THE NEUROEVOLUTIONARY ROOTS OF XENOPHOBIA

By Raisa A. Rahim

Abstract:

Xenophobic tendencies can be observed throughout the animal kingdom, making it likely that this anti-social bias has been evolutionarily inherited. Converging evidence from comparative behavioral, prophylactic behavioral, lesion, neuropsychological, and functional neuroimaging studies elucidate the biological and neurological underpinnings of this adaptive attitude, specifically the basis of racial bias that is promoted through the expression of prejudice and stereotype in humans. Perception of faces contributes heavily to this social categorization, such that neuropsychological damage that impairs this perceptive ability may dampen these discriminations. Though natural selection does not promote "for the good of the group" altruistic behavior in all cases, the development and utilization of empathic attitudes would allow our species to overcome our evolutionary past and move towards a more harmonious future.

Keywords:
Xenophobia | prejudice | stereotype | social categorization | group selection | behavior | functional neuroimaging | prosopagnosia

Definitions:
Xenophobia: fear of and hostility towards objects or animals perceived as foreign or dissimilar to one's own identity
In-group: grouping comprised of members of one's own species or social group
Out-group: grouping comprised of members of species or social groups not of one's own
Personal fitness: an individual organism's evolutionary readiness to survive
Inclusive fitness: an organism's in-group's evolutionary readiness to survive
Discrimination: the ability to differentiate between examples of objects and animals from other examples within the same or different categories
Prejudice: an evaluation held about members of a social group based on stereotypical presumptions
Stereotype: an over-generalization of trait characteristics of members of a social group
Implicit bias: attitudes that influence behavior without conscious awareness

Introduction

In his seminal work "On the Origin of Species", Darwin (1859) proposed that organisms evolve through a process of natural selection. This biological mechanism theorizes that organisms will tend to inherit the most evolutionarily adaptive physical characteristics from their ancestors. These adaptations are rarely novel additions, but are re-purposed from existing ones (de Waal, 2009). According to this logic, all extant organisms are by-products of past environments, equipped with adaptations that previously provided a selective advantage for their ancestral species. Fitness-relevant stimuli (e.g. predators, aggressive conspecifics, potential mates), as well as heuristically similar stimuli, are selectively attended to (Öhman & Mineka, 2001) in order to promote fitness-benefiting behaviors.

For the next century, biologists laid claim that organisms hold an innate ability to function as a prescient, cooperative group. Group selection is at work when traits evolve as a result of differential survival and productivity among groups within a total population (Eldakar & Wilson, 2011). Seemingly an extension of Darwin's logic, group selection was invoked to explain how natural selection may target organisms at the group level instead of the individual.

Group selection requires that the population subset be relatively small and that the trait in question be selectively disadvantageous to the altruistic actor, but that nevertheless propagates within the group. Additionally, the groups must be reproductively isolated to enhance the genetic variation among groups and no individuals can cheat (Smith, 1964). These are severe and unrealistic requirements.

This viewpoint was forcefully challenged in the 1960's and 1970's, when evolutionary biologists such as J. M. Smith and G. C. Wilson asserted that such behavior could not have evolved by natural selection. As natural selection works at the individual level, seemingly inter-organismal behavior could actually have evolved by working on individuals (for review, see Smith, 1964). Within a group of organisms, cheaters have a fitness advantage that makes "for the good of the group" decision-making evolutionarily unfavorable. Additionally, mathematical models showed that the between-groups selection on which group selection is predicated on, is negligible compared to within-groups selection (Wilson & Wilson, 2008).

Any subsequent mention of group selection in the literature was immediately rejected. Instead, any observed behavior that held a semblance to group selection was framed from the perspective of the individual organism. Hence, kin selection (Trivers, 1971) and reciprocal altruism emerged to explain these pro-social behaviors.

When urged to reconsider his theory of reciprocal altruism (Hamilton, 1964) by putting its variables into the Price equation (Price, 1972), a model that is sensitive to both within- and between-groups interaction properties, W. D. Hamilton realized that group selection was at play because the altruistic act was selectively disadvantageous to the actor. (Eldakar & Wilson, 2011). Even Darwin cited instances of selfless behavior, where the recipient is the sole beneficiary of a fitness-relevant inter-organism interaction that could not have arisen through individual-targeting natural selection (Darwin, 1871).

Recently, the multi-level selection theory (Wilson & Sober, 1989) has provided a synthesis in the field. This re-appraisal of the previous mechanism examines organisms at various hierarchical levels, using a species-specific approach to analyze organisms'

behaviors within the context of the selection pressures at play. This theory explains why individuals within a group may resort to selfless behaviors under certain conditions. Such an individually disadvantageous behavior is only feasible when the behavior gives a between-group selective advantage that can overcome the within-group selection problem of unequal reciprocity ("problem of cheaters"; Wilson & Wilson, 2008).

Proponents of this theory claim that evolutionary biologists' blanket dismissal of group selection is based on a fallacy. Just as natural selection works on the gene within an individual or an individual within a population, it is myopic to deny that selection can act in a parallel way on the next highest level on the biological hierarchy under certain circumstances (Wilson & Sober, 1989). In addition, the mathematical models that evolutionary biologists utilize to simulate population characteristics are not designed to be sensitive to between-groups differences (Eldakar & Wilson, 2011; Leimar & Hammerstein, 2006), such that their conclusions are not informative regarding whether or not group selection is in effect.

The principles of natural selection were later applied to ideological inheritance, such as sociocultural norms and individual dispositions. In this view, affective and cognitive responses are adaptive "tools" that promote the individual's personal or inclusive fitness (Gigerenzer, 2008). In the human ancestral environment, it was adaptive to distinguish members of one's own species or social group (in-group) from those that were not (out-group). This distinction allowed for the formation of socially based coalitional alliances (Kurzban, Tooby & Cosmides, 2001; Gottfredson, 1996) based on cooperation and reciprocity within the group. But it also promoted intergroup conflict, discrimination, and even genocide through the mobilization of prejudice and stereotype.

Prejudice and stereotype function as heuristics for social categorization, using evolutionarily adaptive heuristics that allow organisms to make viable predictions of future events to successfully perform fitness-benefiting behavior. These biases can reflect vestigial tendencies that do not necessarily promote an individual's fitness. For example, Kubota et al. (2003) found that participants made decisions based on implicit bias and racial group membership even though such decisions were personally detrimental.

Race is particularly important in human social categorization, as it is perceived as a salient, inherent, and conspicuous physical distinction. A race can be defined as human beings sharing physical attributes, ethnicity, and history (Malinowska, 2016). Some say race is simply a social construct (for review, see Smedley & Smedley, 2005), while others cite the neurological (Rushton & Jensen, 2005), pharmacological (Burroughs, Maxey & Levy, 2002), and genetic (for review, see Jorde & Wooding, 2004) differences between races, although this is under debate (Tishkoff & Kidd, 2004).

Genetic similarity theory (Rushton, Russell & Wells, 1984) extends beyond Hamilton's rule (1964) of gene-based social identity recognition to purport that racial groupings are a function of phenotypic (and therefore, genotypic) similarity. It then promotes an individual's inclusive fitness through alliances that breed trust and cooperation within the group (Kurzban, Tooby & Cosmides, 2001). This is exhibited in highly inbred animals that reduce competition for resources between members (Wilson & Wilson, 2008).

Moreover, after populations diverged from Africa, they were reproductively isolated from each other due to low migration rates (Harpending et al., 1993), increasing genetic variation among populations. Because phenotype varies with genotype, populations

appeared increasingly distinct. The phenotypic similarity (e.g. skin pigmentation) observed within a racial group provides a heuristic for determining who to incur inclusive fitness-benefiting cooperative acts for.

