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Social inference and the evolution of the human brain

Timothy Richard Koscik
University of Iowa

SOCIAL INFERENCE AND THE EVOLUTION OF THE HUMAN BRAIN

by

Timothy Richard Koscik

An Abstract

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of the requirements for the Doctor of
Philosophy degree in Neuroscience
in the Graduate College of
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ABSTRACT

The evolutionary forces that led to the unprecedented expansion of the human brain and the extreme cognitive prowess possessed by humans have always attracted a great deal of attention from the scientific community. Presented here is a novel theoretical perspective, where the driving force on human brain evolution was the need for enhanced ability to infer social values of conspecifics in the face of degradation and loss of chemosensory signalling mechanisms necessary for social communication present in most mammals.

The lack of chemosensory communication of biologically relevant information between humans in the face of the need to make adaptive and accurate social evaluations, led to an exaption of mammalian chemosensory brain regions for the more complex task of inferring social values from behavioural cues that are variable, ambiguous, or otherwise difficult to detect and interpret. This change in social processing from perceptual evaluation to inferential computation placed a premium on cognitive capacity, thus selecting for larger more powerful brains. These selective processes would have left an indelible mark on the human brain, where the human homologues of regions involved in mammalian conspecific chemical communication, in particular the target regions of this study the amygdala and ventromedial prefrontal cortex (VMPC), should be involved in the processing of biologically relevant information and social inference.

Several experiments were conducted to examine the role of these brain regions in social inferential processing using the lesion deficit method. First, given that conspecific chemical communication is particularly relevant for biologically imperative evaluation for the purposes of reproduction, VMPC and amygdala damage may result in abnormal mate-related decisions. Second, normal social attributions exhibit the correspondence bias, however damage to the target regions may result in an abnormal lack correspondence bias. Third, the current hypothesis is contrasted with another leading hypothesis, the Social Brain Hypothesis whose proponents predict a relationship between

group-size and social cognition. Finally, if the target brain regions are truly integral in inferring social information, then damage to these regions will interfere with the ability to utilize transitive inference in social situations, and potentially in using transitive inference in general.

Damage to the target areas produces limited effects on mate-related decisions and preferences. However, the current hypothesis may suggest that the target brain regions are only involved when the problem is inferential in nature rather than simpler perception of social information. In support of this notion, damage to the target regions results in a lack of the correspondence bias when making economic decisions. This alteration in social attributions actually leads to more 'rational' decision-making in this context. In contrast to the predictions of the Social Brain Hypothesis, damage to the target regions produces no observed reduction in social group size, nor is there any observed relationship between perspective-taking ability and group size. Finally, damage to the VMPC produces deficits in using transitive inference in a non-social context perhaps hinting at the underlying computations of this region in inferring social information.

In conclusion, it appears that the notion that the human brain regions that have been exapted from their duties in chemosensation and communication in mammalian brains has at least some validity. Moreover, these brain regions have been shifted by evolution to a more computationally complex process of social inference possibly providing the push toward larger and more powerful human brains.

Abstract Approved:_____
Thesis Supervisor

_____
Title and Department

_____
Date

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Iowa City, Iowa

CERTIFICATE OF APPROVAL

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PH.D. THESIS

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This is to certify that the Ph.D. thesis of

Timothy Richard Koscik

has been approved by the Examining Committee
for the thesis requirement for the Doctor of Philosophy
degree in Neuroscience at the December 2010 graduation.

Thesis Committee: _____
Daniel Tranel, Thesis Supervisor

_____
Natalie Denburg

_____
Robert Franciscus

_____
David Moser

_____
Peggy Nopoulos

_____
Jerry Suls

To my amazing wife

These are some of the things that hydrogen atoms do, given fifteen billion years of evolution.

