

Original Article

Where Evolutionary Psychology meets Cognitive Neuroscience: A précis to Evolutionary Cognitive Neuroscience¹

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Abstract: Cognitive neuroscience, the study of brain-behavior relationships, has long attempted to map the brain. The discipline is flourishing, with an increasing number of functional neuroimaging studies appearing in the scientific literature daily. Unlike biology and even psychology, the cognitive neurosciences have only recently begun to apply evolutionary meta-theory and methodological guidance. Approaching cognitive neuroscience from an evolutionary perspective allows scientists to apply biologically based theoretical guidance to their investigations and can be conducted in both humans and non-human animals. In fact, several investigations of this sort are underway in laboratories around the world. This paper and two new volumes (Platek, Keenan, and Shackelford [Eds.], 2007; Platek and Shackelford [Eds.], under contract) represent the first formal attempts to document the burgeoning field of *evolutionary cognitive neuroscience*. Here, we briefly review the current state of the science of evolutionary cognitive neuroscience, the methods available to the evolutionary cognitive neuroscientist, and what we foresee as the future directions of the discipline.

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Introduction

Evolutionary Cognitive Neuroscience (ECN) integrates comparative neuroscience, archeology, physical anthropology, paleoneurology, cognitive primatology, evolutionary psychology, and cognitive, social and affective neuroscience in an effort to identify and describe the neural mechanisms that have been forged by selection pressures during human evolutionary history that define the human mind, as well as identify comparative neural mechanisms for cognition. In its simplest form, evolutionary cognitive neuroscience is the merging of the fields of evolutionary psychology and cognitive neuroscience using methodology from both disciplines and guidance from evolutionary meta-theory. In this coalescence, the identification of neural substrates of psychological adaptations is paramount. A recent volume (Platek, Keenan, and Shackelford, 2007) presents the first comprehensive overview of this emerging discipline, which is briefly reviewed here (see also Platek and Shackelford, under contract). This article consists of three major sections: 1) historical antecedents to and current state of evolutionary cognitive neuroscience, 2) a brief introduction to methods available to the evolutionary cognitive neuroscientist and possible implementations of such methodologies, as well as references to more sophisticated texts on each methodology, and 3) future directions for the discipline.

Antecedents to Evolutionary Cognitive Neuroscience

Cognitive neuroscience without evolution

Like pre-Darwinian psychology and other social sciences, cognitive neuroscience without evolution will have difficulty accurately describing the functional workings of the human mind. The number of articles appearing in journals such as *The Journal of Cognitive Neuroscience*, *Cognitive Brain Research*, *Brain*, *Neuron*, *Neuroscience*, *Social Neuroscience* and *the Journal of Neuroscience* answering questions about brain-behavior relationships is staggering. What is more astounding, however, is the dearth of articles that present the results of evolutionarily-informed research or interpret the results from an evolutionary perspective.

A cognitive neuroscience approach to ultimate questions without evolutionary meta-theoretical guidance makes little sense, about as much sense as psychological science without evolutionary meta-theoretical guidance. This is not to say that proximate questions cannot be answered by cognitive neuroscience alone. For instance, these methods have been instrumental in providing culturally relevant information for understanding the brain systems implicated in reading disabilities (Price, 2005). However, an evolutionary perspective provides a structure from which to guide empirical investigations and hypothesis generation about brain-behavior relationships.

Psychological mechanisms, domain specificity, and domain generality

Evolutionary psychology assumes that an evolved psychological mechanism (and its corresponding neural substrates) is an information-processing module that was selected during a species' evolutionary history because it reliably produced behavior that solved a

particular adaptive problem (Tooby and Cosmides, 1992). Evolved psychological mechanisms are understood in terms of their specific inputs, decision rules, and outputs (Buss, 1995). Each psychological mechanism evolved to take in a narrow range of information—information specific to a particular adaptive problem. The information (or input) that the organism receives signals the adaptive problem that is being confronted. The input (either internal or external) is then transformed into output (i.e., behavior, physiological activity, or input relayed to another psychological mechanism) via a decision rule—an “if, then” procedure.

Tooby and Cosmides (1992) suggested that the causal link between evolution and behavior is made through psychological mechanisms. The filter of natural selection operates on psychological mechanisms that produce behavior. Natural selection cannot operate on behavior directly, but on the genes associated with the neural substrates that generate the psychological mechanisms that produce the behavior. Williams (1966) noted similarly: “The selection of genes is mediated by the phenotype [psychological mechanism], and in order to be favorably selected, a gene must produce phenotypic reproductive success [adaptive behavior]” (p. 25).

The majority of psychological mechanisms are presumed to be domain-specific. The mind is comprised of content-dependent machinery (i.e., physiological and psychological mechanisms) that is presumed to have evolved to solve specific adaptive problems. Psychological mechanisms can also be expressed as cognitive biases that cause people to more readily attend to some pieces of information relative to others. This presumption of domain-specificity contrasts with the traditional position that humans are endowed with domain-general learning or reasoning mechanisms that are applied to any problem regardless of specific content (e.g., Atkinson and Wheeler, 2004). A system that is domain-general or content-independent, however, is a system that lacks *a priori* knowledge about specific situations or problem domains (Tooby and Cosmides, 1992). Such a system, when faced with a choice in a chain of decisions, must select from all behavioral possibilities (e.g., wink, jump, remember father, smile, point finger, scream). This problem of choosing among an infinite range of possibilities when only a vanishingly small subset are appropriate has been described by researchers in artificial intelligence, linguistics, and other disciplines (see Tooby and Cosmides, 1992, for a review).

Not only are there theoretical arguments against a content-independent system, myriad evidence for domain-specificity comes from, among other areas, evolutionary psychological research (e.g., Cosmides, 1989; Cosmides and Tooby, 1994; Flaxman and Sherman, 2000; Pinker and Bloom, 1990), cognitive research (e.g., Hirschfeld and Gelman, 1994), studies of animal learning (e.g., Carey and Gelman, 1991; Garcia, Ervin, and Koelling, 1966), clinical neurological literature (e.g., Gazzaniga and Smylie, 1983; Ramachandran, 1995; Sergent, Ohta, and MacDonald, 1992), and most recently the arena of functional neuroimaging (e.g., Platek et al., 2005; Takahashi et al., 2006). Practitioners of evolutionary psychology note that relatively domain-general mechanisms that function, for example, to integrate and relay information between domain-specific mechanisms *likely exist* (e.g. attentional systems, anterior cingulate cortex, fluid intelligence, prefrontal cortex, etc.), but the vast majority of mechanisms are presumed to be domain-specific.

Some of the controversy surrounding the relative domain-specificity of the mind seems to be rooted in the use of the term *domain*. Psychologists frequently used the term to refer to particular domains of life, such as the mating domain, kinship domain, and

parenting domain. Subsequently, many have assumed that labeling a mechanism as domain-specific restricts the proposed mechanism to a particular domain, and if evidence can be garnered to show that the mechanism functions in more than one domain (e.g., the mating domain and the kinship domain), then it is taken as evidence for the domain-generality of the proposed mechanism. This, however, is incorrect. A domain, when referring to a psychological mechanism, is a selection pressure, an adaptive problem (Cosmides and Tooby, 1987). Domain, then, is synonymous with *problem*. A domain-specific mechanism refers to a problem-specific mechanism—a mechanism that evolved to solve a specific adaptive problem. Although evolutionary and cognitive psychologists use the term *domain-specific*, perhaps some confusion could be avoided if the more accurate term *problem-specific* were employed. Although some psychological mechanisms operate across different domains of life (e.g., face recognition, working memory, processing speed), they still solve specific problems. Working memory, for example, solves the specific problem of holding information in the mind for a brief period of time. It has been suggested that evolutionary and cognitive psychologists might be better off avoiding these contentious labels and simply describing the proposed mechanism and its function (personal communication, D. M. Buss January 2005).

Unlike early psychologists and behavioral scientists (e.g., Skinner, Watson) who envisioned organisms as “blank slates” capable of making an infinite number of associations, evolutionary meta-theory is beginning to shed light on this flawed theoretical approach to behavior analysis (see Barkow, Cosmides and Tooby, 1992; Buss, 2005; Cosmides and Tooby, 2005). In fact, many of the emerging studies are contending directly with this “standard social science model” of psychology; i.e. that organisms possess one or more general-purpose learning mechanisms and that “biology” plays little role in the manifestation of behavior. Examples of some of the first psychological studies to demonstrate that learning was not mediated by so-called general-purpose learning mechanisms were published several decades ago and mark what might be referred to as the beginning of evolutionary thinking in psychology and a contributing factor to the “cognitive revolution.”

In his landmark study, Garcia (Garcia et al., 1966) discovered that animals learned to avoid novel food products that made them ill in as little as one learning/conditioning trial—something that had not been demonstrated with any other stimulus class previously. Labeled *conditioned taste aversion*, this effect describes an adaptive problem that has since been demonstrated in almost every species tested (the exception to this rule appears to be *Crocodylians*, see Gallup and Suarez, 1987). This adaptation serves an important function—don’t eat food that makes you ill or you might not survive to reproduce; i.e. being ill could result in a number of fitness disadvantages such as death, inability to avoid predation, inability to search and secure mates, and loss of mate value.

