectors in

this form of group cooperation are called “free riders.”

There are many situations, such as common defense, in which the benefits of group cooperation will be shared by everyone in the group, regardless of how much they contributed to producing them. When this is true, those who contribute to the common goal at high levels are at a selective disadvantage compared to those who contribute at low levels (or not at all). The benefits of collective action will be reaped by high and low contributors alike, but the costs of contribution fall disproportionately on the high contributors. Consequently, the low contributors—the free riders—experience higher net payoffs than the high contributors, and those who contribute nothing do best of all. Because net payoffs are translated into offspring produced, decision rules that cause free riding will leave more copies of themselves in the next generation than those that always contribute at high levels. This will continue over generations. Eventually the population will consist entirely of agents who free ride; as a result, no one in this population will contribute to collective actions. Indeed, the total population may end up smaller than it was originally, because it is now composed entirely of agents who do not benefit from resources that can be harvested only by cooperating with others and sharing the resulting benefits.

As in two-party cooperation, adaptations for participating in collective action can be selected for only if they cause contributors to cooperate conditionally. In social exchange, a cooperator can avoid cheaters by switching partners when alternatives are available. This is more difficult in collective actions, because withdrawing from free riders means withdrawing from the group. A better solution is to keep the group, and either exclude free riders from it or else punish them to incentivize higher contributions in the future (Boyd & Richerson 1992, Hauert et al. 2002, Panchanathan & Boyd 2004, Tooby et al. 2006, Tooby & Cosmides 2010).

With these selection pressures in mind, we turn to concepts, categorization, and reasoning.

CONCEPTS AND CATEGORIZATION

Are our brains designed to reliably develop concepts as specific as “cheater” or “free rider,” which categorize people using criteria that satisfy constraints from evolutionary game theory? The idea seems eccentric. Indeed, the study of concepts and categorization started from the assumption that categorization is a unitary and general process, driven by perceptual similarity and shared features (e.g., Bruner et al. 1956, Rips et al. 1973). Some categorization processes do operate widely over many content domains (for review, see Ashby & Maddox 2005), but they coexist in the brain with a large number of content-rich, domain-specific inference systems (for reviews, see Pinker 1997, Boyer & Barrett 2005). These include the theory of mind system (e.g., Baron-Cohen 1995, Leslie et al. 2004, Onishi & Baillargeon 2005, Saxe & Powell 2006), intuitive physics (e.g., Spelke 1990, Leslie 1994), and folk biology (Medin & Atran 1999, Barrett 2005, Mahon & Caramazza 2009).

Each of these systems represents the world using specialized concepts and embodies inferences that, when applied to those concepts, are well designed for solving a different adaptive problem faced by the ancestral hunter-gatherers from whom we are descended. For example, the theory of mind system uses cues such as self-propelled motion and contingent reactivity to distinguish “agents” from other “objects”; proprietary concepts, such as “belief,” “desire,” and “intention,” which are attributed only to entities classified as “agents”; and specialized reasoning circuits for inferring these mental states and using them to predict and explain behavior.

Broad concepts, such as “agents” whose actions reflect their “beliefs” and “desires,” and physical “objects” that move only when acted upon by an outside “force,” are necessary for interacting with the world. But as systems for regulating social interactions, they are blunt instruments.

Intricate rules of obligation, entitlement, and moral violation regulate social interactions, and these differ by domain—consider, for example, the differences between cooperating with a team, negotiating rank in a status hierarchy, courting a romantic partner, trading favors with a friend, and helping a sibling. Evolutionary biologists and behavioral ecologists have developed sophisticated, game-theoretic models of what counts as adaptive social behavior in each of these domains. Implementing these behavioral strategies requires a number of fine-grained social categories and nuanced moral concepts. As a first example, we consider evidence for a domain-specialized concept, “free rider,” designed for regulating cooperation in collective actions.

Concepts for Collective Action: Free Riders Versus Cooperators

Humans are almost unique in the extent to which they participate in collective actions. It is fundamental to the human propensity to work in teams and form coalitions, so understanding the psychological mechanisms that make this zoologically unusual form of cooperation possible is fundamental to understanding organizational behavior, social systems, economics, and even politics (Olson 1965, Brewer & Kramer 1986, Ostrom 1990, Price et al. 2002).

As discussed above, adaptations for contributing to collective actions cannot evolve unless they are accompanied by a desire to exclude or punish free riders: those with motivational systems inclining them to avoid the costs of contributing to a collective action while benefiting from the contributions of others. Economists argue similarly, that rational actors will withdraw from collective actions when free riders are present; indeed, while noting that rational choice theory cannot explain it, behavioral economists and social psychologists have repeatedly shown that people are willing to punish free riders, even when they incur a personal cost to do so (Yamagishi 1986, Fehr & Gächter 2000, Masclet et al. 2003). But what criteria

does the mind use to categorize someone as a free rider?