Humans have inherited a "living kinds module" (Sperber & Hirschfeld, 2004) in order to categorize animate and inanimate objects to support successful interaction with the external environment. In terms of inter-racial interactions, it is unclear whether humans perceive other races as distinct species ("biological kinds module"; Gil-White, 2001) or as out-groups distinct from the in-group ("human kinds module"; MacDonald, 2001). Regardless, humans have developed cognitive systems to categorize conspecifics according to perceived differences between them. These differences allowed for the utilization of anti-social cognitive manifestations (e.g. infrahumanization) that propagate inter-group conflict.

Xenophobic tendencies are prevalent throughout the tree of Life; therefore, human expression of this behavior likely has an evolutionary basis. In a review of the existing literature, I will examine the shared roots of this behavioral response using comparative behavioral, prophylactic behavioral, lesion, neuropsychological, and functional neuroimaging (specifically functional magnetic resonance imaging (fMRI)) approaches.

Results

Comparative Behavioral Evidence

Identity-based inter- and intraspecies discrimination and aggression is widespread throughout the biological world, from plants to primates. Plants participate in chemical warfare with members of the same species as well as different species, as a means of ensuring that they have sufficient resources to survive (Lovett, Ryuntyu & Liu, 1989). In social insects, honeybees discriminate between different colonies by body color (Couvillon et al., 2007). Birds living in flocks exhibit aggression in territorial interactions towards both kin and non-kin (Aguillon & Duckworth, 2015), suggesting that aggressive behavior is not solely a function of genetic similarity.

There is abundant evidence of xenophobic tendencies in mammals, especially in non-human primates. Many species of Old World monkeys live in stable social organizations with dynamic and complex interaction features that resemble human social structures (Amaral, 2002). Chimpanzees have been shown to act aggressively towards foreign males as a means of maintaining the established social dominance hierarchy (Goodall, 1986). Wild rhesus macaques have been observed to express xenophobic attitudes towards conspecifics in territorial interactions (Teas et al., 1982). Interestingly, rhesus monkeys communicate socially through the use of facial expressions (Amaral, 2002), which is analogous to how humans navigate the social environment.

Moreover, in a review by Nagel and Kummer (1974), it was found that Old World monkeys lived in relatively stable social organizations but were very aggressive and territorial towards conspecifics, leading the authors to propose that these factors are related. Though aggression and territoriality in other animals may not be directly translatable to human xenophobic behavior, the fact that similar stimulus characteristics can evoke similar response trajectories suggests the behavior has a shared origin.

Looking at human behavior, xenophobia can be readily observed in interactions ranging from arbitrarily assorted sporting events to race-based inter-group violence. Since these behavioral correlates are universally present throughout the phylogenetic tree, it is likely that this tendency is innate due to inheritance of common descent from our last common ancestor.

Behavioral Prophylaxis

The behavioral immune system (BIS) is comprised of an array of proactive behaviors that supplement the efficacy of the reactive somatic immune system by prompting animals to behave so as to avoid contracting pathogens (for review, see Murray & Schaller, 2016). These behaviors, ranging from cultural sanitation customs to social ostracism, promote spatial avoidance of a BIS-triggering stimulus.

These protective behaviors are preceded by negative-valence emotions like disgust, an adaptive emotion that promotes pathogen avoidance of the disgust-eliciting stimulus. It has been shown to trigger specific responses from the autonomic (Kreibig, 2010) and the central (Baumann & Mattingley, 2012) nervous systems that support the behavioral responses necessary for successful disease avoidance.

The smoke detector theory (Schaller, 2011) for how the BIS is elicited asserts that objects in the environment pose varying degrees of threat; once a threshold of fitness relevance is reached, behavioral avoidance is promoted. Like a smoke detector, the body recognizes that having a false negative to a threatening stimulus has a much greater fitness cost than a false positive. As such, it is evolutionarily adaptive to err on the side of caution and behave in a hyper-sensitive manner to potential external threats.

A member of an out-group may pose a threat in two ways: by exposing locals to parasites that they do not have somatic immunity for, and by not conforming to local sanitation customs (Murray & Schaller, 2016). It is then advantageous to employ a prophylactic cognitive system that heuristically conflates an out-group member with a potential disease threat.

Evidence from Lesion, Neuropsychological, and Functional Neuroimaging Methods

Amodio (2014) proposed two networks (*Figures 1 and 2*) of associated human brain regions for the neural systems that support prejudice and stereotype, two forces that reinforce xenophobic attitudes. Although several of the neural substrates are involved in supporting both processes (e.g. prefrontal cortex), other regions are especially activated during the acquisition and expression of prejudicial (e.g. amygdala, insula) and stereotypical (e.g. temporal lobe) attitudes.

While these neural substrates highlight generalized networks for categorization of the social environment, supplementation of the neural data with measures of direct and indirect race-based biases allows for valid predictions to be made about racial discriminatory tendencies.

Prejudice

Prejudicial attitudes (*Figure 1*) are supported by socially transmitted encoding and stimulus-driven retrieval of group identity-based preconceptions (Amodio, 2014).

Amygdala

The amygdalae are almond-shaped sub-cortical structures situated bilaterally in the medial temporal lobes that are thought to be nuclei for affect-based perception (Anderson & Phelps, 2001), decision-making (Bechara et al., 2003), and memory (McGaugh, 2004). They function together as a "protection device" in order to make relatively automatic appraisals of threat that promote species-typical responses to stimuli (Amaral, 2002). As such, much of the existing literature has examined the amygdala's role in social and emotional processing.

The amygdala has been implicated in the early processing of racial out-group faces (Cunningham et al., 2004). Administration of the Implicit Associations Test (IAT; Greenwald, McGhee & Schwartz, 1998), an indirect measure of implicit racial bias that requires participants to associate valence words (e.g. good, bad) with unfamiliar racial in- and out-group faces, during fMRI data acquisition showed that subjects harbored implicit racial prejudices, which correlated with degree of amygdala activation.

However, a criticism of the IAT's validity holds that the response latencies it measures are not inherently meaningful in terms of bias, as it more closely targets familiarity with stimuli rather than attitude towards them (Phelps & Banaji, 2006). A similar criticism of the fMRI method asserts that increased signal amplitude does not necessarily parallel the mental experience of the scanned individual (Logothetis, 2008).

To address this issue, Phelps et al. (2000) used the IAT in conjunction with the startle eye-blink method (Filion, Dawson & Schell, 1998), a physiological measure of cognitive and affective evaluative processing, fMRI, and a direct measure of racial prejudice. No significant difference was found in amygdala activation of White participants in response to Black or White unfamiliar face stimuli. Results from the two implicit measures did correlate with amygdala activation (though the explicit measure did not), suggesting that the structure is involved in unconscious race evaluations regardless of familiarity.

No race effect was found if stimuli were of familiar Black and White faces (e.g. Denzel Washington, Harrison Ford), suggesting that familiar faces are sub-typed so as to evoke different patterns of amygdala activity and are perceived to hold a different threat component than when exposed to unfamiliar faces (Phelps & Banaji, 2006).

It has been proposed that the varying return of significant results to race-based amygdala activity (Cunningham et al., 2004; Phelps et al., 2000) may reflect discrepancies in stimulus characteristics (Phelps & Banaji, 2006).

Interestingly, both African- and Caucasian Americans had greater amygdala activity to African American unfamiliar faces, suggesting that cultural learning may take precedence in mediating inter-group interactions than familiarity with the social stimulus (Lieberman et al., 2005).