Carl Sagan
Cosmos

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

abAMG – Accessory basal nucleus of the amygdala

ACC – Anterior cingulate cortex

coAMG – Cortical amygdala

ADVR – Anterior portion of the dorsal ventricular ridge

AHA – Amygdalohippocampal area

ANCOVA – Analysis of covariance

AOB – Accessory olfactory bulb

AOT – Nucleus of the accessory olfactory tract

AMG – Amygdala

AVLT – Rey Auditory Verbal Learning Test, 30-min recognition score, correct + correct rejections

bAMG – Basal nucleus of the amygdala

BAI – Beck anxiety inventory

BDC – Brain damaged comparison

BDI – Beck depression inventory

blAMG – Basolateral amygdala

BM – Body Mass

BNST – Bed nucleus of the stria terminalis

BNT – Boston Naming Test

cAMG – Central nucleus of the amygdala

CB – Correspondence Bias

cEA – Central extended amygdala, consisting of cAMG, anterior BNST, and a ring of cell groups around the internal capsule

COWA – Controlled Oral Word Association Test

CT – Computerize tomography

DVR – Dorsal ventricular ridge

EA – Extended amygdala

Face Disc. – Facial Discrimination Test

FSIQ – Full scale IQ on WAIS-III

HPC – hippocampus

IQ – Intelligence quotient

Ka – Thousand years ago

K-Pg – Cretaceous – Paleogene

lAMG – Lateral amygdala

LGN – Lateral geniculate nucleus

LOT – Nucleus of the lateral olfactory tract

Ma – million years ago

mAMG – Medial amygdalar nucleus

MANCOVA – Multivariate analysis of covariance

MDT – Medial dorsal thalamus

mEA – Medial extended amygdala, consist of mAMG, BNST, and cell groups in sublenticular substantia innominata.

MOB – Main olfactory bulb

MR – Magnetic resonance

NC – Normal comparison

OFC – Orbitofrontal cortex

PDVR – Posterior portion of the dorsal ventricular ridge

PFC – Prefrontal cortex

s. l. – senso lato, referring to the intentional 'loose' definitions for species that are not single species in the strict sense.

VIQ – verbal intelligence quotient, on WAIS-III

VMPC – ventromedial prefrontal cortex

VNO – Vomeronasal organ

VTA – Ventral tegmental area

WCST – Wisconsin Card Sorting Test, number of categories completed

WHR – Waist-to-hip Ratio

INTRODUCTION

Regions of the brain involved in social processing are currently under intensive scientific scrutiny. Important insights into which brain regions appear to be involved, how the functions supported by these regions impact overall functioning and success, and a variety of theoretical explanations have been made. However, social neuroscience at times lacks a discernible guiding principle to make predictions about brain regions and cognitive functions. A real risk associated with studying human social behavioural neuroscience without a guiding theoretical principle is to take social behaviours out of context without considering their roots or ultimate causes. By including a consideration of the origins of human sociality, including genetic factors, morphological characteristics, and selective pressures, we will be able to gain insight into human social behaviour in a more comprehensive way such that specific predictions about specific human behaviours, cognitive processes, and neural correlates can be made *a priori* and tested scientifically. By integrating what is known about mammalian biology and behaviour in a cross-species, comparative, evolutionary context, we can properly ground our study of human social behavioural neuroscience, and facilitate understanding of biological considerations of the mind. The selective pressures that create new species through modification of existing features apply not only to body morphology and behaviour but to brain structure and function as well. Understanding the evolutionary heritage of the mammalian brain will allow us to make specific predictions about structure-function relationships in the human brain.

Understanding the pressures that were placed on mammalian brains in evolutionary time and the resultant adaptations that are present in mammals can help us make predictions about the functions of regions of the brains of extant species. In other words, understanding the basic mammalian, neurological architecture and archetypal function can allow interpretation of alterations to this plan endemic to species or

phylogenetic clades. Primates in general and *Homo sapiens* specifically are no exception, and are perhaps the most interesting species to examine given the complexity of the human brain, the flexibility of human behaviour, and the success or ecological dominance of the human species.

In Chapter 1, I will discuss the evolution of mammals, primates, and humans (hominins). This chapter will discuss the major features and adaptations that have evolved, and provide some paleo-ecological context as to how mammals, primates, and hominins evolved.