Economists assume that individuals assess incentives in the immediate situation and make decisions that will maximize their short-term profit. This view suggests that participants in a collective action will classify anyone who has contributed less than themselves (or others) as a free rider (e.g., Masclet et al. 2003). Evolutionary game theory asks a different question: given the structure of ancestral environments, which decision rule for categorizing free riders will best promote its own reproduction over generations? Given the ecological conditions faced by ancestral hunter-gatherers, a concept that classifies everyone who undercontributes as a free rider—to be excluded or punished—is a losing strategy.

Error management. Two categorization errors threaten the evolutionary stability of conditional cooperation: mistakenly treating a free rider as a cooperater (a miss) and mistakenly treating a cooperater as a free rider (a false alarm). In foraging societies, false alarms are more costly than misses. Based on estimates of injury rates and variance in foraging success among existing hunter-gatherers, our ancestors experienced frequent reversals of fortune (Kaplan & Hill 1985, Gurven 2004, Sugiyama 2004). As a result, every individual endowed with neurocognitive mechanisms that cause conditional cooperation will sometimes fail to contribute to a collective action due to errors, accidents, bad luck, or injury. Categorizing these conditional cooperators as free riders will trigger cycles of mutual defection (you defect on the supposed free rider, who defects on you in return. . .). These cycles prevent both parties from harvesting the benefits of repeated mutual cooperation that occur when conditional cooperators correctly recognize one another. Without these benefits, decision rules that cause cooperation are eventually outcompeted by those that cause free riding, and collective action disappears from the population.

This means false alarms were very costly fitness errors for strategies that cooperate con-

ditionally. Misses were less costly: Mistakenly cooperating with a free rider results in a one-time loss, because strategies that cooperate conditionally defect on partners who have defected on them (see above; for agent-based simulations demonstrating this point in the context of two-person cooperation, see Delton et al. 2011).

When false alarms are more costly than misses, natural selection should equip categorization systems with criteria that minimize them, even if that increases the frequency of misses (on error management theory, see Haselton & Buss 2000, Haselton & Nettle 2006). A categorization system that uses level of contribution as its sole criterion for classifying someone as a free rider does exactly the wrong thing: It minimizes misses (the less costly error) at the expense of generating many false alarms (the more costly error). An evolutionarily stable strategy for collective action requires a “free rider” concept that distinguishes between undercontributors, sorting them on the basis of whether they show cues of cooperative versus exploitive intent.

Exploitive designs. Using an unobtrusive measure of social categorization based on recall errors (a “who did what?” protocol, analogous to the “who said what?” protocol developed by Taylor et al. 1978), Delton et al. (2012) showed that people who try to contribute to a collective action but fail are not categorized as free riders—even when they contribute less than others. To be categorized as a free rider, the target must undercontribute in a way suggesting exploitive intent—that is, a motivation to benefit from the collective action without incurring the costs of contributing to it (e.g., by consuming the resource they had promised to contribute or by making no effort to procure the promised resource). These individuals were subsequently judged to be less trustworthy, more selfish, more deserving of punishment, and less desirable as future cooperative partners.

The discovery that targets with exploitive intent are sorted into a distinct mental category—and evaluated more negatively than

targets who try to contribute but fail due to accident or bad luck—is robust. Moreover, it cannot be accounted for by a domain-general process that sifts for any behavioral difference between targets and uses it to categorize them. In a control condition using the same cooperative targets that had previously been categorized (when the other targets were free riders), Delton and colleagues showed that targets who try to contribute, but fail in one of two distinct ways, are not sorted into separate categories.

Moral psychology and free riders. Although these results suggest a domain-specialized system for categorizing free riders, they could also be accounted for if the mind has criteria for distinguishing those who violate moral rules from those who do not. To test this “moral violator” counter-hypothesis, Delton et al. (2012) used the same unobtrusive method to show that the mind distinguishes free riders from other kinds of moral violators. As in the other “who did what?” experiments, subjects saw that everyone who had agreed to participate in the collective action contributed resources on three of five days. But on the other two days, subjects saw that some targets consumed a resource they had promised to contribute to the group (free riders), and others stole a resource owned by the group. Every one of these targets was intentionally violating a moral rule—and illicitly taking a benefit for themselves that was obligated to the group. Nevertheless, subjects sharply distinguished them, as revealed by the categorization measure and the response and character ratings gathered subsequently.

That the mind slices the moral domain so thinly is remarkable: stealing a resource from the group and consuming a resource promised to the group are so similar that most approaches to moral psychology would not distinguish them. These experiments suggest that our minds really are prepared to notice and remember which individuals are free riders on collective actions, making very subtle distinctions between free riders and people who commit other, very similar kinds of moral violations.

REASONING

We take for granted that two parties can make themselves better off than they were before by exchanging things each values less for things each values more (help, favors, goods, services). This form of cooperation for mutual benefit—social exchange—does not exist in many species, but it is as characteristic of human life as language and tool use. From evolutionary game theory, we saw that adaptations for two-party cooperation can be favored and maintained by selection only if they implement a strategy that cooperates conditionally.