Yet a patient with bilateral amygdala damage was shown to have similar responses to direct and indirect measures of racial bias, suggesting that the amygdala is not a sufficient component for the elicitation of prejudicial attitudes (Phelps et al., 2003).

Insula

The insular cortex is implicated in perception (Craig, 2009) and interpersonal experience (Kang et al., 2010), as well as experience of disgust that is elicited through exposure to an object in the external environment or through a social context (for review, see Chapman & Anderson, 2012).

Using a fear-conditioning paradigm, Molapour et al. (2015) found differential activity in the anterior insula and amygdala, depending on whether subjects were exposed to in- or out-group faces, which predicted presence of discriminatory behavior between these two groups.

This study also examined physiological markers to corroborate the fMRI results. In normal participants subjected to a fear conditioning paradigm using examples of racial in- and out-group faces as stimuli, skin conductance response (SCR) was greater for conditioned stimulus (CS) when paired with an

aversive stimulus (US) than when the CS was presented alone, as was expected. Importantly, there was no effect of CS race or an interaction between SCR and CS race at bias acquisition or stimulus recall. Taken together, these results suggest that in- and out-group identity of an interaction partner does not significantly influence the evaluation of the partner.

Acquisition in fear conditioning is produced through direct, personal experience to an aversive stimulus, while that of racial prejudice is through socially transmitted culture-dependent interactions (Phelps & Banaji, 2006). Therefore, it may not be appropriate to extrapolate findings from the former towards the latter.

Prefrontal Cortex (PFC)

The PFC is the anterior-most region of the neocortex. It is the most extensively elaborated structure of the human brain compared to other mammals. It is thought to account for many of the differences in cognitive abilities between humans and non-human primates (for review, see Hrvoc-Mihic et al., 2013). Additionally, it is involved in executive functions such as self-regulation and inhibition of attitudes, such as racial bias (Richeson & Shelton, 2003) that are promoted by sub-cortical structures (e.g. amygdala).

Cunningham (2004) recruited White participants and administered the IAT to investigate the presence of implicit racial bias. All of the participants reported having motivation to inhibit racial prejudices. The subsequent fMRI results showed that the bigger the difference in amygdala activity between subliminal and extended exposure to Black and White face stimuli correlated with greater activation of the dorso- and ventrolateral PFCs. This implies greater effect of PFC modulation. Overall, this study shows that executive function by the PFC can modulate, even override, the relatively automatic appraisals that the amygdala

detects.

These results were further corroborated by Lieberman et al. et al. et al. (2005), who found that amygdala activity negatively correlated with activation of the ventrolateral PFC when encoding same- and other-race faces. The authors propose that this functional coupling may be due to inhibitory neural connections, thereby providing a mechanism for prejudice suppression.

Stereotype

Stereotype activation (*Figure 2*) requires the encoding of culturally driven stereotype concepts, the stimulus-driven selection of these concepts into working memory, and execution of the concepts as behaviors (Amodio, 2014).

Temporal Lobe (TL)

The TL is involved in semantic (Mummery et al., 2000) and episodic (Dolan et al., 2000) memory acquisition and recollection, as well as those of context-driven social knowledge (Zahn et al., 2007). The hippocampus is an especially important sub-cortical structure involved in the memory consolidation (Bernabeu et al., 1997) and recall (Liu et al., 2012) processes. As navigating the social environment requires remembering the intricacies of inter-personal relationships given specific contexts, stereotype encoding and activation is likely to involve regions of the temporal lobes (Amodio, 2014).

Whereas bilateral amygdala damage leads patients to have no SCR to fear conditioning while maintaining explicit knowledge of the CS-US pairing (Phelps & Banaji, 2006), hippocampal damage patients exhibit SCR (intact implicit memory) but have no explicit memory of the CS-US pairing (Phelps, 2004). This may be extended to suggest that hippocampal damage may be correlated with reduced social bias, though this supposition

needs to be investigated in human populations (Burton et al., 2000).

However, the hippocampus was shown to not be significantly involved in the affective response to members of the social out-group (Fourie et al., 2014), suggesting that memory for the out-group does not have an emotional component. This parallels the human tendency to individuate members of the in-group to a greater extent than towards those of the out-group ("other race effect"; Van Bavel, Packer & Cunningham, 2008).

The anterior TL has been implicated in supporting social knowledge, as it is activated when human participants are exposed to conspecifics, but not to inanimate objects (Puce et al., 1998). Likewise, if people of other races are perceived as being of another species (Gil-White, 2001), then recognition and categorization is likely to involve the temporal lobe (Haxby, 2001). Importantly, transcranial magnetic stimulation of the anterior TL and subsequent disruption of its activity has been shown to disrupt the elicitation of implicit stereotypes, suggesting that this region is necessary for stereotype expression (Gallate et al., 2011).

Prefrontal Cortex (PFC)

Although the PFC is involved in supporting prejudicial attitudes, it is more directly involved in stereotype regulation (Amodio, 2014).

The medial PFC is of particular import, as it is involved in socially derived impression formation (Mitchell, Macrae & Banaji, 2005). Although most of the existing literature on the expression and regulation of stereotypes is focused on political affiliations (Wilson & Rule, 2014), the medial PFC has also been implicated in race-based stereotype judgments (Quadflieg et al., 2009).

The lateral PFC, especially the region

designated as the inferior frontal gyrus (IFG) is involved in the utilization of heuristics rooted elsewhere in the brain to selectively incorporate these concepts into working memory in order to promote goal-directed action (Miller, Freedman & Wallis, 2002). Extensive reciprocal connections with the basal ganglia and motor cortex (Swann et al., 2009) provide the pathway for the execution of these actions. Mitchell et al. (2009) found that the IFG is selectively activated when subjects are making stereotype-based judgments. As stereotypes may simply be a means of categorizing and simplifying social organizations (Contreras, Banaji & Mitchell, 2012), the IFG may support racial discriminations as a type of semantic memory.

Neural Network for Race-Based Xenophobic Attitudes

Kubota, Banaji, and Phelps (for review, see 2012) outlined a circuit (*Figure 3*) of regions thought to underlie racially based xenophobic attitude expression.

Several of the neural loci involved in prejudice and stereotype (e.g. amygdala and dorsolateral PFC, reviewed above) are parts of this circuit, although other regions are shown to be uniquely involved in recognition of racial in- and out-group members.

Cingulate Cortex

The anterior cingulate cortex (ACC) is involved primarily in conflict resolution of incoming percepts (for review, see Botvinick, Cohen & Carter, 2004), such as in the Stroop task (an indirect measure of conflict between perception and behavior; Carter et al., 1997). Fibers originating in the amygdala and dorsolateral PFC synapse on the ACC (Etkin et al., 2006), suggesting that early decisions of threat and inhibition of these impressions influence how individuals navigate the complex social environment.

Krill & Platek (2009) used a social exclusion paradigm to find that greater ACC activation was correlated with increased amygdala activation and score on the IAT. This suggests that detecting conflict between personal bias and cultural expectations, in order regulate these attitudes, is underway when controlling race-based bias.

Fusiform gyrus

The fusiform gyrus (FG), especially the frontal face area (FFA), is a necessary region for the perception of faces through visual cues (Steeves et al., 2009; Quadflieg & Macrae, 2011).

