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Evolutionary neuromarketing: Darwinizing the neuroimaging paradigm for consumer behavior

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• *The current paper serves two purposes. First, it reviews the neuroimaging literature most relevant to the field of marketing (e.g., neuroeconomics, decision neuroscience, and neuromarketing). Second, it posits that evolutionary theory is a consilient and organizing meta-theoretical framework for neuromarketing research. The great majority of neuroimaging studies suffer from the illusion of explanatory depth namely the sophistication of the neuroimaging technologies provides a semblance of profundity to the reaped knowledge, which is otherwise largely disjointed and atheoretical. Evolutionary theory resolves this conundrum by recognizing that the human mind has evolved via the processes of natural and sexual selection. Hence, in order to provide a complete understanding of any given neuromarketing phenomenon requires that it be tackled at both the proximate level (as is currently the case) and the ultimate level (i.e., understanding the adaptive reason that would generate a particular neural activation pattern). Evolutionary psychology posits that the human mind consists of a set of domain-specific computational systems that have evolved to solve recurring adaptive problems. Accordingly, rather than viewing the human mind as a general-purpose domain-independent organ, evolutionary cognitive neuroscientists recognize that many neural activation patterns are instantiations of evolved computational systems in evolutionarily relevant domains such as survival, mating, kin selection, and reciprocity. As such, an evolutionary neuromarketing approach recognizes that the neural activation patterns associated with numerous marketing-related phenomena can be mapped onto the latter Darwinian modules thus providing a unifying meta-theory for this budding discipline.*

Introduction

Brain-imaging technology is rapidly becoming a ubiquitous research tool spurned by its increased sophistication as well as its decreas-

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ing cost of production and operation. What were perhaps classically considered tools of the physician, have increasingly become popular among researchers to elucidate the role of the brain in directing behavior. According to The Society for Neuroscience (2006), the handbook produced by the Society for Neuroscience, the advancement of neuroimaging techniques has provided valuable tools for research on the nervous system. Numerous diagnostic methods exist that allow scientists to better understand the functioning of the nervous system. A manifestation of these technological advances is the ability to apply neuroimaging to previously disparate fields; the field of consumer behavior has experienced this with the growing popularity of neuromarketing as a distinct discipline. Lee *et al.* (2007, p. 200) state that "neuromarketing as a field of study can simply be defined as the application of neuroscientific methods to analyze and understand human behavior in relation to markets and marketing exchanges." Broadly speaking, neuromarketing represents the intersection of consumer behavior and cognitive neuroscience. Whereas both disciplines have developed independently rich research streams, their nexus provides countless opportunities for future research. Furthermore, both consumer behavior and cognitive neuroscience have recently, and independently, been infused with evolutionary-based theorizing albeit neuromarketing has not as of yet.

Neuromarketing does not possess an overarching theoretical framework to guide its research agenda. The present paper reviews the extant neuromarketing literature and provides a Darwinian-based framework to help guide this budding field. We begin by briefly reviewing neuroimaging technology and how neuromarketing has developed as a product of research in both cognitive science and consumer behavior. Additionally, we discuss the implications of recent applications of evolutionary principles to both cognitive neuroscience and consumption, and in so doing we suggest ways by which one might Darwinize the neuromarketing discipline. Although multiple theoretical frameworks exist for the study of human behavior, some of which are devoid of evolutionary principles and biological-based theorizing (*cf.* the discussion of the Standard Social Science Model by Tooby and Cosmides, 1992), we contend that the Darwinian meta-framework allows for the most comprehensive interpretation of neuroimaging findings as applied to behavior. A complete and accurate understanding of the human mind cannot occur without recognizing the evolutionary forces that have shaped it. This approach implies that human purposive behavior has some biological basis and is the result of selection for traits that lead to relative fitness for individuals or groups. Evolutionary theorizing can not only enrich the explanatory power of neuromarketing but it can also permit neuroscientists to generate novel hypotheses that would have been otherwise invisible to them if solely operating at the proximate physiological level. Evolutionary theorizing achieves this in part by allowing researchers to ask appropriately guided questions.

Whereas evolutionary approaches have been applied recently to both cognitive neuroscience (Platek *et al.*, 2007) and consumer behavior (Saad, 2007), there exists a long tradition of applying an evolutionary framework in understanding the behavior of a wide range of organisms in various contexts, including humans (Gaulin and McBurney, 2003; Buss, 2005; Wilson, 2007). It is noteworthy to point out that Darwinists recognize that humans are both biological as well as cultural beings, as evidenced by the gene-culture coevolution approach, which explicitly recognizes the importance of both factors in having shaped the phylogenetic history of humans (Richerson and Boyd, 2005). Evolutionary meta-theory contends that the biocultural evolution of humans has endowed man with a brain far beyond a "blank slate" but with a highly evolved toolset prepared to respond to environmental demands (Barkow *et al.*, 1992; Cosmides and Tooby, 1994; Gaulin and McBurney, 2003; Buss, 2005). To the extent that neuromarketing explores the effect of cultural products (e.g., advertising images) on a biological organ (i.e., the human mind), it

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should likely benefit from the application of evolutionary principles. Darwinizing the neuromarketing paradigm can infuse the agenda for this relatively new field with the role that evolution has played in shaping contemporary consumption patterns.