In a similar discovery, DaSilva, Rachman, and Seligman (1977) demonstrated what he referred to as prepared learning. Prepared learning is a phenomenon in conditioning and can occur rapidly because of putative biological predispositions. For example, it has been demonstrated that it is much easier for humans (and animals) to form conditioned emotional responses—in this case, associative fear responses—to evolutionarily-relevant threats such as snakes, insects, and heights than to present-day threatening but evolutionarily novel stimuli. In other words, it is easier to condition humans to develop a fear of snakes, spiders, and heights than it is to condition a fear of guns, cars, and knives.

These studies demonstrated that psychological traits, similar to the design of bodily organs, were crafted by evolutionary forces that allowed our ancestors to survive. The information-processing mechanisms designed to deal with such situations as poisonous food or potential threats to survival evolved as part of our ancestors' recurrent experience with such situations. These studies refute a key premise of the standard social science model—there is no general-purpose learning mechanism. Rather, learning is a consequence of carefully crafted mechanisms dedicated to solving specific evolutionary problems (see Barkow, Cosmides, and Tooby, 1992; Pinker, 2002). Our brains have evolved to be efficient problem-solvers and the problems they are designed to solve are those that our ancestors recurrently faced over human evolutionary history.

Although domain-specificity seems to be the prevailing theoretical model of the brain in evolutionary psychology, we note that there is also support for the existence of domain-general mechanisms in areas of cognition and learning. Chiappe and MacDonald (2005) argue that the domain-general approach explains how humans may solve novel problems and employ novel strategies to old recurrent problems; whereas the theory of domain-specificity does not. Contrary to the claim that humans would have an infinite choice of problem solving strategies without a module to guide them, Chiappe and MacDonald (2005) suggest that we have evolved motivational systems that provide positively or negatively charged cues to aid in novel problem solving. They criticize the definition of adaptation put forth by Tooby and Cosmides (1992) because it includes “recurrence”, implying that there can be no adaptations to deal with novel problems. Their revised definition of adaptation is as such, “an adaptation is a system of inherited and reliably developing properties that became incorporated into the standard design of a species because it produced functional outcomes that contributed to propagation with sufficient frequency over evolutionary time” (Chiappe and MacDonald, 2005, p.11).

Examples of general intelligence and innovative problem solving can be seen in animals as well as humans. For instance, common ravens (*Corvus corax*) can solve problems that have not been part of their evolutionary environment. Henrich (2000) designed a study where ravens had to use novel techniques to get food from a string. Results showed that the ravens were able to solve this novel problem to get the food, not through trial and error, but through putative “insight.” Furthermore, Anderson (2000) discovered that rats were able to combine the steps from separately learned tasks to solve a problem. Research with humans has bolstered the argument for domain-free capabilities. Using measures of working memory capacity such as mathematical processing and a reading span task Turner and Engle (1989) discovered that scores on these tasks predicted reading ability. These results indicate that working memory may include domain-specific and domain-general mechanisms involved in several distributed processing tasks (Kane, Bleckley, Conway and Engle, 2001; Chiappe and MacDonald, 2005). Geary (1995) has devised a theory that incorporates domain-specificity and general intelligence by differentiating between primary biological abilities and secondary biological abilities. The primary abilities include language and simple quantitative abilities; these are domain specific. Secondary abilities, such as reading and mathematics, use these primary ability modules in a general way to solve novel problems. Geary states, “Success at these biologically secondary abilities is strongly correlated with general intelligence” (as cited by Chiappe and MacDonald, 2005, p. 17). Modules are critical for learning and problem

solving, but domain-free mechanisms are key in employing information from the modules to solve new original problems (Chiappe and MacDonald, 2005).

Fear acquisition has been used to support the theory of domain-specificity, as some fears (evolutionarily relevant fears) are easily acquired and not easily extinguished (Öhman and Mineka, 2001; Seligman, 1971). Hugdahl and Johnsen (1989), however, argue that stimuli without any evolutionary significance can “gain control of the fear system” (Chiappe and MacDonald, 2005, p.28). Results showed that participants demonstrated superior conditioning to a gun stimulus paired with a loud noise, than to snake stimuli. The extinction rate of the gun stimuli and the snake stimuli, when both were followed by a shock, was equal. Furthermore, there is evidence of two fear processing systems in the brain. Fear is traditionally associated with amygdala activation, especially evolutionary relevant fear stimuli; however, the hippocampus is activated when individuals are exposed to aversive unfamiliar stimuli. Öhman and Mineka (2001) suggest that the hippocampal activation allows the subject to take in all available information from the environment in order to better understand and assess the aversive stimuli.

The social brain hypothesis argues that the brain (especially the higher primate brain) has evolved to its present form as a result of selection pressures imposed by the very social nature of the primate group structure (Dunbar, 2007; Jolly, 1969 as cited by Dunbar, 2007; Humphrey, 1976, as cited by Dunbar 2007). Chiappe and MacDonald state, “Social learning systems in humans are domain general in the critical sense that they allow us to benefit from the experience of others, even when their behavior was not evolutionarily recurrent in the EEA but is effective in achieving evolved goals in the current environment” (2005, p. 33). Several studies have demonstrated that social learning is not confined to humans. Rats observing conspecifics attaining food have in turn employed the observed technique to obtain food (Heyes, Dawson, and Nokes, 1992). Parrots have also been able to socially learn non-species specific behaviors without reinforcement (Moore, 1996). Social learning among primates “coevolved” with increased size of the executive functions, increased innovative ability, as well as tool use (Reader and Laland, 2002). Chiappe and MacDonald claim that these findings buttress the argument for social learning having increased importance as species employ innovative solutions through processes such as working memory, fluid intelligence, and executive function, which are the foundations of general intelligence.

Evolutionary time lags and the environment of evolutionary adaptedness

Because evolution is an excruciatingly slow process, modern humans and their minds are designed for earlier environments of which they are a product. Our minds were not designed to solve many of the day-to-day problems of modern society but, instead, were designed to solve the recurring problems of our evolutionary past. Examples of evolutionary time lags abound: our difficulty in learning to fear modern threats, such as guns and cars, and our near effortless learning to fear more ancient threats, such as snakes and spiders (DaSilva, Rachman, and Seligman, 1977; Öhman and Mineka, 2001) children’s ease in learning biologically primary mathematic abilities, such as counting, and their difficulty in learning biologically secondary mathematic abilities, such as arithmetic (Geary, 1995); women will not concede to intercourse indiscriminately even though modern contraception can greatly minimize the reproductive costs associated with intercourse; our preference for sugar and fat was once adaptive due to their scarcity, but has

now become maladaptive. These few examples illustrate that our modern behavior is best understood when placed in the context of our environment of evolutionary adaptedness.

The environment of evolutionary adaptedness (EEA) is not a place or time in history but a statistical composite of the selection pressures (i.e., the enduring properties, components, and elements) of a species' ancestral past—more specifically, the *adaptations* that characterize a species' ancestral past (Tooby and Cosmides, 1990). Each adaptation evolved due to a specific set of selection pressures. Each adaptation, in principle, has a unique EEA, but there likely would have been overlap in the EEAs of related adaptations. Tooby and Cosmides (1990) and other evolutionary psychologists, however, use “Pleistocene” to refer to the human EEA because this time period, lasting 1.81 to 0.01 million years ago, was appropriate for most adaptations of *Homo sapiens*.

Although our evolutionary past is not available for direct observation, the discovery and description of adaptations allows us to make inferences about our evolutionary past, and the characterization of adaptations may be the most reliable way of learning about the past (Tooby and Cosmides, 1990). Some adaptations provide unequivocal information about our ancestral past. Our cache of psychological mechanisms associated with navigating the social world tells us that our ancestors were a social species (e.g., Cosmides, 1989; Cummins, 1998; Kurzban, Tooby and Cosmides, 2001; Pinker and Bloom 1990; Trivers, 1971). A multitude of psychological mechanisms associated with cuckoldry avoidance tell us that female infidelity was a recurrent feature of our evolutionary past (Buss, Larsen, and Westen, and Semmelroth, 1992; Buss and Shackelford, 1997; Goetz and Shackelford, 2006; Platek, 2003; Shackelford and Goetz, in press).

Some adaptations, however, do not make clear (at least upon first inspection) their link with our ancestral past. There exists, for example, a mechanism present in the middle ear of all humans that is able to reduce sound intensity by as much as 30 decibels in 50 milliseconds. The attenuation reflex, as it is known, acts by contracting muscles that pull the stirrup away from the oval window of the cochlea, preventing strong vibrations from damaging the inner ear. The attenuation reflex meets the characteristics of an adaptation (e.g., economic, efficient, reliable), yet it is not obvious what selection pressures drove the evolution of this adaptation. What specific noises did our ancestors recurrently hear that would create this noise reducing mechanism? That the muscles appear to contract as we are about to speak suggests that our own loud voices might have been the impetus for this adaptation. Moreover, sound attenuation is greater at low frequencies than at high ones (and humans speak at low frequencies), also suggesting that ululating was a recurrent feature of our evolutionary past. Thus, from discovering and describing adaptations, we can tentatively characterize aspects of our evolutionary environment.