Chapter 2 will focus on the evolution of the brain, again in mammals, primates and hominins. First, a discussion of the major components of the brain common to all vertebrates will be discussed, followed by discussion of the unique aspects of the mammalian brain. This will be followed by an examination of the adaptations present in the primate brain that differentiate primate brains from the common mammalian plan. Finally, hominin brains will be discussed, culminating in a discussion of what features make the human brain structurally unique from those of other primates. Lastly, given the general trend toward larger and larger brains up to including the modern human brain will be discussed; are bigger brains actually better?

Chapter 3 will present several theoretical perspectives on the driving forces behind human brain evolution. A main focus will be on three relatively distinct types of theories, including: climatological, ecological, and sociological hypotheses. A particular emphasis is placed on evaluation of the Social Brain Hypothesis as it is simultaneously a popular, well-accepted theoretical perspective, though it may have some problems or issues that need to be confronted. Moreover the current hypothesis could potentially be incorporated as an important feature or condition within the Social Brain Hypothesis or suggest that a reworking of this theory is necessary.

Chapter 4 will discuss the essential background for the present hypothesis, namely that chemosensation has declined in the lineage leading to humans. A particular

emphasis is placed on the conspicuous decrease in importance of conspecific chemical communication among primates. In the last section in this chapter, the increased need to infer social information from invariant cues as opposed to honest signalling is discussed.

In Chapter 5, the Inferential Brain Hypothesis is presented. Briefly, human brain expansion was driven by the need to extract biologically relevant social information by using inference from behaviours that are simultaneously variable and scattered across time, instead of the relatively simpler perceptual task of observing chemosensory, visual, or auditory signals from conspecifics. This increased cognitive demand and required larger brains with greater processing capacity. In the final portion of this chapter, the specific aims of this dissertation are laid out along with specific hypotheses.

Chapter 6 details the general approach and method utilized in this study, further details on the specific tasks will be given in Chapters 7-10, where each chapter is dedicated to the logic, design, results and discussion that pertains to each of the specific aims. Chapter 7 is focused on the role of target brain regions, including ventromedial prefrontal cortex and amygdala, in a form of biologically relevant decision-making, mate choice. Chapter 8 is focused on the process of social attribution, namely whether or not participants with damage to the target brain regions display normal biases in their attributions. Chapter 9 discusses the results pertaining to perspective-taking. The experiments in this chapter have been used to support the Social Brain Hypothesis. Thus this chapter is aimed toward validating or discounting these claims, given that the current hypothesis makes different predictions compared to the Social Brain Hypothesis. Chapter 10 is focused on the use of inferential processes, namely transitive inference, in both a general, non-social context, as well as in the context of accurately deriving a social hierarchy.

