

Evolutionary psychology and the brain

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The human brain is a set of computational machines, each of which was designed by natural selection to solve adaptive problems faced by our hunter–gatherer ancestors. These machines are adaptive specializations: systems equipped with design features that are organized such that they solve an ancestral problem reliably, economically and efficiently. The search for functionally specialized computational adaptations has now begun in earnest. A host of specialized systems have recently been found, including ones designed for sexual motivation, social inference, judgment under uncertainty and conditioning, as well as content-rich systems for visual recognition and knowledge acquisition.

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Introduction

In this article, we shall review some of the recent evidence for functionally specialized problem-solving machinery in the brain. We shall also discuss how theories of adaptive function have been used to uncover their presence and design.

The phenomenon that Darwin was trying to explain is the presence of functional organization in living systems — the kind of organization that one finds in artifacts that were designed by an intelligent engineer to solve a problem of some kind. Darwin showed how the feedback loops of a blind causal process — natural selection — could create structures that *looked like* they were designed by an intelligent engineer to solve a problem. His detailed studies of plants and animals revealed complex structures composed of parts that appeared to be organized to overcome reproductive obstacles (e.g. the presence of predators) or to take advantage of reproductive opportunities (e.g. the presence of fertile mates). And this made sense: although selection can inject problem-solving machines into the architecture of a species, the only problems it can design machines for solving are ones that had an impact on reproductive rates in the environments in which a species evolved.

Discovering how to dissect the architecture of a species in a way that illuminates its functional organization and explains its presence has been a foundational task for evolutionary biology ever since. To arrive at the appropriate construal, one must conceptualize this architecture as composed of nonrandom parts that interact in such a way that

they solve adaptive problems. This requires theories of adaptive function. These are engineering specifications, which provide analyses of what would count as good design for a particular problem [1]. In so doing, they also provide the criteria necessary to decide whether a property of an organism is a design feature, a functionless by-product, a kludge in the system, or noise.

The functional organization of the brain can be illuminated by applying the same biological theories and principles. The task of cognitive neuroscience is to reverse-engineer the brain: to dissect its computational architecture into functionally isolable information-processing units, and to determine how these units operate, both computationally and physically. A correct dissection is one that illuminates the design of these units and explains their presence. The engineering specifications that a good theory of adaptive function provides are essential to this enterprise. Theories of adaptive function can tell one several things. First, they can suggest what kind of computational machines to look for (e.g. units designed for tasks such as: choosing a fertile mate; minimizing contagion; foraging; caring for children; predicting the trajectories of inanimate objects; predicting the behavior of predators, prey, and other members of one's own species). Second, they can tell us what would count as a good design for solving each of these problems. Third, they can reveal when a unit designed for solving one task will be unable to solve another. The latter is important: when the computational requirements of two tasks differ, one expects selection to have created a *different* computational system for accomplishing each — that is, two different functionally specialized adaptations [2,3••].

This expectation is at variance with associationist and other unitarian views of the brain, which many cognitive neuroscientists have inherited from the parent disciplines of neuroscience and cognitive psychology. As Gallistel [4••] puts it,

“It is odd but true that most past and contemporary theorizing about learning does not assume that learning mechanisms are adaptively specialized for the solution of particular kinds of problems. Most theorizing assumes that there is a general-purpose learning process in the brain, a process adapted only to solving the problem of learning. There is no attempt to formalize what the problem of learning is and thereby determine whether it can in fact be conceived as a single or uniform problem. From a biological perspective, this assumption is equivalent to assuming that there is a general-purpose sensory organ, which solves the problem of sensing.”

Gallistel [4••] has analyzed various learning problems solved by desert ants, bees, pigeons, and other animals, showing:

first, that they are incommensurate; second, that each is solved by a different computational machine that is specialized for that task; and third, that associative theories of learning are incapable of explaining the animal learning data. We will begin with this last result, because associationist expectations about the brain persist and continue to organize research agendas in cognitive neuroscience, despite demonstrations that associationist mechanisms are not capable of explaining many features of human cognition [4**,5**,6,7].

Content-general systems: functional specialization and adaptive design

A computational adaptation can be content-general — that is, it can operate on information drawn from many different domains — yet still be functionally specialized. Classical and operant conditioning provide a case in point. According to traditional accounts, conditioning is produced by associative mechanisms that track spatio-temporal contiguity — the paradigmatic general-purpose learning process. In contrast, adaptationist analyses suggest that the mechanisms that produce conditioning are functionally specialized for efficient foraging in the wild [5**]. Rates of reward differ at different foraging sites and under different foraging conditions: a well-designed mechanism should be sensitive to these differences in rates, detect changes in them, and take into account the statistical uncertainties inherent in a limited number of observations. Foragers need to compute temporal contingencies, not contiguities. Based on this evolutionary task analysis, Gallistel and Gibbon [5**] argue that, formally, this problem corresponds to multivariate nonstationary time-series analysis; they demonstrate that associative mechanisms are incapable of performing the necessary computations, and provide an alternative computational model that is. Their model predicts many known conditioning phenomena that associationist models cannot account for, such as the time-scale invariance of conditioning, the failure of partial reinforcement to influence the speed of acquisition and extinction, and blocking. This model also has important implications for neuroscience research on the cellular underpinnings of learning and memory, because it proposes that conditioning is mediated by representational mechanisms rather than by changes in the strength of associative bonds.