This is not to be taken to indicate, however, that the aim of evolutionary psychology is to make inferences about the past. Evolutionary psychology is not *post hoc* storytelling; its practitioners often use a deductive approach, moving from theory to data. Evolutionary psychologists make predictions derived from hypotheses based on middle-level theories—e.g., Trivers's (1972) parental investment theory—then collect data to test their predictions. For example, Buss et al. (1992) tested the hypothesis proposed by Symons (1979) and Daly, Wilson, and Weghorst (1982) that the sexes would differ in their reactions to a romantic partner's sexual and emotional infidelity. Buss and his colleagues did not happen to collect the appropriate data, analyze the results, and develop a *post hoc* explanation for what they observed. Furthermore, claims of adaptations are typically stated

as tentative until the proposed adaptation has undergone rigorous hypothesis testing (see Schmitt and Pilcher, 2004). The inductive approach, however, should not be disregarded. Moving from data to theory is a common practice in all scientific enterprises (e.g., cosmology, geology, and physics) and is known as “explanation” (Tooby and Cosmides, 1992).

Cognitive neuroscience with evolutionary theoretical guidance

Why do we need another discipline? Why is the ECN approach important? Without evolutionary meta-theoretical guidance, cognitive neuroscience will fail to describe with anything but superficial accuracy the human (and animal) mind. Cognitive neuroscience will simply explain proximate mechanisms (i.e., the “how”) of brain-behavior relationships (most often using theoretical models derived from standard social science models). This is only half the equation. This approach misses the ultimate (i.e., “why”) questions of brain-behavior relationships. By adopting the ECN approach and directly addressing ultimate questions about brain-behavior relationships, scientists will be in a position to better describe the cognitive processes and the neural correlates that they investigate. Likewise, without cognitive neuroscientific methods, evolutionary psychology may not be able to adequately describe and understand the neurophysiological mediators to psychological adaptations, and hence may never be able to accurately describe the evolved nature of the human mind. Without “peering” into the brain with techniques such as modern functional neuroimaging, evolutionary psychological investigations can only describe the cognitive processing of human mental characteristics. Evolutionary psychology can describe function, but is limited in its description of structure, and thus has no ability to relate function to structure, which might be important, especially in comparative investigations of cognitive evolution. The relationship between structure and function is inherently a problem of evolutionary biology; i.e. the genes that give rise to brain structure and its component nuclei and modularity, as well as its ability to process information, were the combined units of selection. The need for an integrated science of the mind that utilizes evolutionary meta-theoretical guidance to cognitive neuroscientific investigations is overdue, but beginning to flourish.

Recently, application of evolutionary meta-theory has been applied directly to investigations of the cognitive neuroscience kind. For example, O’Doherty and colleagues (2003; see also Winston et al., 2007) have begun to investigate neural correlates of facial attraction. O’Doherty et al. discovered that the orbitofrontal cortex appears to be activated when a person finds a face attractive, which suggests that facial attractiveness activates a reward or approach system in the brain. These findings have recently been extended (Winston et al., in press) to reveal a more distributed network of activation in the anterior cingulate cortex (ACC), superior temporal sulcus, and amygdala in response to evaluations about attractiveness. Additionally, activation in the ACC and amygdala appear to be sex-dependent, showing increased activation in men only. These areas also are activated when males are asked to imagine (Takahashi et al., 2006) or observe (Rilling, Winslow, and Kilts, 2004) their mate engaging in infidelity, which suggests that appraisals of attractiveness of females by males is related to their decisions about fidelity and paternal certainty (see Shackelford, Pound, and Goetz, 2005, for review). This work is currently being extended to investigate the role of the menstrual cycle in perceptions of attractiveness among female participants. Patel and Platek (in preparation) employed the new functional

neuroimaging technology, functional Near Infrared Spectroscopy (fNIRS), to investigate women's perception of attractiveness as a function of the menstrual cycle while varying male facial symmetry and masculinity. These findings reveal an interaction between perceptions of attractiveness and the menstrual cycle; i.e. women prefer symmetrical and masculine men more during the period of ovulation. Additionally, these data show that the prefrontal reward centers (PFC) parallel this behavioral response; i.e. women display activation of primarily left ventromedial PFC to symmetrical and masculine males during the period of the estrous cycle when they are at greatest likelihood of conception and the opposite pattern when not at high likelihood of conceiving. Together these data suggest that 1) there are sex differences in the neural processing of attractiveness that might be related to evaluations about paternity and sexual fidelity and 2) that in women, activation appears, at least in part, dependent on hormonal state.

Further, Baron-Cohen and colleagues (e.g., 1985, 2001) have been instrumental in identifying the presence of a neural module dedicated to processing socially-relevant information (see also Frith and Frith, 1999). Baron-Cohen et al. demonstrated that the ability to conceive of others' mental states appears to be 1) a highly modularized neurocognitive process and 2) specifically affected by certain neuropsychiatric pathologies, namely autism (also schizophrenia, see Irani et al., 2007; Platek and Gallup, 2002). Patients with autism (and schizophrenia) appear to have deficits in social cognition, independent of deficits in general intellectual functioning. These data suggest that the capacity for social cognition is circumscribed and modularized and thus can be negatively affected independent of negative consequences in other cognitive domains. Several neuroimaging studies have supported the notion of a modularization of social cognition (e.g., Focquaert et al., unpublished data; den Ouden, Frith, Frith and Blakemore, 2005; Ochsner et al., 2005; Platek et al., 2004, 2006; Vollm et al., 2006).

In an explicit test of an evolutionary psychological theory and follow-up to several behavioral studies, Platek et al. (2004, 2005) employed functional magnetic resonance imaging (fMRI) to investigate sex differences in perceptions of children's faces as a function of facial resemblance. In two studies, they discovered that men, but not women, showed activation in left and medial prefrontal regions of the brain when viewing self-resembling child faces. This finding suggests that 1) men display an approach strategy towards children who share facial resemblance with them (e.g., Davidson, Putnam, and Larson, 2000) and 2) men might inhibit a generalized negative response pattern, or avoidance phenotype, toward children unless the child shares facial resemblance.

Perhaps the most exciting application of neuroscientific methods to evolutionary theory has been done in studies empirically testing modularity. Neuroscientific methods such as fMRI can subject theories and claims to rigorous falsification attempts. A very convincing set of psychological experiments demonstrating evolved structures dedicated to social interaction and exchange have come from studies conducted by Cosmides, Tooby, and their colleagues. By modifying a logic problem known as the Wason Selection Task to reflect evolutionarily important social interactions (e.g., cheater detection), Tooby, Cosmides, and colleagues have demonstrated that the human mind appears to have evolved a cheater detection mechanism that is extremely efficient. They have provided neurological evidence for a cheater detection mechanism by showing that one can incur impairment (i.e., brain trauma) to performance on cheater detection problems but remain relatively unimpaired on other types of problem solving. Their data suggest that parts of

the limbic system are implicated in the ability to detect cheaters in social interactions (Stone, Cosmides, Tooby, Kroll, and Knight, 2002).ⁱ

Domain-specificity research continued as Dehaene, Piazza, Pinel, and Cohen (2003) examined whether the human brain has evolved with a certain “predisposition to represent and acquire knowledge about numbers” (p.487). They used behavioral data, neuropsychological evidence, and fMRI to investigate three parietal circuits for number processing. They discovered that the horizontal intraparietal sulcus (HIPS) region, associated with activation during mental arithmetic and number representation, is the most likely candidate for a domain-specific module. As a follow up, Shuman and Kanwisher (2004) tested whether or not this module was involved in nonsymbolic number processing. They hypothesized that if the HIPS were a module specific to the representation and processing of numbers then the following would be true. First, symbolic and nonsymbolic number tasks (greater than vs. less than) would show activation in the HIPS. Second, Numerical tasks should engender greater activation in the HIPS than non-numerical difficulty-matched tasks. Results failed to support the hypothesis. There was not significant brain activation evidence to provide support for the existence of a domain specific cortical region in the parietal lobe dedicated to the processing of symbolic and nonsymbolic numbers.

These new investigations—applying cognitive neuroscientific methods to answer hypotheses posed from an evolutionary theoretical perspective—are bringing forth a new understanding of how the mind and brain evolved. In fact, these new research programs are re-casting much psychological research conducted through the 20th century into the ECN perspective.