Conditional cooperation requires cognitive systems that not only recognize different individuals, but also remember whether they had cooperated or defected in the past. Memory research shows that faces of cooperators and cheaters are remembered better than faces of individuals who did neither (Bell et al. 2010), and faces of cooperators activate reward centers in the brain (Singer et al. 2004). Indeed, participating in social exchange activates reward centers more than nonsocial activities that provide the same payoffs (Elliott et al. 2006). It also triggers a very specialized form of conditional reasoning (reviewed in Cosmides & Tooby 2005, 2008a,b).

Conditional Reasoning and Social Exchange

The study of conditional reasoning was pioneered by Peter Wason, who began his inquiries with a simple question: Does the brain contain a reasoning system that implements first-order logic? (Wason & Johnson-Laird 1972). First-order logic is very useful: It has rules of inference that generate true conclusions from true premises—a very specialized function. But its procedures are blank—free of content—so they can operate uniformly on information from any domain. Logic’s domain generality is a good feature if your goal is to acquire valid knowledge about the world, no matter what subject you are studying. But this design feature is a bug for a system designed to reason adaptively about social exchange.

Conditional reasoning: reasoning about conditionals—rules with the format “If *P* then *Q*”

Logical violation of a conditional: cases of P and not- Q violate “If P then Q ”

When participating in social exchange, you agree to deliver a benefit conditionally (conditional on the other person doing what you required in return). This contingency can be expressed as a “social contract”, a conditional rule that fits the following template: “If you accept benefit B from me, then you must satisfy my requirement R .” The social contract is offered because the individual providing the benefit expects to be better off if its conditions are satisfied [e.g., if the theater owner receives the price of a ticket (“requirement R ”) in return for access to the symphony (“benefit B ”)]. The target accepts these terms only if the benefit provided more than compensates for any losses he incurs by satisfying the requirement (e.g., if hearing the symphony is worth the cost of the ticket to him). This mutual provisioning of benefits, each conditional on the others’ compliance, is what is meant by social exchange or reciprocation (Cosmides 1985, 1989; Tooby & Cosmides 1996). Understanding it requires a form of conditional reasoning. But the inferential rules required do not conform to the inferential rules of truth-preserving logics (Cosmides & Tooby 1989, 2008a).

For example, there is no logical inference by which “If P then Q ” implies “If Q then P ” (e.g., “If a person is a biologist, then he enjoys camping,” does not imply “If a person enjoys camping, then he is a biologist”). But what if P and Q refer to benefits and requirements, and the conditional rule expresses a social exchange between two parties?

Because conditional cooperation makes entitlement to benefits contingent on satisfying obligations, it is natural to infer that “If you accept benefit B from me, then you must satisfy my requirement R ” also implies “If you satisfy my requirement R then you are entitled to receive benefit B from me” (e.g., when I say, “If you borrow my car, then you have to fill my tank with gas,” I also mean “If you fill my tank with gas, then you may borrow my car”). Logic forbids this inference, but reasoning procedures designed for social exchange require it. An evolutionarily stable strategy for reasoning about conditional rules involving

social exchange requires functionally specialized inference rules like these, which operate on abstract yet content-specific conceptual elements, such as “agent,” “benefit,” “requirement,” “obligation,” and “entitlement”—what Cosmides & Tooby (1989, 1992, 2008a) call social contract algorithms.

To implement decision rules for conditional cooperation, social contract algorithms also require an information search function, designed to look for cheaters. “Cheaters” are individuals with a disposition to violate social contracts by taking the benefit offered without satisfying the requirement on which it was made contingent.

Investigations with the Wason Selection Task

The hypothesis that the brain contains social contract algorithms, which include a subroutine for detecting cheaters, predicts a dissociation in reasoning performance by content: a sharply enhanced ability to reason adaptively about conditional rules when those rules specify a social exchange.

Peter Wason’s four-card selection task is a standard tool for investigating conditional reasoning (see **Supplemental Figure 1**; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). Subjects are given a conditional rule of the form “If P then Q ” and asked to identify possible violations of it—a format that easily allows one to see how performance varies as a function of the rule’s content. Wason developed this task to see if we humans are natural falsificationists: if we spontaneously apply first-order logic to look for cases that might violate a conditional rule. It turns out that people perform poorly on this task: For most conditional rules, only 5% to 30% of normal subjects respond with the logically correct answer, even when the rule describes familiar content drawn from everyday life—such as a disease causing a particular symptom or a rule describing people’s preferences or habits (Wason 1983, Cosmides & Tooby 2008a).

Supplemental Material

Content matters, however. When the conditional rule involves social exchange and detecting a violation corresponds to looking for cheaters, 65% to 80% of subjects correctly detect violations on the Wason selection task (see **Supplemental Figure 2**; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). They succeed even when the rule specifies a wildly unfamiliar social contract (e.g., “If you get a tattoo on your face, then I’ll give you cassava root”). The ability to detect cheaters on social contracts is already present by age 3–4 (Núñez & Harris 1998, Harris et al. 2001), and it is found cross-culturally—not just in industrialized market economies, but also among Shiwiar hunter-horticulturalists of the Ecuadorian Amazon (Sugiyama et al. 2002).