Neuroimaging technology allows researchers to observe how detailed neural mechanisms cultivate subsequent behavior. As suggested earlier, fully comprehending human behavior requires an understanding of how evolutionary processes have selected for the functional patterns and responses of the nervous system. Indeed, Charles Darwin had recognized that evolutionary thinking could be applied to human behavior (Darwin, 1872). The fields of evolutionary anthropology, evolutionary psychology, and evolutionary biology recognize this point as a foundational tenet of their respective subdisciplines. Over the course of human history, natural and sexual selection have shaped our biology. Modern human behavior can thus be best understood by considering the Environment of Evolutionary Adaptedness (EEA), the time frame during which intensive selective processes took place (Tooby and Cosmides, 1990). Much of the underlying architecture of modern human biology may have adapted at the genetic level to this human environment of the Pleistocene epoch. Behavioral phenotypes that evolved in the EEA influence much of our modern tendencies, motivations, and general responses across multiple domains. Humans do, however, also respond adaptively to current ecological demands (Laland and Brown, 2002). In fact, a complete Darwinian perspective recognizes that both adaptations as well as adaptability to local niches are important evolutionary mechanisms (Cartwright, 2000). Human behavior, especially that which is purposive, can therefore be construed as the result of both adaptations and adaptability.

Proximate versus ultimate explanations

Evolutionists recognize the distinction between proximate-level and ultimate-level explanations of behavior. Proximate-level studies attempt to understand *what* specific mechanisms are at work and *how* such mechanisms physically function - this is the physiological approach utilized by most neuroscientists. Ultimate-level studies on the other hand attempt to answer *why* a particular trait may be present. Ultimate causation seeks to comprehend why one particular trait was favored over another in a specific environment, and explains subsequent prevalence of such traits. This occurs by selecting for a particular trait that will allow the organism to thrive and reproduce optimally with respect to others in the environment. For instance, the fight-or-flight response is a complex physiological process which involves the endocrine system (proximate mechanism) and has evolved to allow individuals to respond to stressful situations by either preparing to mount an attack or preparing to flee (ultimate mechanism), in response to various stressors that an individual may face (Carlson, 2005). It is assumed that at some point in human history, individuals developed a fight-or-flight response to outwit sources of competition and predation.

Both proximate-level and ultimate-level explanations should be included in evolutionary neuromarketing. This permits one to identify how the brain responds to stimuli relevant to consumer behavior such as individuals' neurological responses to ads laden with sexual content (proximate) and why, in the adaptive sense, some of these observed responses occur in universally similar manners (ultimate). Evolution works by the process of natural selection acting on traits. To clarify the process of evolution by natural selection, Williams (1966) proposed that evolution could be construed as a statistical bias in the rate of perpetuation of alternatives. That is to say, any trait that is relatively better adapted than others can be expected to also become more pervasive than others. Evolutionary processes are not teleological, insofar as evolution is neither linear nor progressive; rather adaptations to an organism's ecological situation exist to guide survivability and reproductive

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success. Insofar as the behavioral neurosciences are concerned, individual differences in proximate neural substrate allows for preferential success in a given environment because the benefit of certain personality types are context-dependent (e.g., being a risk-taker may be generally dangerous, but useful when wooing potential mates or when searching for new sources of food). Those individuals who succeed best may be expected to produce the most viable offspring for the next generation and are thus the most fit. But discovering how neural substrate actually guides behavior, and how brain variation influences behavioral differences, is only possible through scientific technologies used to map the brain. As neuroimaging technology allows researchers to identify the proximate neural mechanisms that are triggered by a particular stimulus (e.g., viewing a juicy hamburger in a print advertisement), the evolutionary neuromarketing approach will permit researchers to provide ultimate explanations for these activation patterns (e.g., the adaptive reasons that exposure to the image of a juicy hamburger "tickles" the brain's pleasure center). That said the great majority of practical uses of neuroimaging technology is likely to continue to occur at the proximate level (e.g., a neurologist need not be evolutionary informed to reap the diagnostic and clinical advantages that this tool affords).

