Culture, Neurobiology, and Human Behavior: New Perspectives in Anthropology

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Abstract

Our primary goal in this article is to discuss the cross-talk between biological and cultural factors that become manifested in the individual brain development, neural wiring, neurochemical homeostasis, and behavior. We will show that behavioral propensities are the product of both cultural and biological factors and an understanding of these interactive processes can provide deep insights into why people behave the way they do. This interdisciplinary perspective is offered in an effort to generate dialog and empirical work among scholars interested in merging aspects of anthropology and neuroscience, and anticipates that biological and cultural anthropology converge. We discuss new theoretical developments, hypothesis-testing strategies, and cross-disciplinary methods of observation and data collection. We believe that the exigency of integrating anthropology and the neurosciences is indisputable and anthropology's role in an emerging interdisciplinary science of human behavior will be critical because its focus is, and has always been, on human biological and cultural systems.

Introduction

The cross-cultural study of human behavior has captured the fascination of anthropologists for well over 150 years. The beauty of modern anthropology is that it is built on an intellectual foundation that attempts to understand behavior from the perspective of both cultural and human biological systems. But, in spite of our discipline's long history of research, a deep understanding of the complexities associated with human behavior continues to challenge us. Clearly we have a long way to go before we can meet our objective of explicating differences and similarities in culture and human behavior. Over the last decades, neuroscience has become increasingly influential on how we explain behavior. In particular, methodological advancements in this field tempt us into seeing behavior as a linear extension of brain processes. It is, therefore, of paramount importance to point out that behavioral substrates unfold at several explanatory levels – from the molecular, neurobiological, to the information processing of neural network dynamics, to mental states, and eventually social cognition. It stands, thus, to reason that behavior itself can only be comprehensively understood from the highest hierarchical landings, viz. within the social and cultural contexts that shape human thought and action. It is towards this end that we argue for the integration of anthropological and neuroscience research and we predict that in coming decades our understanding of human behavior will enter into a new knowledge domain for the many reasons discussed below.

This article centers on several key questions that have developed out of our discussions and interdisciplinary perspectives. Particularly important are neurobiological and neurochemical components associated with human behavior and how environmental factors might influence these biological processes. There is ample evidence that biological processes and thus human behavior can be modulated by the environment, and the genome might primarily serve as a toolkit to provide templates for expression. In this paper, we specifically explore the following questions: What are the characteristics of various neural responses and behavior reactions under particular social interactions and with respect to cultural differences? Can such neuroscientific data inform anthropology? How can cultural context influence one's behavioral and neural propensities for particular behaviors, and can we measure these behavioral propensities using advanced neural imaging and neurochemical methods? And can such an interdisciplinary dialogue generate synergies that allow addressing new research questions?

Regardless of one's theoretical perspective whether it is cultural ecology, gender studies, evolutionary psychology, applied anthropology among so many more, the approach discussed here is, in our opinion, relevant to all perspectives. It is not our purpose to advocate one theoretical framework over another because we strongly believe that there is great value in promoting diversity of opinions. We will suggest, however, that recent research in the neurosciences are universally relevant to all anthropological theory and that there is great potential for more complete understanding of behavioral patterns if we attempt to bridge the neurosciences to our anthropological inquiries. Indeed, the historical foundation of studies in human behavior, neurological processes and culture began well over 100 years ago (Wundt 1904) and these issues remain relevant to research scientists today. But, it is also important to understand the limitations associated with neurosciences and the potential for over-interpretation before moving forward. The idea of bridging the neurosciences and social research is by no means new; many have advocated the importance for cross-disciplinary approaches and anthropology's involvement in such integrative studies has shown promise as well as potential problems (Boden 2006; Deacon 1997; 2012; Gardner 1987; Gray 2012; Schilhab, Stjernfelt and Deacon 2012).

Paleoanthropology and the Human Brain

The evolution of the human brain is a subject that has generated a great deal of inquisitiveness among anthropologists, neuroscientists and evolutionary biologists and it is where we begin this conversation. It is clear that our neural structures are the product of our mammalian evolution that in turn evolved from brain structures of our mammal-like (synapsid) reptilian ancestors. Neuroanatomical research demonstrates conclusively that human brain structures are built on top of our earlier mammalian (Eccles 1989; Striedter 2005; Wedeen et al. 2012) and pre-mammalian structures. In fact, the conservative nature of major brain divisions across living vertebrates suggests that much of the cerebral organization must already have occurred with the origin of vertebrates or shortly thereafter (Northcutt 2002). For example, reptiles, birds, and mammals all possess forebrains with similar major subdivisions, including an external cortex and subcortical nuclear structures (Kaas 2013). But although we share many neuroanatomical structures with other vertebrates and in particular with other mammals, the intellectual capacity of humans, by any measure, reveals that our brain is truly exceptional in mammalian evolution (Churchland 2011; Deacon 1997; Edelman 1987; Gazzaniga 2008; Heyes and Huber 2000; Kandel and Squire 2000; Koch 2004). The unique evolution of the human brain is particularly evident by the increase in complexity during our hominid evolution. Since the emergence of Australopithecus over 3.5 million years ago, brain volume has not only tripled in size, but most importantly has become structurally more complex