This is not because social contracts activate the inferences of first-order logic. Looking for cheaters requires one to investigate two classes of individuals: those who have accepted the benefit offered in the social contract rule (to see if they failed to satisfy the requirement) and those who have not satisfied the requirement (to see if they took the benefit anyway). In many Wason selection tasks, these choices are (by coincidence) logically correct. But it is simple to create a social contract problem where investigating the same individuals is logically incorrect (see **Supplemental Figure 3**; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). When this is done, people do not respect the rules of logic; they look for cheaters instead (Cosmides 1989, Gigerenzer & Hug 1992).

The claim that the mind contains reasoning procedures specialized for detecting cheaters was (and is) very controversial (Cosmides & Tooby 2005, 2008a,b; Fodor 2008). A common response is that people are good at detecting violations of any conditional rule that is deontic (i.e., that expresses permission, obligation, entitlement, or prohibition), whether it is a social contract or not (e.g., Cheng & Holyoak 1985, Manktelow & Over 1991, Sperber et al. 1995, Fodor 2000). In support of this, they

note—correctly—that people are good at detecting violations of (deontic) precautionary rules, such as “if you work with toxic gases, then you must wear a gas mask” (Cheng & Holyoak 1989, Fiddick et al. 2000). But two separate systems regulate reasoning about these two domains: Brain damage can selectively impair a person’s ability to detect cheaters on social contracts while leaving intact their ability to detect violations of precautionary rules (Stone et al. 2002)—a neural dissociation that is supported by brain imaging studies (Fiddick et al. 2005, Ermer et al. 2006, Reis et al. 2007).

Most tellingly, however, good violation detection is not found for deontic rules that are neither precautions nor social contracts (Cosmides & Tooby 2008a,b). Indeed, social contracts themselves do not elicit violation detection unless this can reveal potential cheaters—individuals with a disposition to illicitly benefit by violating the rule (for explanation, see section Concepts for Collective Action: Free Riders Versus Cooperators). Using the same social contract rule—which was given the same deontic interpretation in all problems—Cosmides et al. (2010) parametrically varied three cues relevant to detecting cheaters. Violation detection was high when potential violators were acting intentionally, would get the benefit regulated by the rule, and the situation allowed violations. But removing any one of these cues independently (and additively) down-regulated detection of social contract violations (see **Supplemental Figure 4**; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). Performance was lower (*a*) when violations reflected innocent mistakes (rather than intentional actions), (*b*) when the violators would not get the benefit regulated by the rule, and (*c*) when the situation made cheating difficult (when violations are unlikely, the search for them is unlikely to reveal those with a disposition to cheat). These results indicate that the reasoning mechanism involved is not designed to look for general rule violators, or deontic rule violators, or violators of social contracts,

or even cases in which someone has been cheated; it does not deign to look for people who violated a social exchange by mistake—not even when they have accidentally benefited by doing so. Instead, this reasoning system is monomaniacally focused on looking for social contract rule violations when this is likely to lead to detecting “cheaters”—defined as agents who obtain a rationed benefit while intentionally not meeting the requirement.

MOTIVATION: THE ROLE OF EVOLVED REGULATORY VARIABLES

During the first wave of the cognitive revolution, researchers focused on the design of systems that evolved for knowledge acquisition, not motivation. Some areas, such as vision science, made progress despite the use of intuitive and informal ideas about their adaptive function. Not all biological functions correspond so transparently to our intuitions, however. Notable among these are adaptive problems relevant to value and motivation.

The adaptive regulation of behavior requires systems that value alternative behavioral choices in ways that tracked their fitness consequences. But what counts? For example, in making choices, how much weight should an organism place on the welfare of a sibling compared to its own? How intimidated should one individual be by the threat posed by another? When does the value of forging relationships with strangers offset the risk of exposure to new pathogens? Computational systems that make trade-offs like these should exist, and their study can benefit from systematic analyses of the biological problems that selected for their design.

Biologically speaking, computing value requires more than a general system for maximizing “utility,” as some economists (and psychologists) conceive it. What constitutes biologically successful valuation (i.e., values enabling choices that promote fitness) differs from one domain to the next. In many cases, the criteria for computing value are fundamentally incommensurable across domains (Cosmides

& Tooby 1987, Tooby et al. 2005). There is no general set of cross-domain choice criteria whose uniform application can adaptively guide food choice, mate choice, group affiliation, response to mate infidelity, incest avoidance, predator avoidance, friend-directed altruism, free rider punishment, cheater avoidance, infant nursing, sexual arousal, food sharing, aggression titrating, contagion avoidance, and so on. When valuation systems require distinct and incommensurable criteria to solve motivational problems (e.g., food choice versus mate choice versus predator avoidance), each incommensurable domain will require (at least) one functionally distinct, domain-specialized component.