Cognitive neuroscience

The cognitive neurosciences possess a rich tradition of utilizing neuroimaging technology in seeking to understand the physiological underpinnings of the mind, specifically how the brain supports and mediates cognition. We conducted a search using the ISI Web of Science database (using *fMRI* as the topic search word in the title of the document or list of keywords) to gauge the prevalence of fMRI studies over the past 15 years. The number of fMRI-based documents increased from six reported papers in 1993 to 2471 papers in 2007 (as of 5 pm on 15 March 2008). That said the great majority of research within the human cognitive neurosciences are fraught with areas of investigation that are not explicitly evolutionary based. Two hundred twenty-eight documents were retained for the more restricted search term *fMRI AND Evol**, which is a gross overestimate of the actual number of evolutionary-inspired papers given that *Evol* in many instances was not used in the Darwinian sense of the term. Only two documents were identified for the search term *fMRI AND Darwin**. This is a great detriment to the discipline as much is lost in the absence of an overarching explanatory framework to bridge disjointed research studies. In a sense, the methodological allure of fMRI has yielded an extraordinarily rich empirical literature, albeit much of it consists of disjointed and atheoretical work. To name but a few examples, neuroimaging studies have addressed emotion in neuroanatomy (see Phan *et al.*, 2002), reward system motivation (Peterson, 2005), and outcome representation (Ursa and Carter, 2005). Furthermore, political ideation and affiliation, including neural responses to political attitudes, have also been studied (Kaplan *et al.*, 2007; see also Tingley, 2006 for a discussion of neuroimaging approaches in political science). The neuroscience of decision-making has also been tackled (Platt, 2002; Paulus, 2005; Shiv *et al.*, 2005a) including the role of the prefrontal cortex in human decision-making (Krawczyk, 2002), and deliberation judgments in decision formation (Opris and Bruce, 2005). It is important to reiterate that despite the richness of scientific fMRI-based empirical work, one might argue that the paradigm suffers from an illusion of explanatory depth (Rozenblit and Keil, 2002). Specifically, the technological sophistication inherent to the fMRI paradigm offers a veneer of profundity to the empirical findings, which in most instances are lacking a unifying meta-framework. The allure of the fMRI technology may in part be due to its ability to produce pictorial representations of the human brain rather than to actual methodological elegance (Fellows *et al.*, 2005). It is also worth

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noting that neuroscientists frequently propose atheoretical reverse inferences regarding specific cognitive processes as depicted in fMRI images, an epistemological process whose deductive validity has been questioned (Poldrack, 2008).

Notwithstanding the impressive advances that have been reported in the burgeoning fMRI literature, the field has attracted continued criticisms. In a statement that would be equally veridical today, Kosslyn (1999, p. 1283) stated the following regarding neuroimaging studies: "Many of the studies summarized in the posters did not seem to be designed to answer questions about the functioning of the brain; neither did they seem to bear on specific questions about the roles of particular brain regions. Rather, they could best be described as "exploratory." People were asked to engage in some task while the activity in their brains was monitored, and this activity was then interpreted *post hoc*." In their recent critique of the brain mapping paradigm, Lee and Chamberlain (2007, p. 23) propose that "...there is also a chance that the end result of the present approach is a set of *neuro-whatever* [italics in original] ad hoc research studies that are not necessarily theoretically driven. In such cases, we may fall unwittingly prey to exactly the kind of blobological approach that has received criticism in social and general neuroscientific circles." Numerous other scholars have questioned the value of the brain mapping paradigm including Uttal (2001) who referred to the endeavor as a new form of phrenology, as well as the Neuroscience Institute (fMRI Colloquium Series) at Stanford University who sponsored a debate on 30 November 2005 titled "The great debate of 2005: Is fMRI just a waste of our time? Can we learn anything useful from functional neuroimaging?" (Accessed on 24 March 2008 at http://rsl.stanford.edu/nis/great_debate_2005.html). It is our contention that some of the criticisms levied against the neuroimaging paradigm in general and neuromarketing in particular would be assuaged via the adoption of evolutionary theory as the organizing theoretical meta-framework.

Whereas cognitive neuroscience concerns itself with the biological mechanisms substratal to information processing and perception, evolutionary cognitive neuroscience seeks to more specifically identify how evolution has shaped such brain-behavior relationships (Krill *et al.*, 2007; Platek, 2007; Platek *et al.*, 2007). The successful application of evolutionary principles to the flourishing field of cognitive neuroscience allows for a multitude of studies, including research on humans and/or animals, to be guided by the same overarching rigorous, experiment-tested and theoretical framework (for a review see Platek *et al.*, 2007). Webster (2007) conducted a review of publication trends in cognitive neuroscience over a period of 20 years to assess the relative influence of evolutionary principles on the field and determined that although there was significant growth of evolutionary-based theorizing in the neurosciences, there was relatively little within the subdiscipline of cognitive neuroscience.

Evolutionary psychologists construe the human mind as consisting of a number of domain-specific computational systems/modules, each of which has evolved to solve an adaptive problem. A "module" as commonly referred to in evolutionary psychology, does not refer to a locationist region of the brain. Rather, a module may contain circuitry across a wide range of neural substrate. Domain specificity speaks strictly to the evolutionary domains directing purposive behavior (e.g., survival, mating, kin selection, and reciprocity; see Saad, 2007, chapter 3) and not to brain locationality. That said specific regions of the brain are associated with particular capacities. This is most apparent in a comparative brain evolution approach between humans and other primates with respect to brain size and associated cognitive ability. The study of brain evolution through comparative and archeological samples is a distinct area of inquiry possessing its own research agenda (Allman, 1999). The field of neural Darwinism is another distinct area of evolutionary neuroscience that suggests that the brain is a somatic selection system full of complex adaptive processes that

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respond to physiological processes within the context of the individual's nervous system (Edelman, 1987). Although these processes are important and fall within the realm of evolutionary neuroscience, they represent applications of evolutionary principles in an arena outside of the current scope. Such is the sophistication of a Darwinian approach, as it provides a fundamental framework of evolutionary principles to tackle a wide range of questions.