(Geary 2005; Jerison 1973; Striedter 2005). There are two major jumps in brain size and encephalization (Jerison 1973) that occur with Homo erectus and then again with the evolution of fully modern anatomical humans that are most likely accompanied by an increase in anatomical and functional complexity. The evolution of the human brain that has been fueled by a dual-inheritance mechanism (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Richerson and Boyd 2005) is probably overbalanced toward an environmental impact in humans compared to other mammals due to the extended period of human brain maturation outside the womb. In fact, brain size and complexity (2/3 growth in the first five years of life) is paralleled by a delay in maturation times. This is due to a stepwise and hierarchical myelination proceeding from diencephalic structures such as the thalamus and hindbrain structures such as the cerebellum and pons to primary cortical sensory areas, to higher cortical areas of the temporal, parietal, and frontal lobes as well as due to distinctly orchestrated regional sequences of sculpting grey-matter densities (Flechsig 1901; Deoni et al. 2011; Toga, Thompson, and Sowell 2006) indicating an evolutionary continuance. Paleoanthropological data clearly support this assumption of prolonged human maturation (Striedter 2005:319).

In addition to the environmental factors, genetic factors have most likely also contributed to the expansion of the human neocortex. Recent research suggests that the SRGAP2 gene underwent several human-specific gene duplications about 3.4, 2.4, and 1 million years ago (Dennis et al. 2012). The SRGAP2 gene encodes for a protein that acts as a regulator of neuronal migration and differentiation. The gene duplication that occurred 2.4 million years ago seems to have given rise to an incomplete, but functional, protein that probably antagonizes the ancestral function of SRGAP2. This *de novo* gene function can interfere with filopodia formation allowing a faster migration of neurons and being thus critical for human neocortical expansion (Guerrier et al. 2009; Guo and Bao 2010). Consequently, the SRGAP2 genes by altering the developmental trajectory of neuronal morphogenesis can then – together with other genes that cause heterochrony in the neocortical surface (Lui et al. 2011; Rakic 2009) – induce neoteny (Charrier et al. 2012) and thus contribute to the cortex expansion in *Homo Neanderthalensis* and *Homo sapiens*, but not in Chimpanzee, Orangutan and Gorilla (Sudmant et al., 2010). Noteworthy, the incomplete gene duplication occurred in the time corresponding to the transition from Australopithecus to Homo.

To comply with the increase in brain size, the human skull must allow for certain flexibility. Intriguingly, archaic human fossils dating to about 2.5 million years ago show evidence that morphologically the human skull developed cranial sutures, gaps in the skull that allow the head to decompress during childbirth (Falk 2012). If we are looking for the ultimate cause for human cognitive abilities and related advancements in human cultural evolution, we may have discovered a strong set of causal factors here. In all likelihood future research will discover multiple genetic mutations that set humans onto their evolutionary trajectory and although some were more important than others, the collective effects were extraordinary. We should recognize, however, that genetic inheritance does not only refer to the vertical genome transfer from parent to offspring, but also to epigenetic inheritance that allow acquired traits that depend on the organism's environment to be passed on to the next generation, an important issue for both biological and cultural evolutionary theory (see Jablonka and Lamb 2010). In addition, other processes such as niche construction (Odling-Smee, Laland, and Feldman 2003; Laland et al. 2015) and the Baldwin effect (Deacon 1997) have probably played a major role in the evolution of cognitive traits. In fact, certain emergent cognitive products of cultural evolution, such as language, can be much more convincingly explained by the multilevel co-evolutionary (i.e., biological and cultural) theories, in particular by the Baldwin effect (Deacon 1997). In this view, processes of progressive replacement facilitate the transformation of acquired habits or physiological responses (learned or environmentally stimulated) into instinctual, ineluctably entrenched mechanisms (developmental genetic production).

From a neuroanatomical perspective, the pre-frontal cortex is most pertinent to our discussions below. It is the region of the brain that is a centerpiece in networks involved in planning, foresight, decision-making, and the regulation of various social emotions including empathy, prosocial behavior, desire to cooperate, love, guilt, anger, aggression, and the desire to punish (Atran et al. 2009; Cacioppo and Berntson 2002; De Waal 2009; LeDoux 1996; Pfaff 2007). During hominid evolution, natural and social selection pressures undoubtedly selected for and co-evolved various genetic traits, neural processes, behavioral propensities, and sociocognitive competencies. Humanity's greatest advantage "is our brain and the ability to communicate, remember, plan, and work together" (Cacioppo and Berntson 2002:4) and the emergence of the social brain was the catapult behind our evolutionary success (Boyd and Richerson 1985; Cavalli-Sforza1981; Deacon 1997; Dunbar 2002; Frith and Frith 2010; Geary 2005; Richerson and Boyd 2005; Tomasello 1999).