Internal Regulatory Variables

By starting with models of specific adaptive problems drawn from evolutionary biology and evolutionary anthropology, evolutionary psychologists have identified candidate problems for which there should be evolved motivational specializations. When this is done, it becomes clear that computational strategies capable of solving these problems require elements that have no counterpart in traditional models of motivation. For example, what drive is reduced by helping family members? By sexual jealousy? By avoiding incest? By punishing free riders? By favoring the ingroup? By expressing anger? From what general goal could they be backward derived?

The kind of programs necessary to solve motivational problems require computational elements that are not exactly concepts, beliefs, representations of goal states, desires, preferences, or drives, but something else: internal regulatory variables (along with evolved specializations that compute them and deliver them to evolved decision-making systems) (Lieberman et al. 2007, Ermer et al. 2008, Tooby et al. 2008, Sell et al. 2009a). Each regulatory variable evolved to track a narrow, targeted property of the body, the social environment, or the physical environment—such as aggressive formidability, relative status,

reliability as a cooperator, or kinship—whose computation provided the necessary inputs to evolved decision rules. These regulatory variables store magnitudes (or parameters), which either express value or provide input to mechanisms that compute value.

Below we illustrate with research exploring the architecture of the kin detection system. Evidence so far indicates that this system produces kinship indexes—variables that regulate motivational systems governing altruism and sexual attraction/aversion.

Genetic Relatedness and Motivation: Siblings, Incest, and Altruism

One family of adaptive problems involving valuation arises from asking how genetic relatedness should affect social behavior. Prior to the integration of the evolutionary sciences with psychology, questions like this were rarely considered. Yet adaptive problems posed by relatedness are nonintuitive, biologically real, and have large fitness consequences.

Kin-directed altruism. The theory of kin selection (Hamilton 1964) was a fundamental advance in the theory of natural selection, which follows from replicator dynamics. A gene can cause its own spread not only by increasing the reproduction of the individual it is in, but also by increasing the reproduction of others who are more likely to carry the same gene than a random member of the population—that is, close genetic relatives. This means that natural selection can favor the evolution of motivational designs that, under the right envelope of conditions, cause the individual to sacrifice his or her own welfare to increase the welfare of a genetic relative. There is evidence supporting the predictions of kin selection theory in species in which close genetic relatives frequently interact, including amoebas, plants, shrimp, social insects, rodents, and primates (reviewed in Lieberman et al. 2007). Given that our ancestors lived in small bands with close genetic relatives, kin selection theory predicts that human motivational sys-

tems governing welfare trade-offs (including altruism) should take kinship into account.

Inbreeding avoidance. A second adaptive problem that arises from proximity to close genetic relatives is inbreeding depression. Recessive alleles that are harmless when matched with a healthy allele can be injurious when matched with duplicates of themselves. Because all people carry many unexpressed deleterious recessives they received from their parents, zygotes produced when two close relatives mate are far more likely to carry defective alleles that match than zygotes produced by individuals who are not related to one another. This leads to a sharp increase in the number of genetic diseases expressed in children produced by incestuous matings—costs that may be further aggravated by parasites differentially exploiting more genetically homogeneous hosts (Charlesworth & Charlesworth 1999, Lieberman et al. 2007). This makes incest a major fitness error, like approaching predators, eating gravel, or killing your children. Consequently, computational designs that cost-effectively reduce inbreeding depression by avoiding mating with close genetic relatives outcompete variants in which mating decisions are unaffected by relatedness. Hence, the human psychological architecture should contain evolved systems designed to inhibit incest.

A Kin Detection System

These two adaptive problems—inbreeding avoidance and kin-directed altruism—both require a kin detection system: a neurocomputational system that is well engineered (given the structure of ancestral environments) for computing which individuals in one's social environment are close genetic relatives. By analyzing the adaptive problem, Lieberman et al. (2007) derived a model of this architecture (see **Figure 1**) and conducted a series of tests of predictions drawn from the model.

According to this theory, the kin detection system uses ancestrally reliable cues to compute and update a continuous variable, a kinship