Work on judgment under uncertainty in humans has also uncovered mechanisms that are relatively content-general, yet functionally specialized. The human cognitive architecture seems to contain statistical inference mechanisms that embody the constraints of Bayes's rule, but that require information in an ecologically valid format (absolute frequencies); moreover, as the Gallistel and Gibbon model suggests, these mechanisms distinguish between frequencies and confidence (i.e. uncertainty; [8]). Humans, like other animals, have decision-making algorithms that take into account the expected value of alternative resources, their variances, and the individual's own need-level, combining these three sources of information in the ways that optimal foraging theory predicts [9,10].

Note that although these systems can operate on a wide array of contents, they are designed for solving problems that arise in a particular domain — foraging — and they are specialized for solving foraging problems. Other adaptive problems, such as learned taste aversions and danger avoidance, also rely on the computation of temporal contingencies and may use some of the same machinery. Despite some overlap, however, the solution to these problems requires additional, functionally specialized machinery (with different brain regions implicated) [11,12]. Selection can specialize the performance of a computational machine by giving it what amounts to innate knowledge about a domain, and this appears to have happened in many domains that come under the heading of 'conditioning' [13,14]. This would include the existence of domain-specialized unconditioned stimulus–unconditioned response (US–UR) relationships (e.g. toxins and enzyme induction [15], snakes and avoidance [16]), as well as content-specific, privileged hypotheses about conditioned stimulus–unconditioned stimulus (CS–US) relationships (e.g. taste and nausea [13,17]). Accordingly, some forms of conditioning enjoin the neostriatum, others the neocortex and amygdala, and yet others the cerebellum [11,12].

Content-specific systems: functional specialization and adaptive design

Another way to specialize and thereby improve the performance of a computational machine is to restrict its domain of application. A domain-restricted device can be endowed with *content*: with assumptions, privileged hypotheses, and inference procedures that are appropriate to a domain, but may be irrelevant or even misleading when applied outside that domain. Configural information about the human face may help infants to recognize their parents, but will be useless for recognizing plants; assuming that invisible mental states (beliefs and desires) exist may help predict the behavior of people but will be useless for predicting the behavior of rocks; inferential procedures specialized for cheater detection will help catch violations of agreements to exchange, but will be useless for detecting violations of logical rules or scientific hypotheses. A system that contains a number of content-rich, expert systems of this kind has a decisive advantage over a system limited to executing content-free 'rational algorithms' derived from probability theory, mathematics, or logic. Rational algorithms are defined by what they lack: content. They are computationally weak precisely because they were designed to produce valid inferences in *all* domains. They can only do so, however, if they are stripped of all information and all procedures that would be helpful in one domain but counter-productive in another.

Category-specific recognition systems can serve as filters for category-specific semantic and inferential systems, so one might expect bundles of content-specific, domain-specialized knowledge to come in vertically integrated packages, sometimes called intuitive ontologies [18]. Social interaction, for example, may require procedures for

quickly recognizing individual human beings (visual recognition), retrieving information about their personalities (semantic and episodic memory [6]), and making inferences about their beliefs, desires, and probable behavior (theory of mind [19]); a bundle that, taken together, is sometimes called folk psychology. This bundle may contain different procedures than those designed for predicting the interactions of inanimate objects (folk physics) or for plants and animals (surely important categories for any omnivorous forager).

An ontology refers to what kinds of things exist in the world, and reviews of the evidence from cognitive neuroscience and development suggest that the cognitive architecture has vertically integrated intuitive ontologies that cleave the world into kinds, such as people, animals, plants, artifacts, and locations [18]. Evidence for content-specific, functional specializations exists for visual recognition, semantic memory, and inference.

Visual recognition

Because people can recognize a wide array of items, many vision scientists have assumed that visual recognition is governed by content-general procedures. However, there is now considerable support for the existence of content-specific, functionally specialized recognition systems for: facial identity [20,21,22*,23,24**,25*,26**,27*,28*] (but see [29*]); particular facial expressions of emotion [30*,31–33]; places [34,35]; and animals [36,37,38**]. It also seems likely from an evolutionary perspective that there are specialized systems for recognizing many other visual categories that have either been only hinted at (actions [39,40]; snakes [41]; body parts [42,43]; fruits and vegetables [44]) or not yet documented (water, plants, blood).