Contemporary Neurosciences

Many natural and social scientists have proclaimed that the next 100 years will be the *Century of the Brain* (Churchland 2011; Damasio 2010; Ramachandran 2011). And in fact, we have witnessed impressive achievements in understanding the intricacies of the human brain and behavior over the last decades. Researchers in neuroscience and cognitive fields have demonstrated that an observed human behavior, in any context, is the last event in a long chain of biological and cultural interactions (Bickle 2009; Changeux 2004; Churchland 2011; Damasio 2010; Kandel, Schwartz, and Jessell 2000; Kandel and Squire 2000; Koch 2004; Ramachandran 2011). The brain´s anatomy is subject to neuroplasticity and depends on experience giving rise to cognitive properties that may be highly adaptive (e.g., prosocial child rearing practices) or non-adaptive (e.g., addictive behavior) dependent upon the specific contextual circumstances (Chalupa et al. 2011). Neuroplasticity, the nervous system´s capacity to reorganize itself throughout life, provides both, contextual (cultural) and historically dependent (previous experience) mechanisms to shape the neural system (Doidge 2007). This idea is fundamental to cultural psychology, a developing field strongly influenced by anthropological research and cross-cultural studies (Han and Poppel 2011; Kitayama and Bowman 2011; Mesquita, Feldman-Barrett, and Smith 2010). Thus, the idea that personality and behavior propensities are innate or hard-wired at birth is clearly disputed by recent neuroscientific research and studies in cultural psychology. Integrating the concept of neuroplasticity into this interdisciplinary field is of paramount importance–as Martínez Mateo at al. (2012) have shown, many recent cultural neuroscientific studies simplify culture as an inflexible set of traits and specificities thus falling prey to a hidden evaluative nature.

Frequently, advancements and a deeper understanding of natural phenomena are attributable to ingenuity in the development of novel technologies. Neurosciences have made significant advancements through the use of high-resolution imaging technologies such as Functional Magnetic Resonance Imaging (fMRI) and Positron Emission Tomography (PET) (Cabeza and Kingstone 2008; Uludag et al. 2015). Neural processes can be visualized and measured with relatively great spatial accuracy[1], providing a basis for decoding how the brain functions, creates memory, and correlates with emotions (Gazzaniga 2008; Kandel, Schwartz, and Jessell 2000; Kandel and Squire 2000). In the laboratory, scientists can create controlled experimental conditions and can observe behavioral responses and the activity of the respective neural correlates simultaneously. Using these technologies, cognitive research and psychological experimental studies have considerably advanced our understanding of neural processes and specific brain regions associated with various human behaviors. It is, however, acknowledged that brain scans alone will by no means reveal all the neural processes associated with human behavior and social processing. Noteworthy, using brain stimulation techniques (such as transcranial direct-current stimulation (tDCS) or transcranial magnetic stimulation (TMS)) that allow a temporary and non-invasive interference in brain activity, might shed light on causal effects that go beyond simple correlations between brain activation and mental function.

However, in order to identify causes underlying neuroplasticity one must also rely on additional lines of research, such as developmental biology, theoretical neurophysics and computational modeling of neural processes. Together these fields will certainly provide a significant base for theory building and hypothesis generation for both the neurosciences and cultural studies (Churchland and Sejnowski 1994; Furman and Gallo 2000; Stephanova and Kolev 2013). Here we understand neuroplasticity to mean that it is "a fundamental property of neurons and the nervous system at all levels (e.g., molecular, cellular, and neuronal networks) across all species. As such, it could be said that it is the basis for all of the neurosciences insofar as almost any aspect of the study of the nervous system involves changing properties of neural elements, either during development, due to natural or artificial alteration in input, or in cases of neural trauma" (Shaw and McEachern 2001:3). To understanding the complexities of memory formation and behavior, important research comes from insights into developmental neuronal synaptic networks. This research agenda allows neuroscientists to identify more precisely brain regions that are associated with social behaviors, emotions, psychological propensities and the like. It is, however, important to point out that a localizationist view of brain organization is certainly a historically-biased concept (Star 1989) and too simplistic a

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[1] fMRI measures the blood flow in a region of neurons. Given the average density of neurons and synapses in the cerebral cortex of about 12 x 10^4 and 9 x 10^8 per mm^3, respectively, each voxel (the pixel of fMRI screens), captures blood flow in the region of approximately 80,000 neurons and more than 4 million synapses averaged over one second in this region. Thus, it is clear that the fMRI signal can just serve as an index of the overall activity of many neurons and processes (Raz 2012).