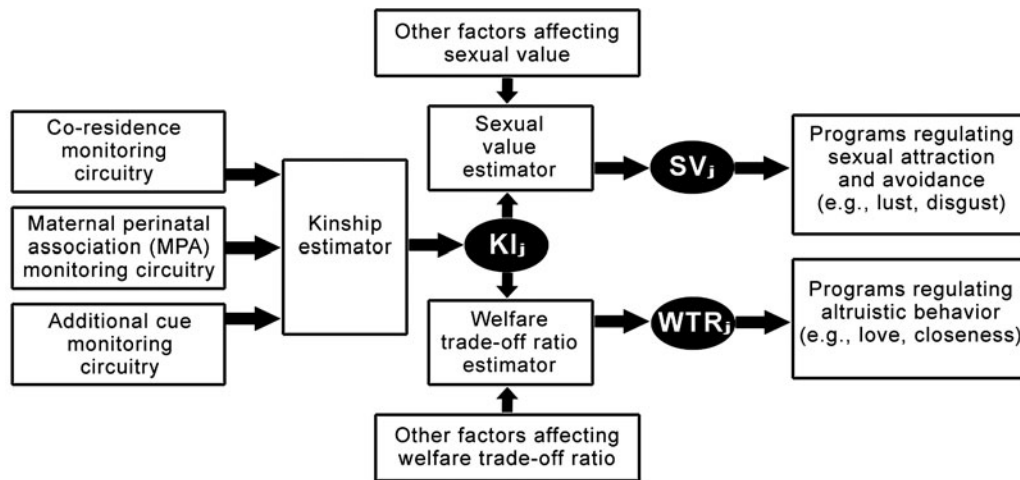


Figure 1

Architecture of a kin detection system, and its relationship to motivational systems regulating altruism (welfare trade-offs) and sexual attraction. The system includes several internal regulatory variables. A high kinship index (KI_j) between self and individual j should lower the sexual value of j to self (SV_j), and increase how much weight one places on j 's welfare when making choices (WTR_j).

index, KI_{ij} , for each familiar other, j . The magnitude of KI_{ij} embodies the system's pairwise estimate of genetic relatedness between self (i) and other (j). Kinship indexes are evolved regulatory variables that should serve as input to neural programs regulating altruism by i toward j and, separately, to programs regulating i 's sexual attraction to j . When KI_{ij} is high, it should up-regulate motivations to provide aid to j , and it should down-regulate sexual attraction by activating disgust at the possibility of sex with j .

Ancestrally reliable cues to genetic relatedness. The adaptive problem of detecting relatedness is hard to solve because genetic relatedness cannot be directly observed. Instead, the system must infer it, based on cues that predict genetic relatedness. A domain-general learning system cannot, by itself, identify and then use whatever transient cues best predict relatedness in the local environment. Discovering which novel cues are best would require the system to already know the genetic relatedness of others—the exact problem the kin detection system needs to solve. Instead, the kin detection system must contain within its evolved design a specification of the core cues that it will use

to determine relatedness—cues picked out over evolutionary time by natural selection because they reliably tracked genetic relatedness in the ancestral social world.

For our hunter-gatherer ancestors, a reliable cue to relatedness is provided by the close association between mother and infant that begins with birth and is maintained by maternal attachment. Maternal perinatal association (MPA) provides an effective psychophysical foundation for the mutual kin detection of mother and child. It also provides a foundation for sibling detection. Among our ancestors, when an individual observed an infant in an enduring caretaking association with the observer's mother, that infant was likely to be the observer's sibling. To use this high-quality information, the kin detection system would need a monitoring subsystem specialized for registering MPA.

Although MPA allows older offspring to detect their younger siblings, it cannot be used by younger siblings because they did not exist when their older siblings were born and nursed. This implies that the kin detection system's psychophysical front end must monitor at least one additional cue to relatedness. The cumulative duration of coresidence between two children, summed over the full period of parental

care until late adolescence, is a cue that could be used to predict genetic relatedness—an expansion and modification of the early ethological proposal about imprinting during early childhood.

Hunter-gatherer bands fission and fuse over time, as their members forage and visit other bands; this means individuals frequently spent short periods of time with unrelated or distantly related persons. However, hunter-gatherer parents (especially mothers) maintained close association with their dependent children in order to care for them. Siblings, therefore, maintained a higher-than-average cumulative association with each other within the band structure. As association is summed over longer periods of time, it monotonically becomes an increasingly good cue to genetic relatedness. This invites the hypothesis that the kin detection system has a system for monitoring duration of coresidence between i and j during i 's childhood, and that its output allows younger offspring to detect their older siblings.

Does a kin detection system regulate sibling altruism and sexual aversion?

To compute the kinship index, the kin detection system requires (a) monitoring circuitry designed to register cues to relatedness (MPA, coresidence during childhood, possibly others) and (b) a computational device, the kinship estimator, whose procedures have been tuned by a history of selection to take these registered inputs and transform them into a kinship index—the regulatory variable that evolved to track genetic relatedness.

If these cues are integrated into a single kinship index—that is, if the kinship index for each familiar individual is a real computational element of human psychology—then two distinct motivational systems should be regulated by the same pattern of input cues. For example, when i is younger than j , i 's kinship index toward j should be higher the longer they coresided during i 's childhood. As a result, i 's levels of altruism and sexual aversion toward j will be predicted by their duration of childhood coresidence.

Lieberman et al. (2007) tested these hypotheses about the computational architecture of human kin detection by quantitatively matching naturally generated individual variation in two predicted cues of genetic relatedness—maternal perinatal association and duration of coresidence during childhood—to individual variation in altruism directed toward a given sibling and opposition to incest with that sibling. When the MPA cue was absent (as it always is for younger detecting older siblings), duration of childhood coresidence with a specific sibling predicted measures of altruism and sexual aversion toward that sibling, with similar effect sizes. When the MPA cue was present (which is possible only for older detecting younger siblings), measures of altruism and sexual aversion toward the younger sibling were high, regardless of childhood coresidence.