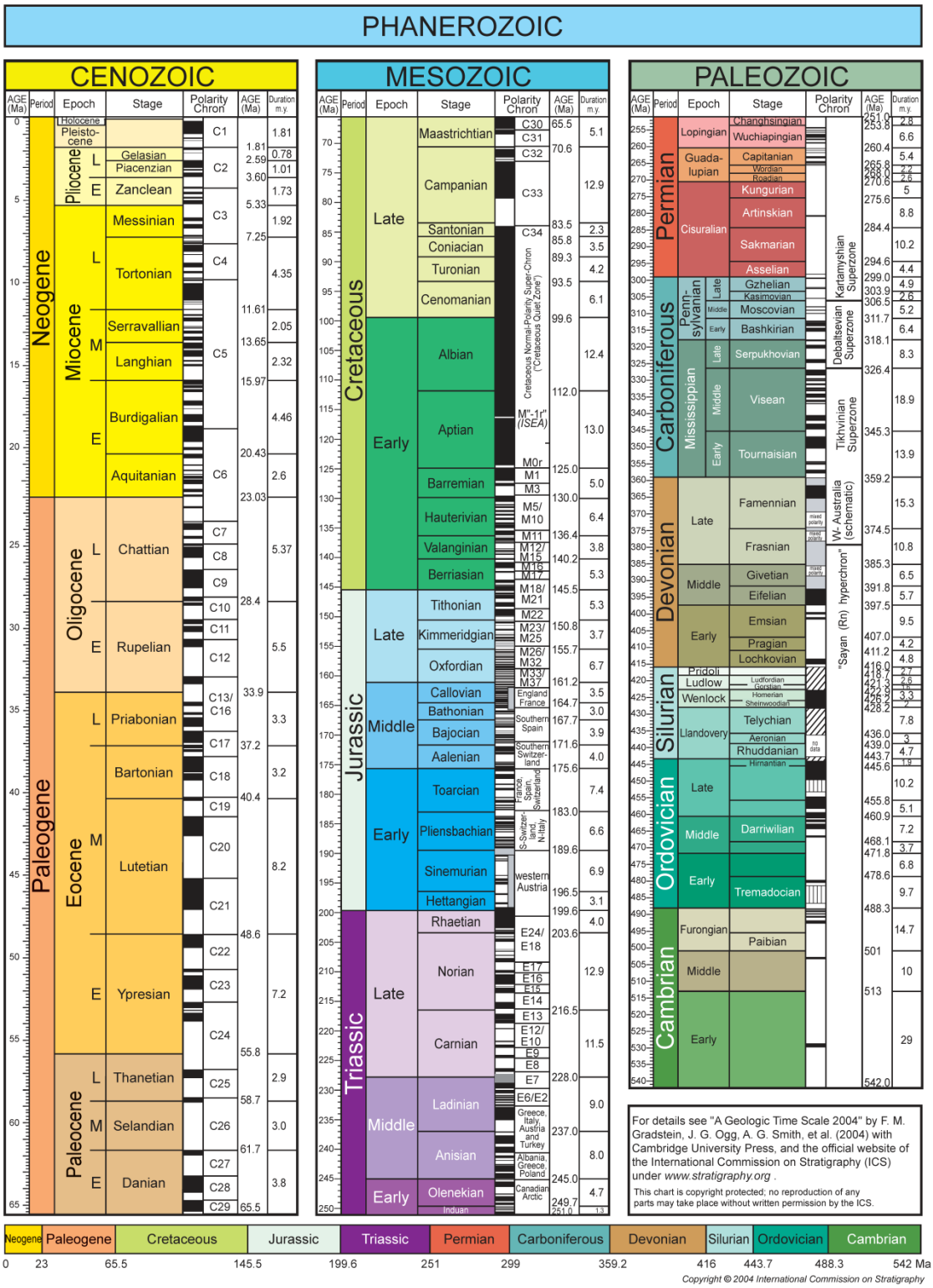
Finally, Chapter 11 will include a general discussion including an evaluation comparing the predictions and the observed results evaluating the value of the present

hypothesis. In the very last section, future directions and new questions that this research has raised will be discussed.

Terms that are printed in **boldface** are defined in Appendix A. Appendix B includes a qualitative analysis of regional brain volumes in primates and non-primate insectivores. These data also bear on the Inferential Brain Hypothesis as brain regions are expected to have evolved in a specific mosaic pattern, emphasizing the decreased chemosensory abilities in humans while predicting retention of chemosensory-related cortical regions.

Figure 1 – The Geologic Timescale – This table presents the accepted and up-to-date timing of major geologic periods throughout the history of multicellular life, and is included here as a reference for the time periods mentioned in the text. Reprinted from Lethaia, 37 (2), Gradstein, F. & Ogg, J, Geological time scale 2004 – why, how, and where next!, p.177, copyright 2004, with permission from John Wiley and Sons.

Geological Timescale



CHAPTER 1

EVOLUTION

Mammalian Evolution

Humans are members of the Mammalia class of vertebrate animals, which are distinct from other vertebrates in the possession of fur and mammary glands. Together, the mammals are a highly successful group of animals that dominate most ecosystems. The most obvious reason for the ecological dominance of mammals is their diversity in form and behaviour. The evolutionary path of mammals is unique and the many adaptations that mammals have evolved have set the stage for the diversity of mammals observed today. A particularly important suite of modifications includes changes to the mammalian skull, which indicate simultaneous changes to the structure of the mammalian brain.