Greater FFA response is observed when participants view racial in-group faces than those of racial out-groups (Golby, et al., 2001), although familiarity with racial out-group faces diminishes this difference (Stahl, Wiese & Schweinberger, 2008; Kim, et al., 2006). Overall, increased duration of exposure reduces race-based differential activity of the FFA (Lebrecht et al., 2009), similarly to duration-modulated amygdala activity to in- and out-group faces (Cunningham, 2004).

Homologous regions in the inferior temporal cortex of macaque monkeys have shown to be selectively tuned to perceiving faces (Rolls, 2000).

Future Directions

Xenophobic attitudes are acquired through the perception of visual input, namely the physical characteristics that distinguish organisms from each other (Ratner & Amodio, 2013). Consequently, it may be fruitful to examine individuals who do not have these visual biases that influence related socio-affective behaviors.

Prosopagnosia (PPG), a.k.a. face blindness, is the result of neuropsychological damage to the

Though prosopagnosia is a perceptive disorder

FG such that the patient can no longer recognize faces as familiar or not. It has been proposed that PPG parallels the autism spectrum disorders (ASD; Pierce et al., 2001), in that both disorders result in patients not being able to perceive social cues provided by facial expressions that are crucial for human communication (Biotti & Cook, 2016). While patients with ASD exhibit deficits in this ability (Dapretto et al., 2006), patients with PPG can still perceive facial expressions denoting emotional states (Duchaine, Parker & Nakayama, 2003), underlining the dissociation between social and affective signals in interaction.

Although it is unlikely that patients with PPG differ from normal populations in other personality traits, it may be that these patients harbor less severe prejudicial tendencies as a direct result of their neuropsychological damage. As the FFA is necessary (Kanwisher & Yovel, 2006), but not sufficient (Steeves, et al., 2006) for the perception of faces, the absence of the capacity to discriminate between familiar and unfamiliar faces based on physical, race-based characteristics may lead to decreased explicit and implicit racial prejudices and stereotypes.

Balas & Nelson (2009) showed that normal populations make racial distinctions based on low-level characteristics, such as musculoskeletal spatial proportions and skin pigmentation. It is unclear whether patients with PPG compensate for their facial recognition deficits by looking to these race-denoting physical characteristics of interaction partners. Gaining a better understanding of the cognitive characteristics of interaction would lend valuable insight into whether racial discrimination is a result of top-down or bottom-up processing, as this makes a significant difference in combatting prejudicial tendencies.

that specifically affects humans, disruption of homologous visual areas involved in

categorization in rhesus macaques (Rolls, 2000) produces similar impairments. While further investigation needs to be conducted to investigate species-specific behavior in response to visual area lesions, the existing literature implies that visually perceived identity recognition may have an evolutionary basis.

Discussion

Xenophobia on an evolutionary timescale was an adaptive behavioral response to the external environment, by promoting behavior in which organisms place their personal or inclusive fitness above those of other organisms not within these categories.

In the modern day, however, xenophobia is a maladaptive trait inherited from our phylogenetic ancestors. With the socioeconomic trend of globalization, people are interacting with racial out-group members to a greater extent than ever before (Diaz & Zirkel, 2012). Denying this fact and actively working against it restricts the gene pool, which could potentially de-stabilize the collective human genome (Lynch & O'Hely, 2001). Socially, xenophobic tendencies perpetuate prejudicial and stereotypical concepts. Consequently, inter-group social harmony is put at risk, potentially leading to such destructive behavior as racial intolerance, infrahumanization, social exclusion, violence, and war.

With the advent of and continuing progress in modern medicine, there is a much lower risk of foreigners transmitting foreign pathogens that the BIS disease avoidance mechanism supports. Moreover, since the human species has the most developed PFC of any animal, our capacity for reasoning and inhibiting the primitive evaluations that are our phylogenetic burden should be the most advanced, as well. Taken together, our species is equipped, now while the brain is still immature and malleable provides a potential means of minimizing the

more than ever, to interact with one another in pro-social ways at lower cost to our personal and inclusive fitness.

Empathy towards the out-group, therefore, acts as the "sole weapon" against xenophobic attitudes (de Waal, 2009). The expression of this emotion requires the organism to practice perspective-taking (Seyfarth & Cheney, 2013). As this cognitive ability is based on interpersonal mentalizations, rather than in response to stimulus-driven appraisals, empathetic attitudes are more effortful to produce (Block-Lerner et al., 2007). It is then adaptive, albeit anti-social, to rely on low-cost heuristics that promote quick, discriminatory decisions about out-group members.

Even though expression of empathetic attitudes is evolutionarily unfavorable, deploying "for the good of the group" group selective behavior benefits the actor by increasing positive-valence affect (Batson & Powell, 2003) and promotes within-group social functioning (Zhou et al., 2002).

The neural substrates especially activated during empathic experience, such as anterior insular cortex and ACC (Gu et al., 2010; Xu, et al., 2009), are also recruited in prejudicial and stereotypical biases, implying that the attitudes are selectively elicited depending on context. Furthermore, this research implies that the brain may be co-opted to be biased to promote empathetic, rather than prejudicial, behavior.

Social development follows a posterior-anterior gradient as the individual's PFC matures (Rubenstein, 2011). Since the PFC inhibits primitive, vestigial evaluations (Cunningham, 2004) such as xenophobic attitudes, the cognitive ability to dampen these biases should strengthen with age. It then follows that training targeted against these anti-social tendencies

effects of these biases.

Positive (non-aversive) exposure to members of the out-group promotes reduced out-group derogation (Pettigrew & Tropp, 2008). But how does digital exposure come into play? In the modern world, media outlets artificially expose people to racial out- groups that they may have never interacted with. As in fear conditioning, if the exposure is paired with threat response-eliciting stimuli, the racial out-group may be associated with a negative percept (Weisbuch, Pauker & Ambady, 2009). Though this "interaction" is not directly aversive, it is one-sided and not necessarily constructive, such that bias towards out-group members may be perpetuated.

Phelps & Banaji (2006) found that racial discriminatory prejudices were difficult to extinguish, even with exposure and familiarity with members of the out-group, especially in the presence of aversive consequences. However, Kurzban, Tooby, and Cosmides (2001) showed that in less than four minutes, grouping based on race was extinguished when arbitrarily assigned inter-racial groups were explicitly directed to attend to the non-racially derived similarities within the group. This evidence shows that, with training, discriminations based on such superficial distinctions as race can be transcended.

Xenophobia is fed in two ways: it increases both love for the in-group, as well as hate for the out-group. Racial discrimination is then two sides of the same coin – favor the racial in-group and simultaneously derogate the racial out-group. This designation of in- and out-group is flexible (Kurzban, Tooby & Cosmides, 2001), lending a potential starting point for combatting these anti-social attitudes.

Although the past two years (at least) have been particularly contentious, explicit discrimination is progressively decreasing worldwide (Wilson, 2011). Perhaps we can one day extend the favor we hold for our in-group to our out-groups, be they other races, other animals, or the planet, itself. We are all more similar than we may appear.

Acknowledgements

References

Aguillon, S. M. & Duckworth, R. A. (2015). Kin aggression and resource availability influence phenotype-dependent dispersal in a passerine bird. *Behavioral Ecology and Sociobiology.* Advance online publication. doi: 10.1007/s00265-015-1873-5

Amaral, D. G. (2002). The primate amygdala and the neurobiology of social behavior: implications for understanding social anxiety. *Biological Psychiatry, 51,* 11-17.