model of brain architecture. There is increasingly clear evidence in favor of a more distributed cognitive processing of highly precise oscillatory rhythms that are distributed over large areas of the cortex (Gray et al. 1989). The synchronization of such neural networks is based on the gradual process of ontogenetic development, from embryogenesis to infancy and late adolescence, and seems to represent the most fundamental driving factor of the phenotypic outcome of brain anatomy (Karmiloff-Smith 2006). Thus, various developmental input, proprioceptive stimuli, and natural as well as social experience lead to temporally more precise and spatially more focused synchronization patterns of neuronal circuits (Uhlhaas and Singer 2011) causing increasingly integrated and connected information processes throughout ontogeny. While early embryonic brain development is probably guided by intrinsic, genetic factors and maternal factors, phenotypic development is largely directed by various extrinsic factors causing significant blending of brain structures in humans as the brain matures[2]. From this it seems clear that neuronal networks are not inheritable but are acquired only by experiences.

The issue that we find most interesting with regard to human behavior is related to how these maturing structures are influenced by experience and precisely how neural networks become wired by experience. Can we map corresponding temporal changes in neural structures based upon phenotypic experiences such as those related to cultural reinforcements that influence the developing human brain? Furthermore, understanding the features of brain structures in humans relative to those of our close primate relatives could reveal the evolutionary history that sets humans apart. We are far from understanding the biological and psychological influences that build the human brain, but drawing from neuroscientific research will move our disciplines closer to our ultimate goal. We believe that evolutionary anthropology and cross-cultural studies that bridge with the neurosciences will be critical lines of research to the investigation of neuroplasticity. And the influence of cultural context and phenotypic histories may well form the core for emerging studies of neuroplasticity (Larson 2006, 2010).

Theoretical arguments and empirical research suggest that we should view the human brain and development of mind from a *Neural Darwinism* conceptual perspective (Edelman 1987). This concept takes the position that genes and environmental factors interact as the brain develops in humans. This view has been summarized by Joseph LeDoux in his book entitled *Synaptic Self*:

> Selection operates on preexisting (synaptic) connections set up by genes (which makes proteins that help guide axons to the right areas) working in concert with nongenetic factors (chemical from the mother, for example). But genes and the chemical environment are not wholly responsible for establishing the initial connections. Selection also assumes that there is a good deal of randomness involved—terminals and dendrites that happen to be in the same vicinity take the opportunity to form synaptic connections, independent of overall guidance plan

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[2] External factors include also epigenetic information. In rhesus monkeys one-fifth of the entire genome is differentially methylated in brain cells compared to blood cells. This large epigenetic difference seems to be a function of early social experience (Suomi 2009). There is good reason to assume that the human genome undergoes epigenetic changes to a similar or greater extent due to extensive gene–environment interactions.

> specified by genes. As a result, in spite of the general genetically programmed plan, the preexisting connections upon which selection ultimately operates also have a unique, individualistic nature, from which experience then does the selecting. Because each person's experiences are different, different patterns of connectivity are selected. Genes thus dictate that we will have a human kind of brain with roughly the same kind of circuits, but random individual differences will exist, and the connectivity of circuits, selected by synaptic activity, will shape the individual's brain (LeDoux 2002:74; also see Edelman 1987).

The evolution of individual behavioral propensities, collective behavior and cultural processes are all interconnected, but the temporal and spatial dimensions by which these interacting variables operate are dramatically different. Ultimately, the approach we offer here seeks to explore how cultural and psychobiological processes could promote stability or change in these expressions. Especially interesting are topics related to language, learning and memory, and the potential Baldwin effect-like phenomena, which might have important implications on neuroplasticity, issues that have rarely been examined in the extant literature (as exceptions see Deacon 2003a; 2003b).

Neural Correlates of Social Cognition and Neuroplasticity

Understanding memory and its neural constituents are fundamental to the exploration of how individuals form concepts of cultural norms, expectations of social interactions both positive and negative, predictions of social outcomes and related rewards and punishments. The ability to use our memories to predict events is important to all individuals in all cultures because humans must be equipped to navigate through extraordinarily complex social, natural and technological landscapes using phenotypic memories that are historically encoded by experience (Bar 2011).

Social learning in humans has provided a mechanism for cultural evolution that is probably rooted in an evolved capacity for theory of mind (Tomasello 1999). Although we are far from understanding the underlying neural structure and mechanisms that allow us to detect the state of mind in others, innovative work using neuroimaging studies of social emotions may contribute to elucidate this issue (Immordino-Yang et al. 2009). For example, the experience of compassion for social pain and admiration for virtue correlates with a strong activity of the posteromedial cortices (PMC–more precisely neuronal assemblies of precuneus, posterior cingulate cortex, and retrosplenial region). Interestingly, the PMC, especially the inferior/posterior sections have been reported to be involved in neural processes associated with introspection and self-awareness (Gusnard et al. 2001; others); thus, seemingly the same neuronal substrate that is involved in self-awareness may have been adopted for making inferences about others and their mental states of mind. Noteworthy, there is evidence for cross-cultural differences in the development of theory of mind (Lillard 1998) and this difference might be related to childhood exposure to collectivist culture versus individualistic culture (Shahaeian 2011). These cultural differences constitute the adult concepts of self and others by either focusing more on self-relevant or group-relevant information (Masuda and Nisbett 2001).