The origin of mammals in the fossil record is accompanied by several defining features, including: (Cifelli, 2001; Luo, 2007; Luo, Kielan-Jaworowska, & Cifelli, 2002)-(for a more detailed list see Kielan-Jaworowska, Cifelli, & Luo, 2004, p. 109)

1. An enlarged braincase, with modifications to frontal and parietal regions
2. Alterations to the jaw, specific to mammalian mastication
    - the jaw consists of a single bone that joins to the skull
3. Alterations to the inner ear
    - the inner ear ossicles formed from other jaw bones

This cranial arrangement provides several advantages to the mammalian form. The presence of a single **temporal fenestra** allows for more jaw-closing musculature and a stronger bite and is diagnostic of inclusion among mammals and mammal-like reptiles (Kemp, 2005, p. 1). Alterations to the middle ear provide more sensitive hearing, particularly in the high frequency range, which may have been adaptive to an **insectivorous** lifestyle (Luo, et al., 2002). The enlarged braincase is of particular interest

to the current discussion and is definitely an important factor in the evolution of *Homo sapiens* which will be discussed in detail later. Interestingly, there is evidence to suggest that these three defining features of inclusion in Mammalia may be consequences of the same developmental perturbation where an enlarged brain case results in displacement of inner ear bones from the jaw (Rowe, 1996).

Living mammals can be defined by several criteria not explicitly found in the fossil record (Gingerich, 1977):

1. Suckling young (hence the term Mammalia)
    - Though lactation may predate true mammals (Oftedal, 2002), it may be integral to mammalian success (e.g., Pond, 1977).
2. Bearing of live young (with the exclusion of **Monotremata**, which lay eggs)
3. **Endothermy**, warm-bloodedness (Grigg, Beard, & Augee, 2004; B. K. McNab, 1978; Ruben, 1995)

In order to truly understand what mammals are it is important to have some sense of their evolutionary history, including the major selective pressures that have influenced mammalian evolution and led to the diversity of modern forms. What may be surprising is just how far back the mammalian branch of life extends, essentially almost back to the point where tetrapods (four-legged animals) first left the water.

Carboniferous – Permian Synapsids

Mammal evolution began in the late Carboniferous period, over 300 million years ago (Ma). Tetrapods had begun the move from aquatic habitats to terrestrial habitats as early as the preceding Devonian period (416 – 359 Ma). These early animals were relatively fish-like and gradually acquired characteristics that ultimately would free tetrapods from aquatic environments (review: Ahlberg & Milner, 2000). A key adaptation was the evolution of a protected egg, allowing total independence of an aquatic environment (Reisz, 1997). The Amniota, named for a particular feature of this

adapted egg, eventually became completely independent of aquatic ecosystems in the early Carboniferous period (~340 Ma) (Kupriyanova, 2009), and continue to dominate the terrestrial biosphere presently. Virtually all terrestrial animals including mammals, birds, reptiles, crocodiles, *etc.* are **amniotes**, excluding Amphibia (frogs, toads, salamanders, *etc.*), Arthropoda (insects, spiders, scorpions, *etc.*), Annelids and other worms (Kemp, 2005). Very early in the history of the amniote tetrapods (perhaps ~310 Ma during the late Carboniferous period, according to molecular data (Kupriyanova, 2009)), the group split into two taxa that would give rise to mammals (**synapsids**) and birds, dinosaurs, modern reptiles, and turtles (**sauropsids** refers to this whole group, **diapsids** includes only dinosaurs and birds) (Kielan-Jaworowska, et al., 2004; Kumar & Hedges, 1998; Laurin & Reisz, 1995; Reisz, 1997). This split represents the first dichotomy within the amniotes, and appears even in the oldest known amniote fossils.