These results support the model in **Figure 1**. At least two cue-monitoring systems must be present, because motivational outcomes were regulated by both MPA and coresidence duration. Moreover, these two inputs regulated two different motivational outputs, altruism and sexual aversion, representing two entirely independent adaptive problems (titrating kin-directed altruism and avoiding incest). The fact that two different motivational systems are regulated in parallel by the same cues to genetic relatedness implicates a single underlying computational variable—a kinship index—that is accessed by both motivational systems. Finally, the kinship estimator must be a part of the architecture because, where both cues are available, the more reliable cue—maternal perinatal association—trumps coresidence duration. The two cues interact in a noncompensatory way, rather than being additive, meaning there is unlikely to be a direct path from the input variables (cues) to the motivational systems they regulate.

This entire computational system appears to operate nonconsciously and independently of conscious beliefs. When beliefs about genetic relatedness conflict with the cues this system uses (as they do when people have coresided with step-siblings), the motivational outputs

(caring, sexual disgust) are shaped by the cues, not the beliefs. It is worth noting that this system influences moral sentiments as well: Those who have opposite-sex siblings associated with a high kinship index are more morally opposed to incestuous relationships, even between third parties (Lieberman et al. 2003, 2007; Fessler & Navarete 2004).

Finally, it is important to recognize that the kin detection system constitutes a learning system: It is designed to learn the genetic relatedness of familiar others. What makes it especially interesting is that it does not resemble the general-purpose learning systems psychologists are used to positing as explanations for behavior. Instead, it is a proprietary learning system, with a dedicated function, whose complex architecture incorporates content-inflected computational elements (e.g., mother, neonate, coresidence). The computational problem-solving strategy evolved to exploit the particular relationships of the ancestral world (foraging patterns, mother-infant association) in order to successfully acquire information it was designed to learn. It is an open question how much of human learning is carried out by domain-specific or content-sensitive devices, and how much by more general-purpose systems.

The case of kin detection (including incest avoidance and kin-directed altruism) is instructive in that it provides an example of what the computational architectures of evolved motivational adaptations are likely to look like. It suggests that the architecture of human motivation is full of registers for evolved variables: kinship indexes, sexual value indexes, coresidence measures, welfare trade-off ratios, and others. These variables acquire their properties and meaning by the evolved behavior-controlling and motivation-generating procedures that compute and access them (Tooby et al. 2008). That is, each has a location embedded in the input-output relations of our evolved programs, and their function inheres in the role they play in the control architecture of these programs. The kinship index is located downstream of input cues, it tracks relatedness, and it is accessed by down-

stream sexual valuation and welfare trade-off motivations.

On this view, there is a hidden, previously unmapped layer of neurocomputational procedures and representations, consisting of (a) internal regulatory variables (e.g., a kinship index), (b) procedures that compute them (e.g., the kinship estimator), (c) psychophysical front ends that monitor cues that serve as inputs to the procedures that compute these variables (e.g., maternal perinatal association monitoring), and (d) the entities that these variables feed, such as decision rules, motivational intensities, emotion programs, and conscious feelings (e.g., disgust at the idea of sexual contact with a sibling). These systems embody an evolved functional logic that reflects the adaptive problems they evolved to solve, and they cause us to experience specific motivations, value specific outcomes, and express specific behaviors given certain inputs. Given the complexity of these systems, one would never discover them using blind empiricism. However, models of adaptive problems give strong guidance in how to construct experimental programs to detect these systems and to map their computational structure.

EMOTION AND THE RECALIBRATION OF REGULATORY VARIABLES

In **Figure 1**, the kinship index feeds systems that compute at least two other regulatory variables: (a) the sexual value index ($SV_{i,j}$), a regulatory variable whose magnitude represents i 's assessment of j 's value as a sexual partner, and (b) a welfare trade-off ratio ($WTR_{i,j}$), a variable whose magnitude represents the weight i puts on j 's welfare when making decisions that impact them both. Ample literature supports the view that many ancestrally reliable cues of a potential sexual partner's health and fertility are integrated to form a sexual value index, whose magnitude is experienced as the person's sexual attractiveness (for review, see Sugiyama 2005). But why posit the existence of welfare trade-off ratios?

Welfare Trade-Offs

In social species, actions undertaken by one individual sometimes impact the welfare of others. Although biologists had previously assumed that selection favored choices that were completely selfish, over the past five decades, evolutionary biologists have identified a series of selection pressures that favor taking the welfare of others into account. That is, there are classes of situations in which the most fitness-promoting choice is not simply to maximize one's own welfare. Instead, under various conditions selection favors placing weight on the welfare of another as well, so that decisions reflect a trade-off between the welfare of self and other. Adaptive problems that favor calibrating such trade-offs include kin selection (Hamilton 1964), reciprocation or exchange (Trivers 1971, Axelrod & Hamilton 1981), aggression and the asymmetric war of attrition (Hammerstein & Parker 1982), and externalities (Tooby & Cosmides 1996).