However, several classical neuroimaging studies investigating social cognition do not take anthropological aspects into account and are thus of limited value for cross-cultural interpretations. It would be highly interesting whether activity of neural correlates of social cognition differ in extent, exact location, or intensity depending on the ethnicity and cultural upbringing (collectivist versus individualist) of (age-matched) subjects.

Interdisciplinary studies combining psychological experiments, social behavior studies, and neuroimaging research show that certain neural correlates (e.g., the posterior cingulate cortex, retrosplenial regions, temporoparietal junction (TPJ), and the precuneus) are highly engaged under controlled social stimuli. But "the processing of social emotions is organized less around the kind of emotional response, be it compassionate or admiring, than around the contents and context of the situation" (Immordino-Yang et al. 2009:8024). Yet both, content and context can be subject to bias in cultural learning (Henrich and McElreath 2007) thereby strongly suggesting that neural responses associated with empathy, compassion, and admiration can be modulated by culture and social relations. In fact, in an fMRI comparison study of African-Americans and Caucasian-Americans, it was demonstrated that neural correlates of empathy and altruistic motivation for in-group members were neurally distinct from correlates of empathy for non-in-group members (Mathur et al. 2010). Similarly, the measured neural activity triggered by the observation of suffering expressed by in-group relative to out-group members indicates greater acquired empathy for one's in-group. In addition, other scholars (also see Singer et al. 2006; Singer and Fehr 2005) found that compassion for physical pain was much stronger and was more immediate than compassion for social pain, the latter being often mediated by culture and the individual's contextual assessment of the situation. Nonetheless both, compassion for physical as well as social pain are associated with strong neural and biophysiological signals (heart rate, respiration, and blood oxygen levels) highlighting the usefulness of neuroimaging techniques to pick-up subtle anatomical and functional differences in the brain that correlate with responses to highly related, but slightly different social stimuli.

Thus, similar to the case of acquired empathy for certain in-group versus out-group members, we believe that interdisciplinary research of cultural neuroscience can ultimately shed light on timely and pressing questions such as how will an individual's brain neurologically adjust when immigrating to a new and unfamiliar society? Can we detect neural differences between an indigenous population and arriving immigrants with respect to social cognition (empathy, compassion and admiration, etc.)? Will these neurological patterns change as immigrants become acculturated over time?

Social neuroscientists are aware of strong interactive systems that operate between the orbital frontal cortex and amygdala. The amygdala plays an important role in the processing of emotional and social cues as well as in the formation and storage of memories associated with emotional events and is thus highly active during social interactions involving an array of sensory inputs including "visual information from faces and facial expression, gaze direction, body posture and movements, as well as auditory information from specific vocal sounds and intonations" (Payne and Bachevalier 2009:39). In addition, the amygdala is crucial for acquisition, storage, and expression of classical fear conditioning (Kubota, Banaji, and Phelps 2012), and most likely also involved in evaluative biases toward out-group members. For example, European-American adults show heightened amygdala activity, even in the absence of conscious awareness, in response to African-American relative to European-American faces (Cunningham et al. 2004) thereby unintentionally and implicitly expressing racial[3] attitudes (Kubota, Banaji, and Phelps 2012). Interestingly, researchers have found that self-reporting of cultural constructs of racial bias is often in conflict with studies that are designed to measure subconscious levels of race bias. The concept of race and in-group and out-group cognitive patterns is complex and dependent on several overlapping brain regions and neural systems (Kubota, Banaji, and Phelps 2012). Firstly, subjects engage both conscious as well as subconscious mechanisms when exposed to facial recognition experiments involving ego-similar and ego-dissimilar facial patterns (black-white, male-female, young-old, etc.). Secondly, individuals make conscious decisions about "racial attitudes" that are, in part, controlled by culture context, phenotypic history, and social conditioning thereby engaging the anterior cingulate cortex and the dorsolateral prefrontal cortex. Thirdly, as mentioned above, the concomitant activation of the amygdala is critical to maintaining and charging emotional states that affect decision-making processes associated with behavioral options (Phelps and LeDoux 2005; Phelps 2006) and thus fuelling evaluative biases. Finally, researchers have also found that neuroendocrine systems are highly activated by in-group and out-group stimuli. For example oxytocin levels vary dependent on race preference or similarity, as do testosterone levels (Bos, Terburg, and van Honk 2010; McCall and Singer 2012).