Foundations for an evolutionary cognitive neuroscience and directions for future research

A formal discipline of evolutionary cognitive neuroscience demands the integration of several branches of psychology, biology, and anthropology, including, but not limited to: comparative neuroscience; archeology, physical anthropology, and paleoneurology; cognitive primatology; evolutionary psychology; and cognitive, social, clinical, and affective neuroscience. In other words, the foundation of ECN is interdisciplinary in nature. The discipline has been synthesized in a recent edited volume published by the MIT Press (Platek, Keenan, and Shackelford, 2007). What is apparent from the formulation of this volume is that for ECN to survive as a discipline, collaborations across disciplines are going to be necessary, and the chapters presented in Platek, Keenan, and Shackelford (2007) highlight this fact. We do not aim to replicate the contents of that volume here, but for purposes of illustration we have reviewed some of the chapter contents and themes. One will notice the application of Tinbergen’s (1963) four “Why’s” and proximate/ultimate dichotomy weaved throughout. This ethological framework is essential to the survival of ECN in that this framework forms the basis for examination of all behaviors from a biological perspective.

Ontogeny of brains and brain size

The prefrontal cortex, temporal cortex, parietal cortex, and striatum seem to be the key brain substrates underlying many of the complex cognitive processes in humans. How did these structures evolve, allowing humans to supercede the cognitive processes of other organisms, especially when it comes to the noted cognitive capacities? Finlay and

Darlington (1995) contend that neurogenesis is strongly related to relative need for structure; i.e. size of a neural substrate will be determined by the organism's need for that substrate for survival and reproductive maximization strategies. Stone (2007) extends this thesis by suggesting that natural selection acted on two factors—neuron number and connectivity—to build brains with more complex cognitive capabilities. These theories complement each other. It has been reported that 96% of brain structure size is predicted by the sizes of the surrounding structures (Finlay and Darlington, 1995). Neurogenesis impacts brain structure, and given that humans have a longer period of prenatal development, more neurons are able to form. Finlay and Darlington surmise that natural selection could have acted on the brain through neurogenesis, but with large correlations between neighboring brain structure sizes, longer gestational period subsequently allows for the entire brain to become larger. This parallels Stone's neurogenesis hypothesis.

Although Finlay and Darlington, as well as Stone, show concurring and supporting evidence for the aforementioned theory of mammalian brain evolution, Barton and Harvey (2000) (also see Clark, Mitra and Wang, 2001, for a review) argue for a mosaic approach to brain evolution. Barton and Harvey found highly significant correlated volumetric evolution relationships within well documented functionally related brain systems. Thus they conclude that mammalian brain evolution implicated size changes focused in particular structures and functional systems.

Box 1: Outstanding research questions about the neural correlates of brain size development

- Are developmental constraints responsible for a coordinated size change among individual brain components?
- Did natural selection act on behavioral capacities thus causing selective size changes? These are not new questions. How can we use evolutionary cognitive neuroscience to test these hypotheses?
- Throughout evolution why did the neocortex increase in surface area, but not in thickness? How is the radial unit hypothesis relevant?
- How did social group size and social interactions impact evolution of cortical size and complexity?

Hemispheric asymmetry, specialization, and handedness

One of the most remarkable commonalities between human and nonhuman primates is brain lateralization, which is implicated in language, spatial abilities, and handedness in humans and may exist in rudimentary forms in non-primates. Annett's (1985) right-shift theory of handedness is a well documented theory of genetic inheritance of handedness in humans. New research is beginning to show that non-human primates may possess a hand preference, which begets the question of whether handedness is related to hemispheric specialization of cognitive capacities. Hemispheric specialization may be an evolutionary step towards the modularity of higher cognitive processes in humans. Hopkins (2007) has been leading the investigation in handedness among non-human primates. Using a paradigm called the TUBE test; he examined handedness among nonhuman primates and discovered lateralized processing in non-human primates, especially in chimpanzees. This, he suggests, lends support to the hypothesis that chimpanzees might also possess lateralization of other important brain functions (e.g.,

communication and spatial abilities). One noteworthy and inexplicable finding illustrated that chimpanzees in captivity tended to exemplify handedness, whereas chimpanzees in the wild did not (McGrew and Merchant, 1997). Evolutionary developmental psychologist, Bjorklund (2006), uses data from great apes and argues that, "...our last common ancestor chimpanzees likely had the behavioral plasticity and sociocognitive precursors to modify their behavior and cognition via maternal effects toward a more human-like intelligence" (p.213). Perhaps the chimpanzees in captivity, as they are reared in a human influenced environment, tend to show increased levels of handedness due to this interaction with humans, who do show a very distinct preference for handedness.

Using Annett's (1985) theory many studies have illustrated that handedness is heritable. Hopkins also attempts to demonstrate a genetic expression of handedness in chimpanzees, but discovers that there is not a significant relationship between handedness in the offspring and maternal or paternal handedness. A study of handedness and birth order indicated that in middle-born offspring there is significant heritability of handedness (Hopkins and Dahl, 2000; Hopkins, Dahl and Pilcher, 2000). The significance of these findings for cognitive evolution is yet unknown, but under close scientific scrutiny.

Box 2. Outstanding research questions about the relationship between handedness and the evolution of higher cognition that is hemispherically specialized.

- What is the relationship between domestication/enrichment/culture and handedness among human populations? Are there epigenetic influences on handedness and if so, what are they?
- What are the ultimate benefits of handedness to an individual and within populations and how does this affect brain formation? Why is handedness heritable in middle born offspring and not others in the birth order?
- What is the relationship across species between handedness and other lateralized brain functions?
- What is the relationship between the evolution of handedness and the evolution of social cognitive (e.g., self-face recognition, theory of mind) processes that are highly lateralized in humans?

Reproduction and kin selection: Social control of reproductive efforts and success

Are there common neurobiological mechanisms shared among animals? While fish seem like unusual subjects of study for evolutionary cognitive neuroscience, according to Fernald (2007), species such as fish are valuable vertebrates to study because they present applicable models for sensory systems, brain organization, and motor outputs. Fernald's (1977) research with African cichlid fish (*Astatotilapia [Haplochromis] burtoni*) demonstrates the interaction between social context and reproductive behavior and how this interaction shapes the brain. African cichlids are territorial. Territorial males (T males) have bold coloring and have control over a specific domain. This domain is enticing for nonterritorial male (NT) cichlids because it is only in these domains where food is available. NT males are therefore camouflaged and colored similarly to females to allow them to purloin food from T cichlid's domains. Fraley and Fernald (1982) discovered that if T males are reared in a group they develop at a slower rate than T males reared alone. Not only are T males reared in isolation larger in body size, but also the size of their gonads

is larger. Fernald suggests that this is a function of having no competition for resources or survival. Other findings include the difference in body size, which is dependent on whether cichlids are raised with brood mates or with adult males (Davis and Fernald, 1990). When maturing among adult males, gonad growth and size is suppressed compared to those reared without adult males around. One of the most fascinating discoveries of the investigation of cichlids is the remarkable change in brain structure as a function of social environment. In the brain of all vertebrates there are gonadotrophin releasing hormone (GnRH) neurons which guide reproduction. Fernald discovered that GnRH neurons are eight times larger in T males as compared NT males (Davis and Fernald, 1990). Can the size of the GnRH neurons in the brain change depending on social environment? The answer appears to be yes. Moving T males into a group with larger T males, the smaller fish become NT males. Conversely, introducing NT males into a group of smaller NT males, the larger males become T males. In examining the brains of these fish (pre- and post-environmental change), it is evident that the size of the GnRH neurons increases in the dominant fish after just four weeks in their new environment. Change in social status was influential enough to change GnRH neuron size in the brain of cichlids. This change was evident in adolescents and adults (Francis, Soma and Fernald, 1993).

Box 3. Outstanding research questions about the evolutionary importance of neuroendocrine interactions.

- What is the relationship between territoriality and sperm competition mechanisms? This type of investigation could lead to discoveries about the neural mechanisms involved in territoriality as well as sperm competition in humans.
- Do these same mechanisms exist across species and in humans?
- Are there effects of social group organization on neural correlates of territoriality?

Neural correlates of love, attachment, and mate choice

When we talk about romantic love it is common for people to generally reference the heart. But, it is the brain, not the heart that is the set of romantic attachment, love, and lust. There appear to be distinct interconnected neural networks that govern the motivational and reward systems involved in romantic love (e.g., Aron, et al., 2005; Winston et al., in press). It is a complex system based upon very specific neurochemical relationships in the brain; and therefore, this system becomes vulnerable when other chemicals are introduced. Fisher and Thomson (2007) have investigated the potential harmful effects of serotonin-enhancing antidepressants. Serotonin enhancing anti-depressants can interfere with oxytocin, vasopressin, and dopamine in the brain producing an array of effects including emotional blunting, decreased obsessive thoughts about a loved one, suppression of loving feelings, altered feelings of attachment, lowered sex drive, as well as inability to experience orgasm and fertility complications. Many of the aforementioned symptoms are essential to the development of a romantic relationship. Ultimately, Fisher and Thomson (2007) have argued that antidepressants interact with the natural neurobiological correlates of attraction and attachment and thus have detrimental effects on one's ability to form a stable pair-bond negatively impacting one's ability to "signal genetic and psychological fitness." The

impacts of these findings are interesting to consider in today's society where anti-depressants and other such drugs are unreservedly prescribed.