Evolutionary consumer behavior

Saad (2007) provides an exhaustive account of ways by which evolutionary theory might inform consumer research. Specifically, Saad demonstrates that consumer scholars have developed sophisticated and rich literature streams void of any ultimate-level explanations. For example, functional areas of interest to consumer scholars including learning, motivation, perception, attitude formation, decision-making, emotions, and personality, have all been investigated without ever recognizing the Darwinian processes that have shaped each of these areas. Accordingly, Saad argues, the consumer behavior discipline provides at best an incomplete account of consumption phenomena by restricting its focus to proximate mechanisms. Saad goes on to demonstrate that cultural products including advertising, song lyrics, movie themes, art, literature, and religion, contain universal contents precisely because these products cater to a common biological heritage. Furthermore, Saad provides compelling evidence that many dark side consumption acts including pathological gambling, compulsive buying, eating disorders, and pornographic addictions, occur in universally predictable manners because they are rooted in a common Darwinian etiology. Of greatest relevance to the current paper, Saad argues that consumption acts can be mapped onto one of four key Darwinian meta-pursuits namely the survival, mating, kin selection, and reciprocity modules.

How might one apply evolutionary theory to neuromarketing? If one were to conduct fMRI-based studies to explore the activation patterns associated with specific marketing-related images, we surmise that numerous universal patterns would emerge. Hence, that the viewing of attractive faces (e.g., celebrity endorsers) or the consumption of pornography might trigger the brain's pleasure center more so in men than it does in women, is rooted in evolutionary-based forces. On the other hand, that men and women might demonstrate similar "pleasure triggers" when consuming food is to be expected given that both sexes have faced the same survival threat associated with caloric scarcity. Hence, an evolutionary neuromarketing approach moves beyond the mere cataloging of differential brain activation patterns, by providing ultimate explanations for these. The ability to identify universal marketing-related fMRI patterns is greatly facilitated by the creation of central repositories of neuroimaging data accessible to all interested parties (cf., the fMRI Data Center at http://www.fmridc.org).

Neuroimaging approaches in economics

Of all business-related disciplines that have incorporated brain-imaging approaches within their methodological toolboxes, neuroeconomics is perhaps the one that has done so most extensively (but see Butler and Senior, 2007a,b; and Senior *et al.*, 2007a for discussions of the nascent field of organizational cognitive neuroscience). Neuroeconomics has been described as the natural extension of bioeconomics (Vromen, 2007). Bioeconomics incorporates evolutionary biology in seeking to understand contemporary economic choice. Neuroeconomics utilizes neuroscience techniques to explore brain mechanisms involved with decision-making and economic analysis (Rustichini, 2005; Sanfey *et al.*, 2006) albeit typically restricted to the proximate realm. Neuroeconomics is an active field with an overriding goal of understanding economically

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relevant brain and behavioral processes (Braeutigam, 2005). A key component of neuroeconomics may be its role in elucidating seemingly irrational choices in various tasks (Huang, 2005). A review of neuroeconomics by Kenning and Plassman (2005) puts emphasis in this field on the role of decision-making and related emotional processes. These studies are, for the most part, absent of any Darwinian interpretation. Evolutionarily relevant work in neuroeconomics has included the role of "theory of mind" in decision-making (Bhatt and Camerer, 2005; Singer and Fehr, 2005) as well as an appreciation that some emotional responses in decision-making may seem more rational when contextualized within mankind's evolutionary past (Cohen, 2005). Processing of the brain's evolved motivational reward circuitry is also believed to be associated with decision-making (Cohen and Blum, 2002). The brain's reward circuitry is important in mediating sensation-seeking behaviors, including risk-taking (*cf.* Knutson *et al.*, 2008 who explored the neural underpinnings of anticipating exposure to erotic photos on men's financial risk-taking).