Most evolutionary models tend to dissect strategic games involving kinship, aggressive formidability, reciprocity, and so on as independent, isolated problems. However, real organisms facing real choices cannot. Humans are often playing a number of games at once with the same individuals. Each act or choice is an expression of the weight the actor places on the target's welfare, and so a single act cannot express inconsistent weights at the same time. Yet different games will rarely converge on the same weighting function for a specific target: A target may be a sibling, for example, yet have cheated recently in a dyadic reciprocation. A person cannot simultaneously give aid (e.g., if the other is indexed as close kin) and withhold aid (e.g., if the other is indexed as someone who has cheated in their reciprocity relationship).

For the neural architecture to be able to decide which self-favoring or other-favoring acts to choose at any given moment, the brain needs a motivational architecture that registers the factors that, taken individually, might call for different weightings, and integrates them (at any given time) into a single welfare trade-off

ratio (Tooby et al. 2008). Multiple converging lines of evidence support the hypothesis that WTRs are not just post hoc theoretical constructs, but exist as real neurocognitive elements within the human motivational architecture—elements that play a role in decision making. A number of empirical studies now support the view that WTRs are person-specific stored values that display remarkable consistency across large numbers of benefit allocations between self and other (Delton 2010).

Anger and the Recalibration of Welfare Trade-Off Ratios

If WTRs actually exist in human brains, then selection can design adaptations whose function is to recalibrate their magnitude in oneself and in others. Gratitude, guilt, and anger may be social emotions that evolved to recalibrate WTRs (Tooby & Cosmides 2008). Evidence supports the view that the gratitude emotion program is activated when someone puts an unexpectedly high weight on your welfare. The gratitude program then recalibrates your WTR toward the generous person upward—serving the function of consolidating cooperative relationships (Lim 2012). Guilt is hypothesized to be activated when a person discovers they have placed too low a weight on someone else's welfare. It also triggers an upward recalibration of the transgressor's WTR toward the victim, so that future treatment is less exploitive (Sznycer 2010).

Within this framework, the greatest amount of research has been done on the recalibrational theory of anger (Sell 2005, Tooby et al. 2008, Sell et al. 2009a). In this view, anger is the expression of a neurocomputational system that evolved to adaptively regulate behavior in the context of resolving conflicts of interest in favor of the angry individual. The anger system is triggered by actions indicating that the other party is placing too little weight on the welfare of the actor (i.e., when their actions express a WTR that is too low). For example, an action by j that imposes a given cost on self is more

likely to activate one's anger program when j did it to gain a small benefit than a large one, because this indicates j 's WTR toward oneself is low (Sell 2005, Lim 2012).

Once triggered, the anger system deploys bargaining tactics designed to incentivize the target of the anger to place greater weight on the welfare of the angry individual in the future. It does this by activating one of two social negotiating tactics: threatening to inflict costs (aggression) or threatening to withdraw expected benefits (i.e., lowering one's own WTR toward the target of the anger). Acts or signals of anger (such as the anger face) communicate that, unless the target starts to place more weight on the angry individual's welfare, the angry individual will inflict costs on the target (in noncooperative relationships) or withdraw benefits from the target (in cooperative relationships)—that is, the angry individual will lower her WTR toward the target unless the target raises his WTR toward her. Experiments show that choices revealing a low WTR trigger anger in cooperative relationships, which in turn leads the angry individuals to lower their own WTR toward their partner (the predicted bargaining response). The magnitude of the subject's anger predicts the magnitude of the subject's WTR recalibration (Lim 2012).

Because interpersonal bargaining power arises from the relative ability to inflict costs or to confer/withhold benefits, the recalibrational model of anger predicts that individuals with enhanced abilities to deploy these tactics will anger more easily, will feel entitled to better treatment (to a higher WTR from others), and will prevail more in conflicts of interest. Their greater ability to inflict costs or withdraw

benefits translates into greater leverage in bargaining—meaning that anger is more likely to be successful for them than for others with less leverage. This suggests that there should be two regulatory variables that summarize these dimensions of social power and feed into the anger system: a formidability index that encodes the individual's self-assessment of his ability to inflict costs (fighting ability) and a conferral index that encodes the individual's self-assessment of his ability to confer/withhold benefits. For our male ancestors, upper-body strength was a major component of the ability to inflict costs on others (by injuring or killing them). Hence, greater strength should set a man's formidability index higher. Even now, people can accurately assess men's strength from sparse visual or vocal cues, and they spontaneously base their assessment of others' fighting ability on it (Sell et al. 2009b, 2010; Fessler et al. 2012). The ability to confer/withhold benefits has many sources, but one factor that is easy to operationalize is sexual attractiveness in women. As predicted by the recalibrational theory of anger, Sell et al. (2009a) found that men with greater upper-body strength were more prone to anger, felt more entitled to better treatment, and prevailed more in conflicts of interest than men with less upper-body strength. In women, attractiveness produced these same effects.

CONCLUSION

Evolutionary psychology is an organizing framework that can be applied to any topic in the psychological sciences. Discovering the design of the mind is easier when evolutionary biology tells us what we might find.

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Discusses gene as unit of selection; stresses importance of design evidence for recognizing adaptations.



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