Box 4. Outstanding research questions about the neural correlates of evolved cognitive adaptation that are utilized during mating and mate selection.

- What is the relationship between 5-HT (and other neurotransmitters, hormones, substances) and attachment? How do variances in 5-HT levels impact fitness?
- What are the specific neural correlates of lust and sexual excitement? Could research using portable brain imaging devices be used to measure neural activation during foreplay, sexual intercourse, and post-copulatory behaviors?
- Are there neural correlates impacted by absorption of chemicals from sperm post-copulatory?

Social Cognition: Mind reading and self-awareness

The study of the evolution of social cognitive mechanisms and self-awareness in humans and non-human primates is contentious and represented by several different theories. Santos and colleagues (2007, also Flombaum and Santos, 2005) present compelling evidence for the capacity of mind-reading in rhesus macaques, a capacity previously thought to exist only in humans and great apes. The findings of her work may serve to expand our understanding of the phylogenetic distribution of neurobiological mechanisms involved in such capacities. These data are contrary to the thesis put forth by Gallup (1982) that only those organisms that could learn to recognize themselves could later develop a sense of other, or theory of mind (see Focquaert and Platek, 2007). The emerging data from cognitive neuroscience suggests that Gallup's hypothesis is at least in part correct. Platek and his colleagues (2004, 2005, and 2006) and Keenan and his colleagues (e.g., 2001, 2003,) have been instrumental in developing this model using modern functional neuroimaging technologies and patient populations (see also Irani et al., in press). It appears that the neural substrates involved in self-recognition, namely the inferior frontal gyrus and inferior parietal lobe in the right hemisphere are integral to the development of an internal self-representational system. These substrates appear also to be involved in processing the mental states of others (e.g. see, Platek et al., 2004, Northoff and Bermpohl, 2004). Additionally, in participants who are inefficient at social cognition, these substrates are recruited differently (e.g., Focquaert et al., in preparation; Platek et al., 2005). Baron-Cohen and his colleagues (e.g., 1985, 2001) have led the way for theorizing about modular deficits in neuropsychiatric patients, namely patients within the autistic spectrum disorders, and suggest that these patient populations represent an instance of specific modular deficit in mind reading and self-processing and might invoke assortative mating for such traits along a systemizing and empathizing quotient.

Box 5. Outstanding research questions about the evolution of social cognition.

- What introspective based social strategies (deception, intentionality, belief, desire, and pretense) are driven by the evolution of self-awareness and theory of mind?
- How exactly do social prostheses (Kosslyn, 2007) and the mirror neuron system interact with the evolution of language, spatial cognition, and self-other action understanding?
- Does one have to be self-aware to employ social prostheses?
- Using the new techniques designed by Santos et al., can other animals (e.g., outside the primate phyla, e.g., *Corvids*) be shown to demonstrate self-processing capacities?

Methods available to the evolutionary cognitive neuroscientist

In addition to traditional cognitive psychological methodology that typically employs dependent variables such as reaction times, performance (e.g., Schützwohl and Koch, 2004), decision judgment tasks (e.g., Singh et al., 1993), and implicit cognitive responses to stimuli (e.g., Thomson et al., under review), evolutionary cognitive neuroscience employs methods that allow direct measurement of brain activation (i.e., brain electric and magnetic responses and neurovascular responses), deficits in functioning among patients with specific lesions and/or neurocognitive impairments, and direct stimulation of the brain (e.g., TMS). Each of these methodological approaches or techniques offers their own degree of trade-off between potential for ecological validity and level of intrusion or obtrusiveness (Simpson and Campbell, 2005). We discuss each of these below.

Measuring brain activation

There are currently two main ways in which brain activation can be measured—directly using magnetoencephalography (MEG) or electroencephalography (EEG), and indirectly by measuring the blood oxygen-dependent neurovascular response using functional magnetic resonance imaging, positron emission tomography, or diffuse optical imaging. MEG and EEG essentially measure changes in the electrical potential of underlying neuronal populations. These techniques, thus, represent a relatively direct measurement of brain electromagnetic activity. Both techniques provide excellent temporal resolution, allowing researchers to plot the time course of stimulus or event evoked activity. The two techniques, however, differ drastically in several ways that can be optimized by the evolutionary cognitive neuroscientist appropriately. MEG, while providing as good temporal resolution as standard EEG using event-related potentials (because it measures the changes in magnetic energy of neurons), also provides fairly accurate spatial resolution and an easier solution to the inverse problem. This implies that MEG has the ability to provide information about the time course of neuronal activation and a relatively close approximation of the localization of such activation. The drawback to MEG is that it is significantly more expensive to purchase and maintain (on the order of 5-10 times as expensive). On the other hand, EEG systems are relatively inexpensive (approx. \$50-100,000 USD). A major drawback of EEG/ERP research is the time and preparation necessary to setup an experiment. For a high-density EEG measurement preparation time can be as long as 1.5-2 hours. This obviously draws from the experiment

by reducing participant motivation, increasing participant frustration, and limiting ecological validity. However, a new generation of mobile EEG/ERP systems are being developed, which rely on advances in electrode technology and wireless transmission of data. This is an obvious advantage to the evolutionary cognitive neuroscientist because it now allows measurement in ambulating participants.

The other major techniques for observing brain activation include those involved in measuring the indirect blood oxygen-dependent level (BOLD) neurovascular response or regional cerebral blood flow and include functional magnetic resonance imaging (fMRI), positron emission tomography (PET), and diffuse optical imaging/functional near infrared spectroscopy (DOI/fNIRS). Because PET utilizes radioisotopes it is not typically employed outside of the clinical domain for reasons of safety; i.e. participants are exposed to radiation in order to measure regional cerebral blood flow (rCBF). Functional magnetic resonance imaging (fMRI) has emerged as the “gold standard” in cognitive neuroimaging and is used in hundreds of laboratories around the world. It works on the principles of differential magnetic properties of the oxygenated and deoxygenated species of hemoglobin. Homogenization of tissue is achieved by using an extremely strong magnet, typically 1.5 Tesla (~20,000 times the magnetic force of the earth’s gravitational pull) a 3 Tesla (~30,000 times the force of the earth’s gravitational pull). Subsequently a radio frequency pulse is passed through the tissue which blocks the homogenization of tissue. Because oxy and deoxy hemoglobin have different paramagnetic properties the return to homogenization of tissue varies in oxygenated and deoxygenated blood allowing the researcher to detect a difference in levels. fMRI is based on the premise that when neurons fire they use oxygen and glucose and the body compensates for the utilization of such substances by increasing blood flow to specific regions that have become activated. Thus, a relative difference in oxygenation (via paramagnetism) ought to be detectable in regions that are recruited for specific processing tasks. In reality the changes in oxygenations are very small, which is why such strong magnets are employed. Detection of changes in oxygenation is nearly impossible with magnets weaker than 1.5 Tesla. fMRI, however, offers limited ecological validity. Participants are typically asked to lay on their back (although new upright magnets are beginning to be used) and remain as still as possible (motion artifact can destroy detection of small changes in BOLD) for the duration of the experiment, which can last up to 2 hours, typically at least 1 hour. The participant is then exposed to a set of stimuli designed to parse out a specific type or processing while controlling for all related neural processing. For example, if you were interested in measuring the neural correlates associated with a commonly researched topic from evolutionary psychology, say sex differences in romantic jealousy you would want to control for the effects of sexual jealousy, emotional jealousy, and perhaps even non-romantic jealousy. This allows you to set up a series of statistical (image) contrasts to identify regions that are uniquely activated by your stimulus of interest. Takahasi et al. (2006), for example, compared sexual jealousy to emotional jealousy to observe the unique activation associated with sexual jealousy when controlling for activations associated with emotional jealousy in males and females.

A newer method for investigating BOLD activation is diffuse optical imaging/functional near infrared spectroscopy (DOI/fNIRS). DOI/fNIRS measures the same signal as fMRI, but does so using light. Oxygenated and deoxygenated hemoglobin possess different absorption coefficients in the near infrared electromagnetic spectrum, thus

by measuring light reflection within the 700-900 nanometer range of the electromagnetic spectrum a researcher can determine (using the modified Beer-Lambert Law, Chance, 1951) the relative and absolute amount of oxygenated and/or deoxygenated hemoglobin present in a region of neural tissue. Researchers using fNIRS need to employ similar controls as those imposed on fMRI, with exception of restraining participants from moving. The newest generation of fNIRS devices are highly mobile and can transmit data wirelessly, allowing subjects to ambulate while having brain activation measured. The technology is also relatively inexpensive when compared to fMRI systems which typically cost between \$2-7 million USD. There are only a few companies manufacturing fNIRS systems for research (e.g., Hitachi, Infrascan, NIRS) and the costs vary from between \$250,000 to as low as \$15,000 USD. There are major drawbacks and limitations to this methodology, however. For example, depth of light transmission is shallow. That is, measurements can only be made from light that passes approximately 1-1.5 centimeters into the head, which only allows you to measure the cortex in adults. Additionally, because you are using light, other tissue absorption coefficients need to be taken into account. The major hurdle for this drawback is hair, which if dark can eradicate any light from entering the skull, let alone landing on the cortex.