Semantic knowledge

For almost 20 years, cognitive neuropsychologists have documented patients who are differentially impaired in accessing semantic information about either animate or inanimate things. However, resistance to the notion that semantic memory may contain category-specific subsystems spawned a number of alternative explanations. Recently, Caramazza and his colleagues [45–47] have argued that these alternatives cannot explain the facts, and have made a very strong case for the existence of both an animate semantic system and an inanimate semantic system. Other neuropsychological cases suggest further cleavages, for example, between edible plants (fruits and vegetables) and other types of food [48–50]. Knowledge about people's personality traits is stored in both episodic and semantic memory, the latter in the form of trait summaries [6]. Studies with amnesics and individuals with autism show that a person who is unable to retrieve behavioral episodes may still be able to access and even update trait summaries [51–53]. Moreover, rules for retrieval are content-specific: retrieving a trait summary primes episodes that are inconsistent with that trait, but not ones that are consistent with it (a pattern that shows adaptive design for bounding the scope of generalizations [6]).

Inferential specializations

Research in cognitive development indicates that there are specialized inference engines for domains such as folk psychology [19,54], folk biology [55,56], naïve physics [57,58], and number [59*,60], which emerge either in infancy or early childhood. Some of the most striking dissociations involve mindreading (inferring other people's mental states) [54,61*,62,63]. For example, although individuals with autism can compute eye direction and know what someone is looking at, they cannot use this information to infer that the person *wants* (mental state) what he is looking at (normal three-year-olds can do this) [19]. The ability to understand mental representations (beliefs) sharply dissociates from the ability to understand physical representations (photographs, maps) [54]. Autism and frontal lobe damage can selectively interfere with mind-reading [19,54,61*,63], which activates different brain regions than making inferences about inanimate objects [64]. Within the domain of social cognition, there is evidence of even more specialized inferential procedures. For example, both functional and neuropsychological evidence indicates that detecting cheaters in social exchange is governed by different reasoning mechanisms than detecting violations of hazard/precaution rules (and both are different from reasoning about nonsocial relationships [65,66]).

Motivation and choice systems: content-specificity and adaptive design

The work reviewed above involves systems designed for acquiring knowledge and information, which are value-free. Such systems would have been useless, however, unless they were coupled to motivational systems that generated adaptive choices and behaviors in ancestral environments. Choice requires standards of value, and these must differ from one domain to the next (e.g. the same criteria cannot govern food choice and mate choice) for behavioral outcomes to track fitness. Moreover, the traditional division of mammalian motivation into systems for sex, hunger, thirst, and survival is too coarse a divide. It fails to capture the intricacies of adaptive design within the systems posited, and omits many systems that are known to exist in other mammals (some of which may exist in humans). This taxonomy omits, for example, adaptations for parenting; these surely exist in the class *Mammalia* (!), and should be interestingly different for females and males [67]. Nor can it accommodate the neurocognitive system that causes virgin male mice to commit infanticide, counts day/light cycles after first intravaginal ejaculation, and switches the male's behaviour from infanticide to parenting at the point at which the pups could be his. Adding an entry for 'aggression' would not help: this does not differentiate among infanticide (found in mice and langur monkeys, but not in many other species), individual jockeying for dominance (most primates), and the system that causes chimpanzees to form multi-male coalitions and raid neighboring groups (a pattern not found in other apes or monkeys [68]).

Recent work showing detailed adaptive design in the mate preferences and sexual motivations of human females

illustrates the inadequacies of positing an undifferentiated 'motivation for sex'. Women's motivation for engaging in sex and their criteria for choosing sexual partners change in theoretically principled ways during fertile and non-fertile phases of the menstrual cycle. Not only do peaks in women's sexual desire occur most frequently during fertile phases [69], but their preferences also change at ovulation. Although mate preferences in females are designed to assess a man's willingness and ability to invest in her offspring, as well as his genetic quality (e.g. heritable disease resistance), one would expect cues indicating genetic quality to be weighted more heavily when the probability of conception is highest. During fertile phases, women find testosterone-related facial characteristics, which may honestly advertise immunocompetence, more attractive than they do during non-fertile phases [70*,71*]. Moreover, this preference shift is more extreme for women contemplating short-term matings [70*]. Similarly, women prefer the scent of men with other, nonfacial markers of genetic quality during fertile periods, but have no systematic preference during non-fertile periods [72,73*,74].

Conclusions

If cognitive neuroscience is to succeed in dissecting the brain into functional units, a more theoretically driven approach to dissociating different systems will be necessary. For the most part, the dissociations found in object recognition and semantic systems have been found by noting patterns of spared and impaired performance in brain-damaged subjects. But a theoretically agnostic approach restricts the range of discoverable dissociations to those the subject happens to notice (e.g. inability to recognize faces) and those for which assessment tools already exist. Only by proactively searching for dissociations between evolutionarily motivated categories — including systems governing motivation and choice — will cognitive neuroscientists discover the full spectrum of functionally specialized mechanisms.

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