Various forms of risk-taking have been investigated from a neuroeconomic perspective. This includes the use of the Ultimatum Game to study the neural basis of decision-making (Sanfey *et al.*, 2003). Risky decisions appear to require increased cognitive effort over non-risky alternatives, as deduced by calling upon the prefrontal and parietal cortices as observed through fMRI (Gonzalez *et al.*, 2005). Neuroeconomic studies have also investigated risk as measured through one's propensity for engaging in financial risk-taking in decision processing (Kuhnen and Knutson, 2005; Huettel *et al.*, 2006; Knutson and Bossaerts, 2007). When monetary rewards are used in the delayed discounting task (measure of impulsivity), subjects showed preferential activation of the midbrain dopamine system and paralimbic cortex (McClure *et al.*, 2004a) suggesting that impulsive decisions call upon particular brain regions in assessing rationality. Using fMRI, it has also been reported that gain outcomes stimulate a region of the mesial prefrontal cortex whereas expectancy of escalating monetary gains stimulate a subcortical region of the ventral striatum (Knutson and Peterson, 2005). Financial risk observed through an economic classical choice task, wherein payoffs and likelihood of outcomes were manipulated in response to risk aversion and risk seeking in gains, showed recruitment of a dorsomedial neocortical system and a ventromedial system via PET scan (Smith *et al.*, 2002). Sexual risk-taking among youth has also been explored within the neuroeconomics framework (Gutnik *et al.*, 2006) albeit from a non-evolutionary perspective. The neural basis for risk-taking behavior is of interest to a broad range of practitioners beyond the business sciences, including those in public health and addiction studies. But, one's tendency for risk-taking represents only one aspect of decision-making as studied by neuroeconomics, as context and affective states are also important.

Whereas much of the consumer psychology literature has historically been influenced by the "cold cognition" approach, a growing number of consumer scholars recognize the importance of affective states when making decisions. This has been supported by neuroimaging findings suggesting that emotional systems have a significant role in decision-making. The somatic marker hypothesis, which suggests that rational decision-making depends on emotional processing, has been used to address the role of affective responses (Bechara and Damasio, 2005). Also studied is the emotional capacity and neural influence of empathy as it relates to economic decision-making (Singer and Fehr, 2005). Shiv *et al.* (2005b) report that subjects with neural system dysfunctions typically make more emotion-based investment decisions, performing better than subjects who do not suffer from preexisting medical conditions. Emotional processing has also been linked to product choice as it relates to negotiating distinct circuitry for product preference and price distinctions (Knutson *et al.*, 2007). Purchasing decisions and product preferences are subject to social influence, both of which may be

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mediated by trust in the product and retailer. Trust is important when making consequential decisions, fittingly trust appears to have a neurobiological and hormonal basis (Zak *et al.*, 2004, 2005a) with trust in others influencing performance on economic tasks (Fehr *et al.*, 2005; Zak *et al.*, 2005b). Relatedly, the neural basis for moral judgments has been investigated, a topic of relevance to business ethics (Greene *et al.*, 2001; Greene *et al.*, 2004). Investigations in neuroeconomics remain broad, with applications in various fields.

If there is a common element across the great majority of neuroeconomic studies, it is perhaps the absence of guiding theoretical frameworks that can help organize the otherwise disjointed findings. Along those lines, Lee and Chamberlain (2007, p. 20) recently proclaimed, "Certainly, a small number of studies have examined economic decision-making and marketing information processing, but these efforts appear to have little overall coherence and no overarching research program is obvious." Effectively, the paradigm has simply replaced paper-and-pencil tasks with "aesthetically pleasing" brain images, which otherwise leave us no closer to a deep and complete understanding of economic decision-making. In order to fully elucidate the mind of *Homo Economicus* requires that neuroeconomists investigate tasks in domains of evolutionary import (e.g., mate choice) rather than restricting their focus to domain-independent processes such as the framing effect.

Evolutionary domains for neuromarketing research

Given its status as a young discipline, the theoretical, empirical, and practical scope of neuromarketing is still being developed (Lee *et al.*, 2007; Senior *et al.*, 2007b). Neuromarketing research has included investigation of culturally familiar brand names (Gordon, 2002), and indeed such work has already shown that familiar brands activate regions of the prefrontal cortex (Schaefer *et al.*, 2006) and engage the brain longer during shopping behavior (Ambler *et al.*, 2004). This is congruent with the assertion made by Gontijo *et al.* (2002) that brand names in the lexicon appear to have "special neuropsychological status" distinct from other names. The neural processes inherent to how brand extensions are categorized have also been examined (Ma *et al.*, 2008). The cognitive processes that consumers utilize when categorizing products has recently received renewed interest in the marketing literature as a result of the growing number of composite products in the marketplace (*cf.* Gill and Dubé, 2007; Gill, 2008). It has also been shown that dissociation exists between brand judgments and person judgments, suggesting that distinct brain activity occurs as a function of the types of judgments made (Yoon *et al.*, 2006). Finally, Plassmann *et al.* (2008) demonstrated that participants, who were led to believe that they were to taste wines of varying prices, reported increased pleasantness and displayed increased neural activity when tasting the more expensive wine (even though in reality all of the wines were the same). One common theme throughout the existing neuromarketing literature is that it is void of evolutionary-based theorizing (see Fugate, 2007 for a recent review of the neuromarketing discipline).