Neuropsychological patients

The use of neuropsychological patients with specific lesions (e.g., Gazzaniga and Smylie, 1983; Keenan et al., 2003; Platek et al., under review; Ramachandran, 1995; Sergent, Ohta, and MacDonald, 1992) is common in behavioral neurology, clinical neuropsychology, and cognitive neuroscience (e.g., Farah and Feinberg 2000). Additionally, the use of patients with neuropsychiatric disorders that appear to be represented by modular deficits in cognition is also common (Stone et al., 2002; Sugiura et al., 2000). Recently, utilization of these patients to test hypotheses from evolutionary cognitive neuroscience for the presence of evolved cognitive adaptations has become popular (e.g., Baron-Cohen et al., 2001; Stone et al., 2002). The use of patients with focalized lesions allows researchers to investigate the role of specific neural substrates in a cognitive process that they're interested in. A classic example is that of Paul Broca, who was interested in language development. He noticed, upon post-mortem inspection, that several of his patients who experienced language production deficits had focalized damage to the left inferior frontal lobe. This finding has now been confirmed by several research programs (including neuroimaging) over the past century and this region has come to be known as Broca's Area. Similarly, Baron-Cohen et al. (1985) noticed that patients with autistic disorder appeared to be particularly inept at social cognitive reasoning, while retaining functioning in other cognitive domains (e.g., general intelligence). He (and others) have theorized that this specific deficit in social cognitive processing represents an instance of a modular deficit in an evolved domain-specific (social reasoning) cognitive mechanisms. This finding has also been replicated several times over using a number of methodologies, including functional neuroimaging, and has been extended to other similar candidate populations (e.g., Irani et al., 2006). There even appears to be a genetic loading for the possession of such modules, which lends further support to the evolutionary interpretation; i.e. these modules are heritable (see Irani et al., 2006).

Stimulating the brain

Transcranial magnetic stimulation (TMS) is a technique based upon Faraday's Law of induction which states that an activated transducer will charge another transducer, not activated, but that is close in proximity and otherwise not activated. Since neurons are essentially electromagnetic transducers, that means that introduction of a strong electromagnetic pulse into the brain can result in neurons becoming activated. This technique is highly invasive and demands intense screening of participants for seizure pathologies, but if used correctly and safely can reveal significant information about the functional and spatial relationship between brain and behavior. The two most common techniques used for TMS in cognitive neuroscience are known as single-pulse and repetitive. Single-pulse TMS allows a researcher to interfere with normal cognition by delivering a singly TMS to a region hypothesized as being implicated some process. If the timing is correct, the participant will experience an inability to complete a task or set of tasks. Single-pulse TMS allows researchers to functionally localizeⁱⁱ regions of the brain implicated in cognitive processing. Repetitive TMS on the other hand involves delivering long trains of stimulation, which subsequently result in down (or up) regulation of a spatially localized population of neurons. This technique has been dubbed the "virtual lesion" technique (Pascual-Leone, Walsh and Rothwell, 2000) because the result is such that the region stimulated becomes under (or over) responsive. The effect is transient and participants soon recover to normal, but during the time of the virtual lesion (~10-30 minutes) the researcher can engage the participants in a number of cognitive tasks. The virtual lesion method is similar to testing patients with focalized lesions or brain damage, but there is no need to be concerned with long-term neural reorganization or the development of neurocognitive compensatory mechanisms.

Future directions for methods in ECN: Interdisciplinary approaches

It is likely that the most exciting advancements in technology for understanding the evolved mind are going to come from interdisciplinary collaborations. One of the most fertile of which, cognitive neurogenetics, is growing in popularity. Cognitive Neurogenetics involves researchers in cognitive neuroscience and genetics, or genomics. Essentially, it involves measuring brain responses as a function of allelic expression. For example, possession of the val/met single nucleotide polymorphism (SNP) for the COMT gene is associated with less efficient frontal lobe processing, as measured using fMRI (e.g., Winterer et al., 2006). The implications for such findings for the evolution of frontal lobe circuits involved in executive function and social cognition are currently underway.

Conclusion

The synthesis of this broadly defined set of research programs might seem at first as an amalgamation of unrelated research disciplines. However, this is in fact not the case. The overarching theme of evolution, specifically brain-behavior evolution, serves to tie together the topics that lay at the foundation of ECN. Although the research questions are quite different among evolutionary cognitive neuroscientists, the goal is the same: to uncover the workings and the evolutionary history of the mind. Further, as an explicit extension of evolutionary behavioral neurobiology, the ECN approach aims to understand a large spectrum of species differences and similarities, in addition to understanding the unique evolved capacities of the human mind and its neurobiology. Hence, the discipline is

inherently comparative and should include investigations and comparisons within species and across species. These new studies and reinterpretations of previous findings will add not only to our understanding of how the brain works and how the brain and behavior interact, but also why the brain and behavior interact and work in ways that contribute meaningfully to an organism's (human or non-human) survival or reproduction. Because of the synergistic combination of two vibrant fields—evolutionary psychology and cognitive neuroscience—the sum of which (ECN) is greater than its constituent parts, we are in the position to also learn more about how the brain goes awry. For example, in Platek, Keenan, and Shackelford (2007), Baron-Cohen (2007) and Stevens et al. (2007) discuss how modular deficits in patients with autism and schizophrenia can be interpreted and best understood from the ECN perspective.

We hope that this article impresses upon the reader the current drive in research programs designed from an ECN perspective, as well as makes clear to the reader the need for future research from this perspective. The ECN approach attacks investigation of the human mind as a modularly organized (yet clearly dependent) set of cognitive structures (see Barkow, Cosmides, and Tooby, 1992). We hope, in fact, that this article and the related volume (Platek, Keenan, and Shackelford, 2007) invigorate researchers to consider this new strategy for future investigations and apply this theoretical stance to research they might already have conducted. The development of new laboratories and research groups dedicated to the ECN approach is likely. Furthermore, by adopting an ECN approach, scientists will be in a position to think about uniquely human traits such as higher-level consciousness, theory of mind, and self-awareness. In fact, ECN might be the only approach that can give rise to such an understanding. Evolutionary cognitive neuroscience might be the newest “science of the mind.”

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References

- Anderson, B. (2000). The g factor in non-human animals. In G.R. Bock, J.A. Goode, and K. Webb (Eds.), *The Nature of Intelligence* (pp.79-95). New York: Wiley.
- Annett, M. (1985). *Left, Right, Hand, and Brain: The Right-shift Theory*. London: Erlbaum.
- Aron, A., Fisher, H.E., Mashek, D.J., Strong, G., Li, H.F., and Brown, L.L. (2005). Reward, motivation and emotion systems associated with early stage intense romantic love: An fMRI study. *Journal of Neurophysiology*, *94*, 327-337.
- Atkinson A.P., and Wheeler, M. (2004). The grain of domains: The evolutionary-psychological case against domain-general cognition. *Mind and Language*, *19*, 147-176.
- Barkow, J.H., Cosmides, L., and Tooby J. (1992). *The Adapted Mind*. New York: Oxford University Press.
- Baron-Cohen, S. (2007). The assortative mating theory of autism. In S.M. Platek, J.P. Keenan and T.K. Shackelford (Eds.), *Evolutionary Cognitive Neuroscience* (pp 499-515). Cambridge, MA: MIT Press.