In addition, there is strong interconnectivity between the amygdala and hippocampal formation, which is critical to modulation of stored memory of previous experiences (Costa-Mattioli et al. 2005). Infancy is a critical period during which these neural systems develop in both humans and other primates. In effect, social signals are detected and stored from the first days of life and the orbital frontal cortex, amygdala and the hippocampal formation are important to the maturation of an infant's response system, in which normal development is highly dependent on the mother's nurturing and interaction behavior (De Haan and Gunnar 2009). fMRI studies have demonstrated that an increased automatic, subconscious activity of the amygdala in response to African-American faces does not reflect an innate process, but rather learned cultural knowledge that emerges during adolescence (Telzer et al. 2013). Importantly, selectively increased amygdala activity to out-group members can be reduced by perceptual familiarity (Cloutier, Li, and Correll 2014) providing potentially important implications for prejudice reduction strategies that rely on contact or individuation-based familiarity. In our view, anthropology in conjunction with social and cognitive neurosciences will play a major role in devising scientific investigations of the neural, behavioral, and cultural components of prejudice. It is important to recognize, however, that generalizations about propensities for phenotypic prejudice, gender bias, and behavioral tendencies for membership in conservative or liberal parties has captured the attention of the modern media. The science on which these grandiose reports are based is often the product of poor data collection strategies (small sample size and small effect sizes), over-explanation of neuroimaging results, inadequate statistical analyses (sample error and differences between replicate and independent data sets), and inclination to publish results that are new and counter to traditional perspectives (Carpenter 2012). Indeed,

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[3] The terms "race" and "race bias" are used in much of the contemporary literature dealing with this subject. Anthropologists have rightfully rejected the traditional concept of "race" and the cited authors reject the traditional term as well; they clearly understand that "race" is a cultural construct.

several studies have been subjected to reevaluation and scholars could not replicate the results.

The bottom line is that the integrity of studies in the social and cognitive neurosciences will be evaluated on how well research stands up to the scrutiny of scientific inquiry and not speculative or "common sense" interpretations (P. Churchland 2007; Hull 1988).

Formalized Social Cognition

Experimental games designed to emulate real world experiences of cooperation and fair play evidence neural processes associated with cultural context, prosocial behavior, and conformist propensities (Camerer 2009; Fehr 2009; Gazzaniga 2009; Glimcher et al. 2009; Singer and Fehr 2005). Players who experience mutually supporting and cooperative responses from other players show strong evidence of both neural (excitement in the dorsal striatum) and neurochemical rewards (Creamer 2009; Delgado et al. 2003; Fehr 2009; Knutson et al. 2009; Kosfeld *et al.* 2005; Sanfey and Dorris 2009). Particularly important is the neuropeptide oxytocin, which is strongly related to human trusting and trustworthy behavior (Churchland 2011; Zak 2008). In a revealing experiment by Kosfeld and colleagues, a neuropharmacological nasal spray of oxytocin[4] was administered to players just before they engaged in trust games that made the players much more willing to trust other players (Glimcher et al. 2009; Kosfeld et al. 2005). Other controlled psychological experiments demonstrate that the neurotransmitter dopamine is strongly tied to prosocial and cooperative interactions among individuals (Knafo, Israel, and Ebstein 2011; Skuse and Gallagher 2011; Wise 2004;). In fact, stimuli associated with cooperative or prosocial interactions increased the anatomical production of both dopamine and oxytocin in human subjects (Churchland 2011; De Dreu et. al. 2010; Donalson and Young 2008; Zak 2008). In recent years numerous researchers have replicated these experimental results, unequivocally demonstrating that dopamine and oxytocin induce both cooperative and prosocial behaviors (Knafo, Israel, and Ebstein 2011).

On the other hand, researchers have found that reaction to cheaters and non-cooperative players also induces strong psychological and neural reactions among subjects involved in fairness games (Kosfeld *et al.* 2005; Fehr *et al.* 2005; Fehr 2009; among others). Interestingly, de Quervain and co-authors (2004) found humans have a detectable propensity to seek retribution when another individual cheats them. The emotional dynamic (schadenfreude) felt by their human subjects was measured using positron emission tomography (PET) at a time in the game when an opponent would choose not to reciprocate and/or to defect in the game. Haruno and Frith have generated very compelling evidence from neuroimaging research and game experiments showing that "automatic emotional processing in the amygdala lies at the core of prosocial value orientation" and that humans have a strong intuitive aversion to inequitable and unfair behavior (Haruno and Frith 2010:160).

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[4] It should, however, be noted that evidence is still missing whether oxytocin, a relatively lipophilic peptide molecule, can actually cross the blood-brain barriere. Thus, most studies using nasal oxytocin sprays only provide indirect evidence of oxytocin effects on the brain as cerebrospinal fluids are usually not measured.