Amodio, D. M. (2014). The neuroscience of prejudice and stereotyping. *Nature Reviews Neuroscience, 15,* 670-682. doi: 10.1038/nrn3800

Anderson, A. K. & Phelps, E. A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events*. Nature, 411,* 305-309. doi: 10.1038/35077083

Balas, B. & Nelson, C. A. (2009). The role of face shape and pigmentation in other-race perception: An electrophysiological study. *Neuropsychologia, 48,* 498-506. doi: 10.1016/j.neuropsychologia.2009.10.007

Batson, C. D. & Powell, A. A. (2003). Altruism and Prosocial Behavior. *Handbook of*

Psychology, 19, 463-484. doi: 10.1002/0471264385.wei0519

Baumann, O. & Mattingley, J. B. (2012). Functional topography of primary emotion processing in the human cerebellum. *NeuroImage, 61,* 805-811. doi: 10.1016/j.neuroimage.2012.03.044

Bechara, A., Damasio, H. & Damasio, A. R. (2003). Role of the Amygdala in Decision-Making. *Annals of the New York Academy of Sciences, 985,* 356-369. doi: 10.1111/j.1749-6632.2003.tb07094.x

Bernebeu, R., Bevilaqua, L., Ardenghi, P., Bromberg, E., Schmitz, P., Bianchin, M.,... Medina, J. H. (1997). Involvement of hippocampal cAMP/cAMP-dependent protein kinase signaling pathways in a late memory consolidation phase of aversively motivated learning in rats. *Proceedings of the National Academy of Science of the United States of America, 94,* 7041-7046.

Biotti, F. & Cook, R. (2016). Impaired perception of facial emotion in developmental prosopagnosia. *Cortex, 81,* 126-136. Doi: 10.1016/j.cortex.2016.04.008

Block-Lerner, J., Adair, C., Plumb, J. C., Rhatigan, D. L. & Orsillo, S. M. (2007). The case for mindfulness-based approaches in the cultivation of empathy: Does nonjudgmental, present-moment awareness increase capacity for perspective-taking and empathic concern? *Journal of Marital and Family Therapy, 33*, 501-516. doi: 10.1111/j.1752-0606.2007.00034.x

Botvinick, M. M., Cohen, J. D. & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: an update*. Trends in Cognitive Sciences, 8,* 539-546. doi:

10.1016/j.tics.2004.10.003

Burroughs, V. J., Maxey, R. W. & Levy, R. A. (2002). Racial and ethnic differences in response to medicines: towards individualized pharmaceutical treatment. *Journal of the National Medical Association, 94* (10 Suppl), 1-26.

Burton, S., Murphy, D., Qureshi, U., Sutton, P. & O'Keefe, J. (2000). Combined Lesions of Hippocampus and Subiculum Do Not Produce Deficits in a Nonspatial Social Olfactory Memory Task. *Journal of Neuroscience, 20,* 5468-5475. doi: 10.1101/lm.862308

Carter, C. S., Mintun, M., Nichols, T. & Cohen, J. D. (1997). Anterior cingulate gyrus dysfunction and selective attention deficits in schizophrenia: [15O]H2O PET study during single-trial Stroop task performance*. The American Journal of Psychiatry, 154,* 1670-1675. doi: 10.1176/ajp.154.12.1670

Chapman, H. A. & Anderson, A. K. (2012). Understanding disgust. *ANNALS OF THE NEW YORK ACADEMY OF SCIENCES, 1251,* 62-76. doi: 10.1111/j.1749-6632.2011.06369.x

Contreras, J. M., Banaji, M. R & Mitchell, J. P. (2012). Dissociable neural correlates of stereotypes and other forms of semantic knowledge. *Social Cognitive And Affective Neuroscience, 7,* 764-770. doi: 10.1093/scan/nsr053

Couvillon, M. J., Caple, J. P., Endsor, S. L., Kärfcher, M., Russell, T. E., Storey, D. E. & Ratnieks, F. L. W. (2007). Nest-mate recognition template of guard honeybees (Apis mellifera) is modified by wax comb transfer. *Biology Letters, 3,* 228-230. doi: 10.1098/rsbl.2006.0612

Cunningham, W. A. Johnson, M. K., Raye, C. L., Gatenby, C. J., Gore, J. C. & Banaji, M. R. (2004). Separable neural components in the processing of black and white faces. *Psychological Science, 15,* 806-813. doi: 10.1111/j.0956-7976.2004.00760.x

Craig, A. D. (2009). Emotional moments across time: a possible neural basis for time perception in the anterior insula. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364,* 1933-1942. doi: 10.1098/rstb.2009.0008

Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y. & Iacoboni, M. (2006). Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience, 9,* 28-30. doi: 10.1038/nn1611

Darwin, C. (1859). On the Origin of Species By Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life.

Darwin, C. (1871). The Descent of Man and Selection in Relation to Sex. Retrieved from http://www.fulltextarchive.com/pdfs/The-Descent-of-Man-and-Selection-in-Relation.pdf

de Waal, F. (2009). *The Age of Empathy:Nature's Lessons for a Kinder Society.* New York, NY: Three Rivers Press.

Diaz, J. & Zirkel, S. (2012). Globalization, Psychology, and Social Issues Research: An Introduction and Conceptual Framework. *Social Issues, 68,* 439-453. doi: 10.1111/j.1540-4560.2012.01757.x

Dolan, R. J., Lane, R., Chua, P. & Fletcher, P. (2000). Dissociable temporal lobe activations during emotional episodic memory retrieval. *NeuroImage, 11,* 203-209. doi: 10.1006/nimg.2000.0538

Duchaine, B. C., Parker, H. & Nakayama, K. (2003). Normal recognition of emotion in a prosopagnosic. *Perception, 32,* 827-838. doi: 10.1068/p5067

Eldakar, O. T. & Wilson, D. S. (2011) Eight Criticisms Not to Make About Group Selection. *Evolution, 65,* 1523-1526. doi:10.1111/j.1558-5646.2011.01290.x

Etkin, A., Egner, T., Peraza, D. M., Kandel, E. R. & Hirsch, J. (2006). Resolving Emotional Conflict: A Role for the Rostral Anterior Cingulate Cortex in Modulating Activity in the Amygdala. *Neuron, 51,* 871-882. doi: 10.1016/j.neuron.2006.07.029

F. de Waal. (2005, September 1). The Evolution of Empathy [Web blog post]. Retrieved from http://greatergood.berkeley.edu/article/item/the_evolution_of_empathy

Filion, D. L., Dawson, M. E. & Schell, A. M. (1998). The psychological significance of human startle eyeblink modification: a review. *Biological Psychology, 47,* 1-43.

Fourie, M. M., Thomas, K. G. F., Amodio, D. M., Warton, C. M. R. & Meintjes, E. M. (2014). Neural correlates of experienced moral emotion: an fMRI investigation of emotion in response to prejudice feedback. *Social Neuroscience, 9,* 203–218. doi: 10.1080/17470919.2013.878750

Gallate, J., Wong, C., Ellwood, S., Chi, R. & Snyder, A. (2011). Noninvasive brain stimulation reduces prejudice scores on an implicit association test. *Neuropsychology, 25,*

185-192. doi: 10.1037/a0021102

Gigerenzer, G. (2008). Why Heuristics Work. *Perspectives on Psychological Science, 3,* 20-29. doi: 10.1111/j.1745-6916.2008.00058.x

Gil-White, F. J. (2001). Are Ethnic Groups Biological "Species" to the Human Brain?. *Current Anthropology, 42*, 515-554.