- Baron-Cohen, S., Leslie, A.M., and Frith, U. (1985). Does the autistic child have a “theory of mind?” *Cognition*, 21, 37-46.
- Baron-Cohen, S., Wheelwright, S. and Hill, J. (2001). The “reading the mind in the eyes” test revised version: A study with normal adults, and adults with Asperger Syndrome or high functioning autism. *Journal of Child Psychology and Psychiatry*, 42, 241-252.
- Barton, R.A. and Harvey, P.H. (2000). Mosaic evolution of brain structure in mammals. *Nature*, 405, 1055-1057.
- Bjorklund, D.F. (2006). Mother knows best: Epigenetic inheritance, maternal effects, and the evolution of human intelligence. *Developmental Review*, 26, 213-242.
- Buss, D.M. (1995). Evolutionary psychology: A new paradigm for psychological science. *Psychological Inquiry*, 6, 1-20.
- Buss, D.M. (Ed.). (2005). *The Handbook of Evolutionary Psychology*. New York: Wiley.
- Buss D.M., Larsen R., Westen D., and Semmelroth J. (1992). Sex differences in jealousy: Evolution, physiology, and psychology. *Psychological Science*, 3, 251–255.
- Buss, D.M., and Shackelford, T.K. (1997). From vigilance to violence: Mate retention tactics in married couples. *Journal of Personality and Social Psychology*, 72, 346-361.
- Byrne, R. and Whiten, A. (Eds.) (1988). *Machiavellian Intelligence*. Oxford: Oxford University Press.
- Carey, S., and Gelman, R. (1991). *The Epigenesis of Mind*. Hillsdale, NJ: Erlbaum.
- Chance, B. (1951). Rapid and sensitive spectrophotometry, III. A double beam apparatus. *Review of Scientific Instruments*, 22, 634-638.
- Chiappe, D. and MacDonald, K. (2005). The evolution of domain-general mechanisms in intelligence and learning. *Journal of General Psychology*, 132, 5-40.
- Clark, D.A., Mitra, P.P., Wang, S.S.-H. (2001). Scalable architecture in mammalian brains. *Nature*, 411, 189-193.
- Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, 31, 187-276.
- Cosmides, L., and Tooby, J. (1987). From evolution to behavior: Evolutionary psychology as the missing link. In J. Dupre (Ed.), *The Latest on the Best* (pp. 277-306). Cambridge, MA: The MIT Press.
- Cosmides, L., and Tooby, J. (1994). Origins of domain specificity: The evolution of functional organization. In L.A. Hirschfeld and S.A. Gelman (Eds.) *Mapping the Mind* (pp. 85-116). New York: Cambridge University Press.
- Cosmides, L. and Tooby, J. (2005). Neurocognitive adaptations designed for social exchange. In D. Buss (Ed.) *Evolutionary Psychology Handbook* (pp.584-627) New York: Wiley
- Cummins, D. D. (1998). Social norms and other minds: The evolutionary roots of higher cognition. In D. D. Cummins and C. Allen (Eds.), *The Evolution of Mind* (pp. 30-50). New York: Oxford University Press.
- Daly, M., Wilson, M., and Weghorst, S. J. (1982). Male sexual jealousy. *Ethology and Sociobiology*, 3, 11-27.
- DaSilva, P., Rachman, S.J., and Seligman, M.E.P. (1977). Prepared phobias and obsessions: Therapeutic outcomes. *Behaviour Research and Therapy*, 15, 210-211.

- Davidson, R.J., Putnam, K.M., and Larson, C.L. (2000). Dysfunction in the neural circuitry of emotion regulation-- A possible prelude to violence. *Science*, 289, 591-594.
- Davis, M.R. and Fernald, R.D. (1990). Social control of neuronal soma size. *Journal of Neurobiology* 21, 1180-1188.
- Dehaene, S. Piazza, M., Pinel, P. and Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Psychology*, 20, 487-506.
- den Ouden, H.E.M., Frith, U., Frith, C. and Blakemore, S.J. (2005). Thinking about intentions. *NeuroImage*, 28, 787-796.
- Dunbar, R.I.M. (2007). Brain and cognition in evolutionary perspective. In S.M. Platek, J.P. Keenan, and T.K. Shackelford (Eds.), *Evolutionary Cognitive Neuroscience* (pp. 21-46). Cambridge, MA: MIT Press.
- Farah, M.J. and Feinberg T.E. (2000) *Patient-Based Approaches to Cognitive Neuroscience*. Cambridge, MA: MIT Press.
- Fernald, R.D. (1977). Quantitative observations of *Haplochromis burtoni* under semi natural conditions. *Animal Behavior*, 25, 643-653.
- Fernald, R.D. (2007). The social control of reproduction: Physiological, cellular, and molecular consequences of social status. In S.M. Platek, J.P. Keenan, and T.K. Shackelford (Eds.), *Evolutionary Cognitive Neuroscience* (pp. 197-216). Cambridge, MA: MIT Press.
- Finlay, B.L. and Darlington, R.B. (1995). Linked regularities in the development and evolution of mammalian brains. *Science* 268, 1578-1584.
- Fisher, H.E. and Thomson, A.J., Jr. (2007). Lust, romance, attachment: Do side effects of serotonin-enhancing antidepressants jeopardize romantic love, marriage, and fertility? In S.M. Platek, J.P. Keenan, and T.K. Shackelford (Eds.), *Evolutionary Cognitive Neuroscience* (pp. 245-283). Cambridge, MA: MIT Press.
- Flaxman, S.M., and Sherman, P. (2000). Morning sickness: A mechanism for protecting mother and embryo. *Quarterly Review of Biology*, 75, 113-148.
- Flombaum, J.I., and Santos, L.R. (2005) Rhesus monkeys attribute perceptions to others. *Current Biology*, 15(5), 447-452.
- Focquaert, F. and Platek, S.M. (2007). Evolution of self-awareness: Ultimate theories, selection pressures, and proximate explanations. In S.M. Platek, J.P. Keenan and T.K. Shackelford (Eds.), *Evolutionary Cognitive Neuroscience* (pp 457-497). Cambridge, MA: MIT Press.
- Fraley, N.B. and Fernald, R.D. (1982). Social control of developmental rate in the African cichlid, *Haplochromis burtoni*. *Zeitschrift für Tierpsychologie*, 60, 66-82.
- Francis, R.C., Soma, K.K., and Fernald, R.D. (1993). Social regulation of the brain-pituitary-gonadal axis. *Proceedings of the National Academy of Sciences USA*, 90, 7794-7799.
- Frith, C.D., and Frith, U. (1999). Interacting minds—A biological basis. *Science*, 286, 1692-1695.
- Gallup, G.G., Jr. (1982). Self-awareness and the emergence of mind in primates. *American Journal of Primatology*, 2, 237-248.
- Gallup, G.G., Jr., and Suarez, S.D. (1987). "Biotic revenge" and the death of the dinosaurs. *The Scientist*, Jan. 26, p. 10.
- Garcia, J., Ervin, F.R., and Koelling, R.A. (1966). Learning with prolonged delay of reinforcement. *Psychonomic Science*, 5, 121-122.

- Gazzaniga, M.S., and Smylie, C.S. (1983). Facial recognition and brain asymmetries: Clues to underlying mechanisms. *Annals of Neurology*, *13*, 536-540.
- Geary, D.C. (1995). Reflections of evolution and culture in children's cognition: Implications for mathematical development and instruction. *American Psychologist*, *50*, 24-37.
- Goetz, A.T., Shackelford, T.K. (2006). Sexual coercion and forced in-pair copulation as sperm competition tactics in humans. *Human Nature*, *17*, 265-282.
- Henrich, B. (2000). Testing insight in ravens. In C. Heyes and L. Huber (Eds.), *The Evolution of Cognition* (pp.289-305). Cambridge, MA: MIT Press.
- Heyes, C., Dawson, G., and Nokes, T. (1992). Imitation in rats: Initial responding and transfer evidence. *Quarterly Journal of Experimental Psychology*, *45*, 229-240.
- Hirschfeld, L.A. and Gelman, S.A. (1994). *Mapping the Mind*. New York: Cambridge University Press.
- Hopkins, W.D. (2007). Hemispheric specialization in chimpanzees: Evolution of hand and brain. In S.M. Platek, J.P. Keenan, and T.K. Shackelford (Eds.), *Evolutionary Cognitive Neuroscience* (pp. 95-119). Cambridge, MA: MIT Press.
- Hopkins, W.D., and Dahl, J.F. (2000). Birth order and hand preference in chimpanzees (*Pan troglodytes*): Implications for pathological models of human handedness. *Journal of Comparative Psychology*, *114*, 302-306.
- Hopkins, W.D., Dahl, J.F., and Pilcher, D. (2000). Birth order and left-handedness revisited: Some recent findings in chimpanzees (*Pan troglodytes*) and their implications for developmental and evolutionary models of human handedness. *Neuropsychologia*, *38*, 1626-1633.
- Hugdahl, K. and Johnsen, B.H. (1989). Preparedness and electrodermal fear-conditioning: Ontogenetic vs. phylogenetic explanations. *Behavioral Research and Therapy*, *27*, 269-278.
- Irani, F., Platek, S.M., Panyavin, I.S., Calkins, M.E., Kohler, C., Siegel, S.J., Schachter, M., Gur, R.E., and Gur, R.C. (2006). Self-face recognition and theory of mind in patients with schizophrenia and first-degree relatives. *Schizophrenia Research*, *88*, 151-160.
- Kane, M.J., Bleckley, M.K., Conway, A.R., and Engle, R. (2001). A controlled-attention view of working memory capacity. *Journal of Experimental Psychology: General*, *130*, 169-183.
- Keenan, J.P., McCutcheon, B., and Pascual-Leone A. (2001). Functional magnetic resonance imaging and event related potentials suggest right prefrontal activation for self-related processing. *Brain and Cognition*, *47*, 87-91.
- Keenan, J.P., Wheeler, M.A., and Ewers, M. (2003). The neuropsychology of self. In A. S. David and T. Kircher (Eds.), *The Self and Schizophrenia: A Neuropsychological Perspective*. Cambridge: Cambridge University Press.
- Kosslyn, S.M. (2007). On the evolution of human motivation: The role of social prosthetic systems. In S.M. Platek, J.P. Keenan and T.K. Shackelford (Eds.), *Evolutionary Cognitive Neuroscience* (pp. 541-554). Cambridge, MA: MIT Press.
- Kurzban, R., Tooby, J., and Cosmides, L. (2001). Can race be erased? Coalitional computation and social categorization. *Proceedings of the National Academy of Sciences*, *98*, 15387-15392.