Not all phenomena that are tackled within the neuromarketing rubric fall within relevant evolutionary domains (e.g., identifying the neural activation patterns when viewing humorous ads). McClure *et al.* (2004b) analyzed subjects' preference for non-carbonated versions of the soft drinks Coke and Pepsi. Participants tasted both drinks while undergoing fMRI and results indicated that brand knowledge for Pepsi had relatively minimal influence on behavioral response. However, brand knowledge of Coke positively influenced preference, and was associated with recruitment of the dorsolateral prefrontal cortex and the hippocampus, regions of the brain associated with affect and emotion. Although soft drink choice does not appear to have evolutionary significance, many such studies could indeed be mapped onto the four key Darwinian modules alluded to earlier and

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further discussed in the next sections. It seems that human product choice is a complex process, which calls on multiple capacities of the mind (Lee *et al.*, 2007). As humans are also subject to various cultural phenomena, human behavior is comprised of biological predispositions and cultural mediation. Of particular evolutionary importance would be a product's taste and safety (survival) along with how a product influences one's social status (mating). Accordingly, various advertising images and celebrity endorsers in part shape a consumer's brand impression. This suggests that social influences via brand image may be involved in the production of increased neural activity for an emotive response, in guiding behavioral choice for a soft drink brand. An example of the mind's adaptive responses manifested as choice for a contemporary beverage.

In the ensuing sections, we show how neuroimaging studies arising from a wide range of behavioral neuroscience areas could be mapped onto the four Darwinian meta-domains discussed earlier (survival, mating, kin selection, and reciprocity). In so doing, we hope to demonstrate that evolutionary theory can serve as a consilient framework for the neuromarketing discipline. This classification attempts to make sense of the biological architecture of the human mind when applied to consumer behavior, and accordingly it highlights the epistemological benefits of possessing an overarching framework to guide neuromarketing research. Some of the papers cited below do in fact specifically address the role of evolutionary biology in shaping the neural mechanisms that guide purposive behavior.

Survival

Survival can be construed as an individual's basic drive to stay alive through reproductive age and compete against others for basic resources such as food, water, shelter, and protection from predators. However, the role of the survival domain in contemporary human behavior may manifest itself in alternate forms. The survival drive can include the ability to make assessments of the surrounding environment for signs of danger. As such, the human mind should be prepared to quickly respond to unpleasant situations that have the potential to threaten one's survival. Stimuli that cause an individual to negatively respond emotionally should instigate the brain to be more prepared to mount a response. Perhaps, it is no surprise then that fMRI shows increased activation of emotion processing regions when subjects viewed visual stimuli that caused negative mood (Herwig *et al.*, 2007). As a tenuous future does not help ensure survival, an individual's ability to assess the environment through reactions of others is important to survival. Differential responses were observed in the amygdala to neutral and fearful faces, with faster responses for fearful and potentially dangerous faces (Reinders *et al.*, 2006). Additionally, theory of mind tasks and the Ultimatum Game were used to assess the neural basis for an individual's ability to interpret cues from social partners (Rilling *et al.*, 2004), which is an important adaptation to human social life. Theory of mind is the ability to be aware of the mental states of others, and presumably developed in human history along with evolutionary developments in the prefrontal cortex (Povinelli and Preuss, 1995).

Advertising often incorporates the use of celebrity endorsers, and to an evolutionist it is no surprise that this tactic should prove effective in light of the advantages inherent in emulating the behaviors and product choices of high-status individuals. Consumers are taught that by copying the endorser's decisions, they too can possess valuable resources including safe and nutritious foods. Feeding behavior, including the recognition of safe foods that contain essential dietary compounds as determined by evolved taste perception, has been essential to human survival (Boyd and Silk, 2006). Although one might expect sex differences in the foraging for food one should not expect sex differences in the consumption of food. It is fitting then that fMRI has shown explicit activation

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common in both male and female subjects during food craving (Pelchat *et al.*, 2004). Conversely, sex differences do exist when choosing groceries (a form of food foraging), with males showing greater activation in the right temporal cortices and females in the left posterior cortices (Braeutigam *et al.*, 2004). Individuals seem to possess an uncanny ability to recall which foods were previously enjoyable versus those that were harmful to self and/or others. Cerebral activation related to a perceived expression of disgust has related this ability to survival and sociality (Phillips *et al.*, 1997). Hence, in this case, an integral element of human memory appears to be linked to a domain-specific pursuit central to human survival.