Fourie, M. M., Thomas, K. G. F., Amodio, D. M., Warton, C. M. R. & Meintjes, E. M. (2014). Neural correlates of experienced moral emotion: an fMRI investigation of emotion in response to prejudice feedback. *Social Neuroscience, 9,* 203–218. doi: 10.1080/17470919.2013.878750

Gallate, J., Wong, C., Ellwood, S., Chi, R. & Snyder, A. (2011). Noninvasive brain stimulation reduces prejudice scores on an implicit association test. *Neuropsychology, 25,* 185-192. doi: 10.1037/a0021102

Golby, A. J., Gabrieli, J. D. E., Chiao, J. L. (2001). Differential responses in the fusiform region to same-race and other-race faces. *Nature Neuroscience, 4,* doi: 10.1038/90565

Goodall, J. (1986). *The chimpanzees of Gombe.* Boston: Houghton Mifflin Publishing.

Gottfredson, L. S. (1996). Race, Evolution, and Behavior: A Life History Perspective. Politics and the Life Sciences, 141-143.

Greenwald, A. G., McGhee, D. E. & Schwartz, J. L. (1998). Measuring individual differences in implicit cognition: the implicit association test. *Journal of Personality and Social Psychology, 74,* 1464-1480.

Gu, X., Guise, K. G., Naidich, T. P., Hof, P. R. & Fan,

J. (2010). Functional Dissociation of the Frontoinsular and Anterior Cingulate Cortices in Empathy for Pain. *Journal of Neuroscience, 30,* 3739-3:744. doi: 10.1523/JNEUROSCI.4844-09.2010

Harpending, H. C. , Sherry, S. T., Rogers, A. R. & Stoneking, M. (1993). The Genetic Structure of Ancient Human Populations. *Current Anthropology 34,* 483-496. doi: 10.1086/204195

Haxby, J. V., Gobbini, M. A., Furey, M. L., Ishai, A., Schouten, J. L. & Pietrini, P. (2001). Distributed and Overlapping Representations of Faces and Objects in Ventral Temporal Cortex. *Science, 293,* 2425-243 0. doi: https://doi.org/10.1126/science.1063736

Hrvoc-Mihic, B., Bienvenu, T., Stefanacci, L., Muotri, A. R. & Semendeferi, K. (2013). Evolution, development, and plasticity of the human brain: from molecules to bones. *Frontiers in Human Neuroscience, 7.* doi: 10.3389/fnhum.2013.00707

Jorde, L. B. & Wooding, S. P. (2004). Genetic variation, classification and 'race'. *Nature Genetics, 36,* S28-S33. doi: 10.1038/ng1435

Kang, Y., Williams, L. E., Clark, M. S., Gray, J. R. & Bargh, J. A. (2011). Physical temperature effects on trust behavior: the role of insula. *Social Cognitive and Affective Neuroscience, 6,* 507-515. doi: 10.1093/scan/nsq077

Kanwisher, N. & Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 361,* 2109-2128. doi: 10.1098/rstb.2006.1934

Kim, J. S., Yoon, H. W., Kim, B. S., Jeun, S. S., Jung, S. L. & Choe, B. Y. (2006). Racial distinction of the unknown facial identity recognition mechanism by event-related fMRI. *Neuroscience Letters, 397,* 279-284. doi: 10.1016/j.neulet.2005.12.061

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: a review. *Biological Psychology, 84,* 394-421. doi: 10.1016/j.biopsycho.2010.03.010

Krill, A. & Platek, S. M. (2009). In-Group and Out-Group Membership Mediates Anterior Cingulate Activation to Social Exclusion. *Frontiers in Evolutionary Neuroscience, 1.* Advance online publication. doi: 10.3389/neuro.18.001.2009

Kubota, J. T., Banaji, M. R. & Phelps, E. A. Phelps, E. A. (2012). The neuroscience of race. *Nature Neuroscience, 15,* 940-948. doi:10.1038/nn.3136

Kubota, J. T., Jian, L., Bar-David, E., Banaji, M. R. & Phelps, E. A. (2013). The Price of Racial Bias: Intergroup Negotiations in the Ultimatum Game. Psychological Science, 24, 2498-2504. doi: 10.1177/0956797613496435

Kurzban, R., Tooby, J. & Cosmides, L. (2001). Can race be erased? Coalitional computation and social categorization. *Proceedings of the National Academy of Sciences, 98,* 15387-15392. doi: 10.1073/pnas.251541498

Lebrecht, S., Pierce, L. J., Tarr, M. J. & Tanaka, J. W. (2009). Perceptual Other-Race Training Reduces Implicit Racial Bias. *PLoS One, 4,* e4215. doi:10.1371/ journal.pone.0004215

Leimar, O. & Hammerstein, P. (2006). Facing the Facts. *Journal Compilation of the European Society for Evolutionary Biology, 19,* 1403-1405. doi: 10.1111/j.1420-9101.2006.01156.x

Lieberman, M. D., Hariri, A., Jarcho, J. M., Eisenberger, N. I., & Bookheimer, S. Y. (2005). An fMRI investigation of race-related amygdala activity in African American and Caucasian-American individuals. *Nature Neuroscience, 8*, 720–722. doi: 10.1038/nn1465

Liu, X., Ramirez, S., Pang, P. T., Puryear, C. B., Govindarajan, A., Deisseroth, K. & Tonegawa, S. (2012). Optogenetic stimulation of a hippocampal engram activates fear memory recall. *Nature, 484,* 381-385. doi:10.1038/nature11028

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature, 453,* 869-878. doi: 10.1038/nature06976

Lovett, J. V., Ryuntyu, M. Y. & Liu, D. L. (1989). Allelopathy, chemical communication, and plant defense. *Journal of Chemical Ecology, 15,* 1193-1202. doi:10.1007/ BF01014822

Lynch, M. & O'Hely, M. (2001). Captive breeding and the genetic fitness of natural populations. *Conservation Genetics, 2,* 363-378. doi: 10.1023/A:1012550620717

MacDonald, K (2001). An integrative evolutionary perspective on ethnicity. *Politics and the Life Sciences, 20,* 67-80.

Malinowska, J. K. (2016). Cultural neuroscience and the category of race: the case of the other-race effect. *Synthese, 193,* 3865-3887. doi: 10.1007/s11229-016-1108-y

Marks, Jonathan (2015). *Tales of the Ex-Apes:*

How We Think about Human Evolution, Ed. 1. University of California Press.

McGaugh, J. L. (2004). The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annual Review of Neuroscience, 27,* 1-28. doi: 0.1146/annurev.neuro.27.070203.144157

Miller, E. K., Freedman, D. J. & Wallis, J. D. (2002). The prefrontal cortex: categories, concepts and cognition. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 357,* 1123-1136. doi: 10.1098/rstb.2002.1099

Mitchell, D. G. V., Luo, Q., Avny, S. B., Kasprzycki, T., Gupta, K., Chen, G., ... Blair, R. J. R. (2009). Adapting to dynamic stimulus-response values: Differential contributions of inferior frontal, dorsomedial, and dorsolateral regions of prefrontal cortex to decision making. *Journal of Neuroscience, 29,* 10827-10834. doi: 10.1523/ JNEUROSCI.0963-09.2009

Mitchell, J. P., Macrae, N. C. & Banaji, M. R. (2005). Forming impressions of people versus inanimate objects: social-cognitive processing in the medial prefrontal cortex. *Neuroimage, 26,* 251-257. doi: 10.1016/j.neuroimage.2005.01.031

Molapour, T., Golkar, A., Navarette, C. D., Haaker, J. & Olsson, A. (2015). Neural correlates of biased social fear learning and interaction in an intergroup context. *NeuroImage, 121,* 171-183. doi: 10.1016/j.neuroimage

Mummery, C. J., Patterson, K., Price, C. J., Ashburner, J., Frackowiak, R. S. & Hodges, J. R. (2000). A voxel-based morphometry study of semantic dementia: relationship between temporal lobe atrophy and semantic memory. *Annals of Neurology, 47,* 36-45.