Recent psychological game experiments conducted by the *Preferences Network*, an interdisciplinary cohort of scholars that share an interest in cross-cultural testing of "self-regarding" and "outcome oriented" hypotheses, has generated significant insights related to social cooperation (Gintis et al. 2005; Henrich et al. 2004). The results of their highly innovative cross-cultural research using ultimatum, public goods, and dictator games demonstrate conclusively that among the 15 different small scale societies of foragers, horticulturalists, nomadic herders and full-time agriculturalists, no society evidences the selfishness pattern; all societies show a commitment to fairness and unselfish behavior. There is, however, high inter- and intra-cultural variability in perspectives of fairness, ranging from 30% to 70% sharing contribution in the ultimatum game. These results have not been further investigated by neuroimaging studies, and the authors argue here that this kind of ethnographic research would be greatly enhanced using neuroscientific methods designed to explore similarities and differences in neuroanatomy and neurochemistry of cross-cultural populations. For example, it would be interesting to find out whether a difference in the activity of neuronal correlates (e.g., the PMC that is usually activated during tasks of self-awareness/making inferences about others′ mental states) can be found at different stages of the game[5], e.g., before making an offer, when receiving an "unfair" offer, or when experiencing schadenfreude. And it would be particularly informative whether such differences correlate with the subjects′ cultural background. E.g., do people from a cultural background of collectivism engage more in perspective-taking (have higher PMC activity) before making an offer? Are there cultural differences in who is more/less forgiving to cheaters, e.g. does the punishment of defectors result in a higher PMC activity in people from collectivist or individualist cultures? Moreover it would be particularly revealing to investigate the activity of the subjects′ amygdala when making "unfair" offers. Do people from a cultural background of strong individualism display a lower activity of the amydgala indicating increased "self-righteousness." Or do people from different ethnicities have comparable amygdala activity, but display differences in the activity of the dorsolateral prefrontal cortex suggesting similar fear response, but acquired impulse control of the subconscious fear reaction?

Such complementary approaches are exactly the kind of research that we envision to bridge anthropology, neurosciences, and other disciplines. Our position is grounded in the theoretical assumption that the human organism is both a biological and cultural entity and it is precisely these interactions that should be examined if we are to form a more complete understanding of human behavior.

Our objective here is to present a research framework that includes evolutionary theory and techniques grounded in the neurosciences that will hopefully complement existing theoretical work and mathematical modeling of human behavior, especially prosocial interactions (Bowles 2004; Bowles and Gintis 2011; Gintis 2000, 2009; Hauert et al. 2007; Hauert, Traulsen, and De Silva nee Brandt 2008; Henrich 2004; Nowak 2011, 2012; Ostrom and Walker 2003; Richerson and Boyd 2000, 2005; among others).

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[5] However, one needs to take the hemodynamic response of fMRI studies into account that is about 4–6 seconds. This requires a precise temporal planning of the multi-paradigm set-up, something that is done for many other studies in which reaction time of subjects is an important parameter that must be controlled for.

Cultural Neurosciences and Neuroanthropology

The goal of *Cultural Neuroscience* is to examine human cognition and "how the underlying neural mechanisms are affected by culture and identity – a frame in which human cognition develops and evolves" (Han and Poppel 2011:v). The concept of neuroplasticity puts forward that the human brain is constantly being constructed by experience and the states of social interaction, emotional development, self-reflection/introspection and behavior during ontogeny (Chalupa 2011). At the same time these cognitive mechanisms provide a substrate for creating our own social and cultural environment that function as a learning niche for the next generation (Sterelny 2003) thereby facilitating an upwardly spiral effect of cognitive traits in response to social stimuli.

Neurophilosophers suggest that the quest for scientific predictability is our end goal, using statistical analyses of correlations and interactions among variables including neural, environmental and behavioral factors. If we can predict behaviors and actions, then in effect we have achieved an understanding of the process. But sorting out cause and effect relationships from non-associated correlations is a formidable challenge for interdisciplinary scholars. It is an extraordinarily difficult undertaking that begins at the molecular level and ends at the human population level. The implication is that each level of interaction has relational effects on variables that are higher and lower. Many scholars recognize this dimensional conundrum and seek to discover hierarchical relationships giving us cause to believe that the future holds great promise for understanding the complexity of human behavior. Cultural neuroscience, in our view, will play a vital role toward this end and already has by providing both a theoretical framework and empirical basis for understanding variability in human social behavior (Chiao 2009; Chiao and Bebko 2011; Chiao and Blizinsky 2010).