Kin selection

Kin selection recognizes that individuals can augment their inclusive fitness by investing in and behaving altruistically toward their kin (Hamilton, 1964). We focus on kin selection and not the process of group selection, but it is worth noting that this remains a contentious issue amongst evolutionists (West *et al.*, 2007; Wilson, 2008). However, the resurgence of group selection as "multilevel selection theory" has provided rich data in support of the notion that selection not only acts at the individual level but also at the group level (Wilson and Sober, 1994; Borrello, 2005; Wilson and Wilson, 2007). Kin selection involves kin recognition processes and rests on the premise that organisms are able to differentiate kin from non-kin. Evolutionary theory predicts sex differences along some key processes associated with the kin module. For example, the neural correlates of maternal love are evolutionarily important and have been accordingly investigated (Bartels and Zeki, 2004). On a related note, adults display preferential reward-associated medial orbitofrontal cortex activation to images of unfamiliar infant faces over unfamiliar adult faces, suggesting an evolutionarily rooted positive response to infants (Kringelbach *et al.*, 2008). This is likely related to the general penchant that humans exhibit toward organisms possessing neotenous features (e.g., kittens, puppies, and human infants). For human males, kin recognition is particularly important as they solely face the evolutionary threat of parental uncertainty. Kin recognition has been demonstrated using fMRI to show that human males use facial resemblance to detect relatedness, with particular recruitment of the left superior, middle, and medial frontal gyri (Platek *et al.*, 2004). Males are expected to process their likelihood of genetic relatedness to children, and when a high likelihood is established they may subsequently demonstrate increased paternal investment (Platek *et al.*, 2005). Facial resemblance, in particular, is influential in decision-making for establishing trustworthiness and attractiveness (DeBruine, 2002; Neff and Sherman, 2002). Perceptions of the face, including perceived facial expressions, are also important in mediating social relationships. There has been increased interest in social brain sciences and the concept of self in negotiating social interactions (Heatherton *et al.*, 2004). Kin selection is ultimately an important aspect of sociality.

Reciprocal altruism

Reciprocal altruism explains altruistic behavior directed towards non-kin (Trivers, 1971). An organism behaves altruistically when providing some benefit to another at a cost to itself. This seemingly selfless behavior is useful, as the beneficiary of the altruistic act is typically expected to reciprocate in the future. This response of "Tit-for-Tat" is an evolutionarily stable strategy within the context of the Prisoner's Dilemma (Maynard Smith, 1982). Little has been done in neuromarketing thus far that falls within the purview of reciprocal altruism. The cross-cultural practice of gift giving is one area where reciprocal altruism may be influential within consumer behavior. The giving and receiving of gifts has been considered in consumer behavior research (*cf.* Clarke, 2006), albeit without the use of

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neuroimaging technology. However, understanding how the brain responds whilst engaging in the all-important gift giving ritual may provide useful information into the form and function of the computational systems inherent to the reciprocal altruism module. To explore the neural bases for cooperation and competition, fMRI results suggest that both actions call upon executive function through frontoparietal networks, but cooperation is processed by the brain as more socially rewarding (Decety *et al.*, 2004). Perceptions of altruism have been associated with the superior temporal cortex (Tankersley *et al.*, 2007). The application of social cognition to neuromarketing will help expand knowledge of the neural mechanisms for altruism. Neuroeconomic studies on cooperative games (Rilling *et al.*, 2002) and economic trust games (McCabe *et al.*, 2001) are examples of applying social cognition within the reciprocity module. Notions of in-group connectivity further mediate reciprocal altruism. Images of race are one cognitive proxy that people use in determining coalitional affiliations (Kurzban *et al.*, 2001). Therefore, viewing an ad containing an endorser of the same race as the viewer might also trigger regions of the brain associated with coalitional thinking. The neural underpinnings of social exchange are particularly relevant to understanding the reciprocity module in human sociality.

Mating

Mating is a complex process consisting of numerous evolved responses to help direct mate choice and the subsequent production of viable offspring. In choosing mates, humans seek compatible and attractive partners. That said evolutionary theory posits sex differences with regards to some aspects of mating, as the relative costs of mating loom much larger for women (see Saad and Gill, 2003 for a sequela of this universal sex difference in the context of the gift giving courtship ritual). Takahashi *et al.* (2006) used neuroimaging technology to show sex differences with regards to participants' reactions to sexual and emotional infidelity. Although both sexes showed recruitment of the visual cortex, men had greater activation in regions such as the amygdala and hypothalamus, which are associated with sexual and aggressive behaviors whereas women displayed greater activation in the posterior temporal sulcus, which are associated with intention and deception. Although jealousy is important in maintaining and protecting pair bonds (Buss, 2000), attraction is the first response in initiating a desired pair bond, a topic to which we turn to next.

Human attraction consists of highly evolved mechanisms designed to identify prospective suitors with superior genes with whom to have offspring (Buss, 2005). Attraction is based on several signals and cues including facial morphology, body shape, voice quality, and smell (Gaulin and McBurney, 2003; Buss, 2005). Studies have shown the significance of facial attractiveness in selecting potential mates, with particular activation of the orbitofrontal cortex when assessing facial attractiveness in others (Hamann, 2005; Ishai, 2007; Bray and O'Doherty, 2007; Winston *et al.*, 2007). Generally speaking, the perceptual processes associated with the viewing of beautiful faces recruit distinct parts of the human brain (Senior, 2003). In fact, one fMRI study found that when choosing a prospective dinner date based on exposure to opposite-sex faces, a unique network of cortical activation was obtained as compared to that triggered for unimportant decisions (Turk *et al.*, 2004). On a related note, both men and women display increased neural response to facial photographs of targets whose sex is congruent with one's self-reported sexual orientation (Kranz and Ishai, 2006). Although an individual might be physically attractive, that does not necessarily mean it is advisable to choose that particular individual for a mate. It may be best to choose a mate who also possesses adequate resources. Accordingly, mate preference is often determined through the results of intrasexual selection. For instance, the outcome of social competitions can establish social rank within a group. Social status can