Murray, D. R., & Schaller, M. (2016). The behavioral immune system: Implications for social cognition, social interaction, and social influence. *Advances in Experimental Social Psychology, 53,* 75-129. doi: 10.1016/bs.aesp.2015.09.002

Nagel, U. & Kummer, H. (1974). Variation in cercopithecoid aggressive behavior. In R. L. Holloway (Ed.), *Primate Aggression, Territoriality, and Xenophobia* (pp. 159-184). New York: Academic Press.

Öhman, A. & Mineka, S. (2001). Fears, Phobias, and Preparedness: Toward an Evolved Module of Fear and Fear Learning. *Psychological Review, 108,* 483-522. doi: 10.1037//0033-295X.108.3.483

Pettigrew, T. F. & Tropp, L. R. (2008). How does intergroup contact reduce prejudice? Meta-analytic tests of three mediators. *European Journal of Social Psychology, 38,* 922-934. doi: 10.1002/ejsp.504

Phelps, E. A. (2004). Human emotion and memory: interactions of the amygdala and hippocampal complex. *Current Opinion in Neurobiology, 14,* 198-202. doi: 10.1016/j.conb.2004.03.015

Phelps, E. A. & Banaji, M. R. (2006). Animal Models of Human Attitudes: Integrations Across Behavioral, Cognitive, and Social Neuroscience. In J. T. Caccioppo, P. S. Visser & C. L. Pickett (Eds.), *Social Neuroscience: People Thinking about Thinking People.* Cambridge, MA: MIT Press.

Phelps, E. A., Cannistraci, C. J. & Cunningham, W. A. (2003). Intact performance on an indirect measure of race bias following

amygdala damage. *Neuropsychologia, 41,* 203-208.

Phelps, E. A., O'Connor, K. J., Cunningham, W. A., Funayama, E. S., Gatenby, J. C., Gore, J. C. & Banaji, M. R. (2000). Performance on Indirect Measures of Race Evaluation Predicts Amygdala Activation. *Journal of Cognitive Neuroscience, 12,* 729-738. doi:10.1162/089892900562552

Pierce, K., Müller, R. A., Ambrose, J., Allen, G. & Courchesne, E. (2001). Face processing occurs outside the fusiform 'face area' in autism: evidence from functional MRI. *Brain, 124,* 2059-2073. doi: 10.1093/brain/124.10.2059

Price, G. R. (1972). Selection and covariance. *Nature, 227,* 520-521. Doi: 10.1038/227520a0

Puce, A., Allison, T., Bentin, S., Gore, J. C. & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience, 18*, 2188-2199.

Rushton, J. P., Russell, R. J. H. & Wells, P. A. Genetic Similarity Theory: Beyond Kin Selection. *Behavior Genetics, 14,* 179-193. doi: 10.1007/BF01065540

Quadflieg, S., Flannigan, N., Waiter, G. D., Rossion, B., Wig, G. S., Turk, D. J. & Macrae, C. N. . (2011). Stereotype-based modulation of person perception. *Neuroimage, 57,* 549-557. doi: 10.1016/j.neuroimage.2011.05.004

Quadflieg, S., Turk, D. J., Waiter, G. D., Mitchell, J. P., Jenkins, A. C. & Macrae, C. N. (2009). Exploring the neural correlates of social stereotyping. *Journal of Cognitive Neuroscience, 21,* 1560-1570. doi:10.1162/jocn.2009.21091

Ratner, K. G., & Amodio, D. M. (2013). Seeing "us vs. them": Minimal group effects on the neural encoding of faces. *Journal of Experimental Social Psychology, 49,* 298-301. doi: 10.1016/j.jesp.2012.10.017

Richeson, J. A. & Shelton, J. N. (2003). When prejudice does not pay: effects of interracial contact on executive function. *Psychological Science, 14,* 287-290.

Rolls, E. T. (2000). Functions of the Primate Temporal Lobe Cortical Visual Areas in Invariant Visual Object and Face Recognition. *Neuron, 27,* 205-218. Doi: 10.1016/S0896-6273(00)00030-1

Rubenstein, J. L. R. (2011). Development of the Cerebral Cortex: Implications for Neurodevelopmental Disorders. *Journal of Child Psychology and Psychiatry, 52*, 339-355. doi: 10.1111/j.1469-7610.2010.02307.x

Rushton J. P. & Jensen, A. R. (2005). THIRTY YEARS OF RESEARCH ON RACE DIFFERENCES IN COGNITIVE ABILITY. *Psychology, Public Policy, and Law, 11,* 235-294. doi: 10.1037/1076-8971.11.2.235

Schaller, M. (2011). The behavioural immune system and the psychology of human sociality. *Philosophical Transactions of the Royal Society Series B, 366,* 3418–3426. doi:10.1098/ rstb.2011.0029

Seyfarth, R. M. & Cheney, D. L. (2013). Affiliation, empathy, and the origins of theory of mind. *Proceedings of the National Academy of Science of the United States of America, 110 (Supplement 2),* Advance online publication. 10349-10356. doi: 10.1073/pnas.1301223110

Smedley, A. & Smedley, B. D. (2005). Race as biology is fiction, racism as a social problem is real: Anthropological and historical perspectives on the social construction of race. *The American Psychologist, 60,* 16-26. doi: 10.1037/0003-066X.60.1.16

Smith, J. M. (1964). Group Selection and Kin Selection. *Nature, 201,* 1145-1147. doi: [10.1038/2011145a0](10.1038/2011145a0)

Sperber, D. & Hirschfeld, L. A. (2004). The cognitive foundations of cultural stability and diversity. *Trends in Cognitive Science, 8,* 40-46. doi: 10.1016/j.tics.2003.11.002

Stahl, J., Wiese, H. & Schweinberger, S. R. (2008). Expertise and own-race bias in face processing: an event-related potential study. *Neuroreport, 19,* 583-587. doi: 10.1097/WNR.0b013e3282f97b4d

Steeves, J., Dricot, L., Goltz, H. C., Sorger, B., Peters, J. Milner, A. D., ... Rossion, B. (2009). Abnormal face identity coding in the middle fusiform gyrus of two brain-damaged prosopagnosic patients. *Neuropsychologia, 47,* 2584-2592. doi: 10.1016/j.neuropsychologia.2009.05.005

Steeves, J. K. E., Culham, J. C., Duchaine, B. C., Pratesi, C. C., Valyear, K. F., Schindler, I., ...,, Humphrey, G. K., Milner, A. D. & Goodale, M. A. (2006). The fusiform face area is not sufficient for face recognition: Evidence from a patient with dense prosopagnosia ad no occipital face area. *Neuropsychologia, 44,* 594-609.