Neuroanthropology, although a relatively recent development in anthropology, is grounded in many of the principles discussed in this article. It is a research domain that derives from Psychological Anthropology, a subdiscipline that has a long history in the field. Scholars that have focused on the neurosciences realize the value of investigating the relationships between the biological and cultural components of human behavior. Recently, Lende and Downey (2012) have presented pioneering efforts on how to apply anthropological theory and methods to real problems involving the human mind with which contemporary society is confronted, such as PTSD among American veterans, addiction, coping with cancer, and other examples. It is expected that as this approach matures its contributions to the study of human behavior will be significant.

CONCLUSIONS

> *...imagination was needed to realize fully that not the behavior of bodies, but behavior of something between them, that is, the field, may be essential for ordering and understanding events.*
>
> Albert Einstein and Leopold Infeld 1938:295

At the beginning of this article we posed several questions related to neural evolution, cognitive development, social interaction, and culture context. We then explored a wide range literature relevant to our topic areas allowing us to draw several conclusions. First, we hope we have demonstrated that the human brain has universal scaffolding, which is the product of humanity's long-term evolution that is shaped by particular cultural and environmental experiences. This position clearly places research emphases on neuroplasticity, cultural context, social cognition, and phenotypic experiences. Understanding the interplay among all these variables will be a monumental task; however, the theoretical and operational research tasks that we propose here will allow us the opportunity to generate the right kinds of questions and collect relevant data sets, integral to measurable and replicable empirical results required in modern science. We expect that advanced mathematical modeling and theory development will propel cultural studies forward in a manner that will explicate human behavior holistically. Indeed, examples of this type of research are already advancing our understanding of human behavior (Gintis 2000; Gintis 2009; Nowak 2011; Odling-Smee et al. 2003; Richards and Boyd 2005). The challenge now is to integrate the neurosciences making studies of human behavior yet more robust.

Second, there is a clear need to integrate research related to neurodevelopment and neuroplasticity studies in anthropology. Particularly the first few years of life as well as adolescence are critical periods when an individual are most susceptible to enculturation, concepts of normative behavior, and rules of conspecifics interactions, value systems associated with family and community members, etc. (Uhlhaas and Singer 2011). We expect that the study of cultural reinforcement, neuroplasticity, and anthropology could be extremely informative, especially in regard to cross-cultural child rearing practices, prosocial development, learning and formation of memory structures, and language and cognitive development. Research associated with early intervention of pre-school education, neurodevelopment and dietary programs demonstrate incontrovertibly that much could be gained by proactive anthropologists and neuroscientists being advocates in their communities (Reynolds 2011:360). What is not well understood is how human neurobiology and cultural experience produce negative or positive outcomes, a research arena that cries out for immediate attention from cultural and applied anthropologists. To this end, studies that track individuals over an extended period of time (infant to elderly) who are subject to neuroimaging techniques and recordation of life experiences would be most instructive. Interestingly, we may be able to neuroanatomically map and measure differences in the degree of emotions, feelings, and behavioral expression associated with specific cultural dimensions.

Third, we believe that progress in cross-cultural studies in anthropology and neurosciences will benefit from the use of advanced instrumentation, offering scholars unprecedented opportunities to observe human subjects at various levels of investigation when individuals are subject to laboratory and field experiments, like fairness, ultimatum, public good, and dictator games. Particularly relevant will be the efforts to employ neuroimaging methods to try and isolate neural pathways and anatomical brain areas that may be associated with specific cross-cultural responses in human subjects. Significant progress has been made in conducting experiments during which multiple subjects are undergoing simultaneous neuroimaging (Montague et al. 2002). Indeed, psychological experiments involving group neuroimaging coupled with neuroendocrine systems research of multiple subjects may well revolutionize the study of neurobiology and behavior. Though, comparability of cross-cultural data sets will require an understanding of cultural context, normative belief systems, and the nature of how individuals express covert and overt behaviors. This type of research will require interdisciplinary groups and carefully designed experiments and data collection. Concerted efforts must be made to explicitly define concepts such as neuroplasticity, culture, groups, behaviors (prosocial, empathy, prejudice, etc.), and propensities.

An understanding of neuroplasticity, behavioral flexibility and context are all key factors to any explanations of human behavior, a position that is strongly consistent with the principles of the "The Extended Synthesis" in evolutionary developmental biology (Pigliucci and Muller 2010). Would Boas, Kroeber, Mead, Benedict, and White approve of this merging of anthropology and the neurosciences? We think so, and in particular, they would embrace the idea that the human mind is shaped by experience and that modern science can provide us with tools unimaginable to these pioneers of anthropology. What we advocate here is a logical progression in cross-cultural research and human behavior to explore relationships among neural processes, synaptic maturation, brain development, neural wiring, neurochemical homeostasis, and behavior in response to cultural influences. While cultural studies, independent of neuroscience, will of course continue to be the focus of anthropology, new students will hopefully be made aware of the value of interdisciplinary collaboration and cross-fertilization that is unique, inexplicable from a single discipline's perspective. This will establish something new and most importantly relevant to modern society and a new generation of scholars.

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