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also be associated with survival (e.g., highest ranking individual eats first), but in the context of intrasexual competition it falls within the purview of mating. Using images of cars as a proxy for social value in wealth and dominance, sports cars - which rated socially more attractive than other vehicles - initiated reward activity in the ventral striatum, orbitofrontal cortex, anterior cingulate, and occipital regions of the male brain (Erk *et al.*, 2002). These regions are important to the reward circuitry in the brain, as they are influential in producing motivated responses and presumably regulating social interactions. Sports cars serve as a male-specific sexual signal, highlighting a man's social capital and financial stability, traits highly desired by women within the mating arena. Perhaps, it is an expected finding from an evolutionary perspective that males viewing pictures of attractive female faces also had preferential activation of the ventral striatum and reward circuitry (Aharon *et al.*, 2001; Erk *et al.*, 2002).

Love has evolved as an adaptation to guide mate choice as well as maintain biparental investment for the successful rearing of viable offspring (Fisher, 1994, 1998). Hence, in the human context, the mating module incorporates elements of lust (sex drive) and romantic love (emotive attraction) both of which are evolutionarily based. Evolutionary anthropologist Helen Fisher and her colleagues have conducted fMRI studies to identify regions of the brain associated with different aspects of love (see Fisher, 2004). Fisher argues that love is a set of three motivational brain systems (lust, attraction, and attachment), which have evolved as specific neural mechanisms to direct reproduction (Fisher, 1994, 1998, 2004; Fisher *et al.*, 2002). This is supported by other neuroimaging studies on the neural correlates of romantic love (Bartels and Zeki, 2000, 2004) and emotional systems associated with early stage romantic love (Aron *et al.*, 2005). Fisher also suggests that there may be overlap between the brain's visual cortex and regions associated with having sex with a loved one. This point elucidates the strong male-based consumption of the visually stimulating pornography industry, and largely sex-specific female facial ornamentation as a means of providing visually pleasing stimuli to male partners. Although both males and females exhibit increased arousal in the presence of opposites-sex nude photographs, the greatest visually evoked mean magnetic response occurred in male subjects (Costa *et al.*, 2003). On a related note, exposure to erotic films has yielded sex differences in brain activation, with men displaying greater activation in the hypothalamus, which is associated with lust (Karama *et al.*, 2002). Needless to say, the adult entertainment market, which according to the 2006 Annual Survey of the US Adult Entertainment Industry conducted by AVN Media Network had approximately $12.9 billion in retail sales in 2006 (AVN Media Network, 2007), is an area ripe for an evolutionary neuromarketing approach, as evolved brain systems are in large part driving the male-based consumption of pornography.

Conclusion

The neuromarketing paradigm is in its infancy and as such is replete with research opportunities. As might be expected, the paradigm is somewhat atheoretical and as such consists of largely disjointed one-shot empirical studies that typically amount to "fishing expeditions" for distinct neural activation patterns. A case in point is the set of 50 neuroimaging studies cited in the current paper, 33 of which are non-evolutionary with the remaining 17 being evolutionary based. The percentages of papers within each of these two sets that posited *a priori* hypotheses are 18.2 and 88.2 per cent, respectively, suggesting that evolutionary-inspired research is far more likely to generate research that is based on the scientific method and less so on haphazard data collection. Evolutionary theory provides a consilient framework for the neuromarketing paradigm. The human mind consists of highly evolved adaptations to guide purposive behavior. Contextualization of these adaptations should be at the forefront of any research examining

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the neural correlates of consumption. As advances in neuroimaging technology allow for an improved understanding of the architecture of the brain, a guiding framework remains exceptionally important. For instance, in using neuroimaging technology to study political advertisements and consumer affiliations, it is unlikely that one will uncover "conservative" or "liberal" centers in the brain. It is equally unlikely that one will uncover a distinct module in the brain responsible for the processing of celebrity endorsements. However, research can be guided in the pursuit of regions associated with decision-making and status recognition. This is *a priori* expected from a Darwinian perspective because the brain represents many highly evolved adaptations to guide purposive behavior. The brain will certainly show preferential activation in various consumer behavior tasks, but it is the role of the researcher to determine what such recruitment means with respect to evolved human biology. By providing examples of how evolutionary principles have already been applied to consumer behavior and cognitive neurosciences, future possibilities for neuromarketing have hopefully been crystallized. By organizing research into the evolutionarily relevant meta-domains, a roadmap for the future of evolutionary neuromarketing has been established.

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