Swann, N., Tandon, N., Canolty, R., Ellmore, T. M., McEvoy, L. K., Dreyer, S.,... Aron, A. R. (2009). Intracranial EEG Reveals a Time- and Frequency-Specific Role for the Right Inferior Frontal Gyrus and Primary Motor Cortex in Stopping Initiated Responses. *Journal of Neuroscience, 29,* 12675-12685. doi: 10.1523/JNEUROSCI. 3359-09.2009

Teas, J., Feldman, H. A., Richie, T. L., Southwick, C. H. (1982). Aggressive behavior in the free-ranging rhesus monkeys of Kathmandu, Nepal. *Aggressive Behavior, 8*, 63-77. doi: 10.1002/1098-2337(1982)8:1<63::AID-AB2480080105>3.0.CO;2-9

Tishkoff, S. A. & Kidd, K. K. (2004). *Nature, 36,* S21-S27. doi: 10.1038/ng1438

Trivers, R. L. (1971). The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology, 46,* 35-57. doi: 10.1086/406755

Van Bavel, J. J., Packer, D. J. & Cunningham, W. A. (2008). The neural substrates of in-group bias: a functional magnetic resonance imaging investigation. *Psychological Science, 19,* 1131-1139. doi: 10.1111/j.1467-9280.2008.02214.x

Weisbuch, M., Pauker, K. & Ambady, N. (2009). The Subtle Transmission of Race Bias via Televised Nonverbal Behavior. *Science, 326,* 1711-1714. doi: 10.1126/science.1178358

Wilson, D. S. & Sober, E. (1989). Reviving the Superorganism. *Journal of Theoretical Biology, 136,* 337-356. doi: 10.1017/S0140525X00036104

Wilson, D.S. & Wilson, E. O. (2008). Evolution "for the Good of the Group". *American Scientist, 96,* 380-389. doi: 10.1511/2008.74.1

Wilson, J. P. & Rule, N. O. (2014). Perceptions of Others' Political Affiliation Are Moderated by Individual Perceivers' Own Political Attitudes. *PLoS One, 9,* e95431. doi: 10.1371/journal.pone.0095431

Wilson, W. J. (2011). The Declining Significance of Race: Revisited & Revised. *Daedalus, 140,* 55-69. doi: 10.1162/DAED_a_00077

Xu, X., Zuo, X., Wang, X. & Han, S. (2009). Do You Feel My Pain? Racial Group Membership Modulates Empathic Neural Responses. *The Journal of Neuroscience, 29,* 8525-8529. doi: 10.1523/JNEUROSCI.2418-09.2009

Zahn, R., Moll, J., Krueger, F., Huey, E. D., Garrido, G. & Grafman, J. (2007). Social concepts are represented in the superior anterior temporal cortex. *Proceedings of the National Academy of Science of the United States of America, 104,* 6430-6435. doi: 10.1073/pnas.0607061104

Zhou, Q., Eisenberg, N., Losoya, S. H., Fabes, R. A., Reiser, M., Guthrie, I. K., … Shepard, S. A. (2002). The Relations of Parental Warmth and Positive Expressiveness to Children's Empathy-Related Responding and Social Functioning: A Longitudinal Study. *Child Development, 73*, 893-915. doi: 10.1111/1467-8624.00446
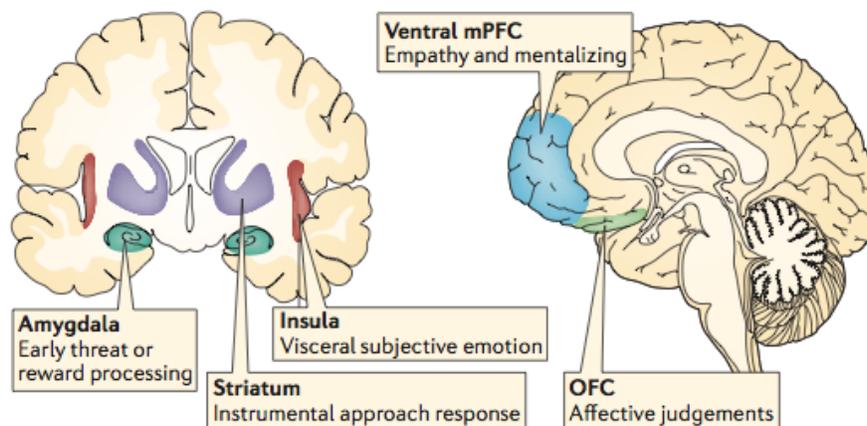
Figures:

Figure 1. **Neural Network of Prejudice Encoding and Activation.** Re-printed from Amodio (2014). The amygdala, insula, and PFC are especially activated substrates for harboring prejudicial attitudes.
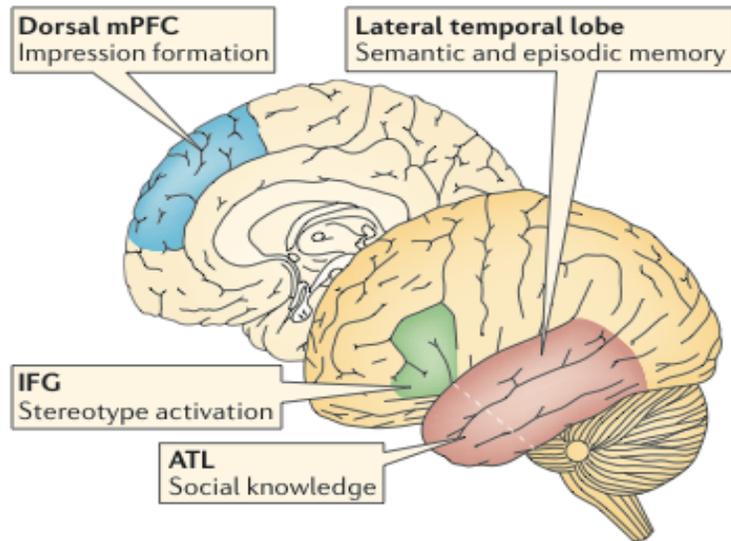
Figure 2. **Neural Network of Stereotype Activation and Regulation.** Reprinted from Amodio (2014). The temporal lobe and PFC support stereotypical judgments by supporting the encoding and retrieval of socially relevant concepts.
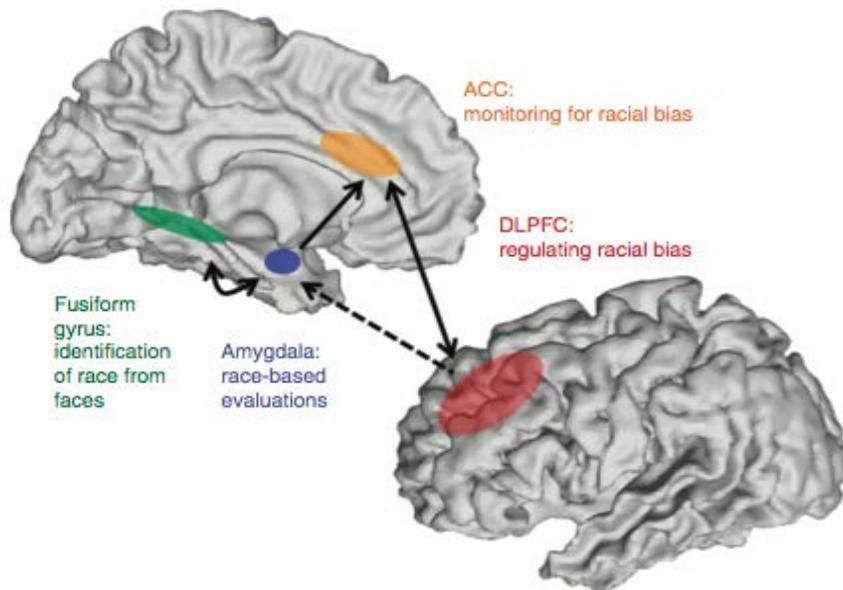

Figure 3. **Neural Network of Race-based Social Categorization.** Reprinted from Kubota et al. (2012). The cingulate cortex and the fusiform gyrus are especially activated when making discriminations of social interaction partners, in addition to the amygdala, PFC, etc. that support prejudice and stereotype expression and regulation.