- McGrew, W.C., and Merchant, L.F. (1997). On the other hand: Current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology*, 40, 201-232.
- Moore, B. R. (1996). Evolution of imitative learning. In C.M. Heyes and B.G. Galef (Eds.), *Social Learning in Animals: The Roots of Culture* (pp. 245-265). San Diego: Academic Press.
- Northoff, G. and Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences*, 8, 102-108.
- O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D.M., and Dolan, R.J. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, 41, 147-155.
- Öhman, A., and Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, 108, 483-522.
- Ochsner, K.N., Beer, J.S., Robertson, E.R., Cooper, J.C., Grabieli, J.D.E., Kihlstrom, J.F., D'Esposito, M. (2005). The neural correlates of direct and reflected self-knowledge. *NeuroImage*, 28, 797-814.
- Pascual-Leone, A. Walsh, V., and Rothwell, J. (2000). Transcranial magnetic stimulation in cognitive neuroscience: Virtual lesion, chronometry, and functional connectivity. *Current Opinion in Neurobiology*, 10, 232-237.
- Pinker, S. (2002). *The Blank Slate*. New York: Viking.
- Pinker, S., and Bloom, P. (1990). Natural language and natural selection. *Behavioral and Brain Sciences*, 13, 707-727.
- Platek, S.M. (2003). An evolutionary model of the effects of human paternal resemblance on paternal investment. *Evolution and Cognition*, 9, 189-197.
- Platek, S.M. and Gallup, G.G., Jr. (2002). Self-face recognition is affected by schizotypal personality traits. *Schizophrenia Research*, 57, 81-86.
- Platek, S.M., Irani, F., Sheiser, D., Schneider, J., and Glosser, G. (under review). Effect of anterior temporal lobectomy on self-face recognition.
- Platek, S.M., Keenan, J.P., Mohamed, F.B. (2005). Sex differences in neural correlates of child facial resemblance: An event-related fMRI study. *NeuroImage*, 25, 1336-1344.
- Platek, S.M., Keenan, J.P., and Shackelford, T.K. (Eds.). (2007). *Evolutionary Cognitive Neuroscience*. Cambridge, MA: MIT Press.
- Platek, S.M., Loughhead, J.W., Gur, R.C., Busch, S. Ruparel, K. Phend, N., et al. (2006) Neural substrates for functionally discriminating self-face from personally familiar faces. *Human Brain Mapping*, 27, 91-98.
- Platek, S.M., Raines, D.M., Gallup Jr., G.G., Mohamed, F.B., Thomson, J.W., Myers, T.E., Panyavin, I.S., Levin, S.L., Davis, J.A., Fonteyn, L.C.M., and Arigo, D.R. (2004). Reactions to children's faces: Males are still more affected by resemblance than females are, and so are their brains. *Evolution and Human Behavior*, 25, 394-405.
- Platek, S.M. and Shackelford, T.K. (under contract). *Foundations in Evolutionary Cognitive Neuroscience*. Cambridge University Press, Cambridge, UK.
- Price, C.J. and Mechelli, A. (2005). Reading and reading disturbance. *Current opinion in Neurobiology*, 15, 231-238.
- Ramachandran, V.S. (1995). Anosognosia in parietal lobe syndrome. *Consciousness Cognition*, 4, 22-51.

- Reader, S.M. and Laland, K.N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Science*, 99, 4436-4441.
- Rilling, J.K., Winslow, J.T., and Kilts C.D. (2004). The neural correlates of mate competition in dominant male rhesus macaques. *Biological Psychiatry*, 56, 364-375.
- Santos, L.R., Flombaum, J.I., and Phillips, W. (2007) The Evolution of human mindreading: primate can inform social cognitive neuroscience. In S.M. Platek, J.P. Keenan, and T.K. Shackelford (Eds.), *Evolutionary Cognitive Neuroscience* (pp. 433-456). Cambridge, MA: MIT Press.
- Schmitt, D.P., and Pilcher, J.J. (2004). Evaluating evidence of psychological adaptation: How do we know one when we see one? *Psychological Science*, 15, 643-649.
- Schultzwohl, A. and Koch, S. (2004). Sex differences in jealousy: The recall of cues to sexual and emotional infidelity in personally more and less threatening contexts. *Evolution and Human Behavior*, 25, 249-257.
- Seligman, M.E.P. (1971). Phobias and preparedness. *Behavior Therapy*, 2, 307-320.
- Sergent, J., Ohta, S., and MacDonald, B. (1992). Functional neuroanatomy of face and object processing: A positron emission topography study. *Brain*, 115, 15-36.
- Shackelford, T.K., and Goetz, A.T. (in press). Adaptation to sperm competition in humans. *Current Directions in Psychological Science*.
- Shackelford, T.K., Pound, N., and Goetz, A.T. (2005). Psychological and physiological adaptation to human sperm competition. *Review of General Psychology*, 9, 228-248.
- Shuman, M. and Kanwisher, N. (2004). Numerical magnitude and the human parietal lobe: Tests of representational generality and domain specificity. *Neuron*, 44, 557-569.
- Singh, D. (1993). Adaptive significance of female physical attractiveness: Role of waist-to-hip ratio. *Journal of Personality and Social Psychology*, 65, 293-307.
- Simpson, J.A. and Campbell, L. (2005). Methods in evolutionary sciences. In D.M. Buss, (Ed.) *The Handbook of Evolutionary Psychology*, Wiley, New York, NY.
- Stevens, S.T., Guise, K., Christiana, W., Kumar, M., and Keenan, J.P. (2007). Deception, evolution, and the brain. In S.M. Platek, J.P. Keenan, and T.K. Shackelford, (Eds.), *Evolutionary Cognitive Neuroscience*. The MIT Press, Cambridge, MA.
- Stone, V. (2007). The evolution of ontogeny and human cognitive uniqueness: Selection for extended brain development in the hominid line. In S.M. Platek, J.P. Keenan, and T.K. Shackelford (Eds.), *Evolutionary Cognitive Neuroscience* (pp. 65-94). Cambridge, MA: MIT Press.
- Stone, V., Cosmides, L., Tooby, J., Kroll, N., and Knight, R. (2002). Selective Impairment of Reasoning about Social Exchange in a Patient with Bilateral Limbic System Damage. *Proceeding of the National Academy of Science*, 99, 11531-11536.
- Sugiura, M., Kawashima, R., Nakamura, K., Okada, K., Kato, T., Nakamura, A., Hatano, K., Itoh, K., et al. (2000). Passive and active recognition of one's own face. *NeuroImage*, 11, 36-48.
- Symons, D. (1979). *The Evolution of Human Sexuality*. New York: Oxford University Press.
- Takahashi, H., Matsuura, M., Yahata, N., Koeda, M., Suhara, T., and Okubo, Y. (2006). Men and women show distinct brain activation during imagery of sexual and emotional infidelity. *NeuroImage*, 32, 1299-1307.

- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift fur Tierpsychologie*, 20, 410-433.
- Tomasello, M. and Call, J. (1997). *Primate Cognition*. New York, NY: Oxford University Press.
- Tooby, J., and Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, 11, 375-424.
- Tooby, J., and Cosmides, L. (1992). The psychological foundations of culture. In J.H. Barkow, L. Cosmides, and J. Tooby (Eds.), *The Adapted Mind* (pp. 19-136). New York: Oxford University Press.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, 76, 35-57.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man: 1871-1971* (pp. 136-179). Chicago: Aldine.
- Turner, M.L. and Engle, R.W. (1989). Is working memory capacity task dependent? *Journal of Memory and Language*, 28, 127-154.
- Vollm, B., Richardson, P., McKie, S., Elliot, R., Deakin, J.F.W., and Anderson, I.M. (2006). Serotonergic modulation of neuronal responses to behavioral inhibition and reinforcing stimuli: An fMRI study in healthy volunteers. *European Journal of Neuroscience*, 23, 552-560.
- Williams, G.C. (1966). *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Winston, J. S., O'Doherty, J., Kilner, J.M., Perrett, D.I., and Dolan, R.J. (2007). Brain systems for assessing physical attractiveness. *Neuropsychologica*
- Winterer, G., Musso, F., Vucurevic, G., Stoeter, P., Konrad, A., Seker, B., et al. (2006). COMT Genotype predicts BOLD signal and noise characteristics in prefrontal circuits. *NeuroImage*, 32, 1722-1732.

ⁱ A complete survey of evolutionary cognitive neuroscience must include a survey of the non-human literature; however this survey is beyond the scope of this paper. Interested readers can consult the text *Primate Cognition* (Tomasello and Call, 1997) as well as a number of recent papers that apply the ECN framework (e.g., Rilling et al., 2004).

ⁱⁱ Here functional localization is differentiated from spatial localization for the simple fact that TMS represents a causal interference with brain function, while other techniques that offer spatial resolution (e.g., fMRI) are correlative in nature. That is, the BOLD signal is a correlation of activity in a region of interest, or set of regions associated with some stimulus delivery, while TMS is the direct influence over brain function during delivery of stimuli. Hence, since TMS can alter behaviour it is said to measure functional localization.