The synapsids, sometimes referred to as the 'mammal-like' reptiles, became the dominant terrestrial animals during the Permian period, which lasted from 299 to 251 Ma (Gradstein & Ogg, 2004). The climate of the Permian period saw a progressive warming from ~2^{o} cooler than today during the Permo-Carboniferous glaciation (Royer, Berner, Montañez, Tabor, & Beerling, 2004) to ~5^{o} warmer than today by the mid-Permian (Kemp, 2006). Additionally, oxygen content in the atmosphere was declining from a high of 35% ~300 Ma to 27% ~267 Ma (21% today); carbon dioxide levels by contrast were rising from a minimum ~300 Ma to 1000 parts per million ~267 Ma (3 times higher than today) (Kemp, 1983; Royer, et al., 2004). Seasonal and latitudinal gradients in climate likely had a profound effect on determining which animals would survive and thrive, particularly those which benefited from increased endothermy.

Throughout the middle to late Permian period (299 – 251 Ma), synapsids dominated terrestrial ecosystems. Advanced synapsids began to appear around 270 Ma, the **therapsids**, which rapidly expanded to include temperate zones between 30 and 60^{o} both north and south of the equator (Kemp, 2005) and eventually completely excluded

their more primitive relatives, which survived only within 30^{o} of the equator (Kemp, 2006). From the fossil record, therapsids appear as a diverse group of related herbivores, carnivores, and a possible insectivore (Kemp, 2005). By the late Permian, **cynodonts**, characterized by a well-developed secondary palate separating the nasal passage for breathing and the oral passage for feeding, had evolved from advanced therapsids (Kielan-Jaworowska, et al., 2004). The order Mammalia, including all extant species, has been placed within an advanced group of cynodonts that managed to survive the end-Permian extinction (Kielan-Jaworowska, et al., 2004).

End-Permian Extinction and Triassic Mammalian Origins

The end-Permian extinction event (251 Ma) was a brief, non-catastrophic event that occurred synchronously across the globe and wiped out 90 – 95% of all species (Benton & Twitchett, 2003). One of the leading hypotheses for the sequence of events that led to the survival of only 5% of all species on Earth, suggests that rapid and dramatic climatic change was the root cause (Wignall, 2001), where simultaneously, world-wide photosynthesis slowed and temperatures rose. The surviving animals must have had sufficiently diverse diets to survive on what food remained and were located in sufficiently protected habitats to survive extreme seasons (Kemp, 2005).

About a dozen synapsid lineages are known or inferred to have survived the end-Permian event. Among these were at least two cynodont lineages that gave rise to mammals by the end of the Triassic period (Rubidge & Sidor, 2001). The earliest known animals to possess the defining features of mammals appeared during the late Triassic period, approximately 220 Ma ago (Cifelli, 2001; A. Crompton & Jenkins Jr, 1973; Gingerich, 1977). These early mammals likely had high levels of overall activity, high growth rates, and predator-prey ratios typical of endothermic animals (Kielan-Jaworowska, et al., 2004). By the late Triassic, despite being a diverse group, Mesozoic mammals were relatively rare and were overshadowed by the rapidly rising diapsids, the

dinosaurs. The remaining mammals were small and likely nocturnal. In order to survive in colder, dark habitats, this period of mammalian evolution may have led to the adaptations of endothermy, the mammalian reproductive system (Hopson, 1973), and necessitated a change in sensory apparatus in order to exploit low-light niches.

Mesozoic Mammals

The Mesozoic era lasted from 251 to 65.5 Ma ago,[1] capped by the end-Permian extinction event at its beginning and the Cretaceous-Paleogene extinction event at its end. The ancestral mammal descended from a long-standing sequence of small carnivores with an increasing ability to regulate their internal environment. These early mammals were small; 5 – 10 g, roughly the size of the smallest modern mammals; and were relatively rare (Kemp, 2005; Kielan-Jaworowska, et al., 2004). This ancestral mammal was endothermic (Grigg, et al., 2004), insectivorous, likely covered in fur, had a relatively large brain for its body size, and was most likely nocturnal in an arboreal environment.

The pattern of small-sized mammals persisted throughout the 155 Ma Mesozoic (Kemp, 2005; Kielan-Jaworowska, et al., 2004) though there is no consensus on the evolutionary causes for this maintenance of small size. Maintenance of this small size throughout the entire Mesozoic era is quite remarkable considering the great range in size prior to the end-Permian event and following the end-Cretaceous extinction event. It has been suggested that small size may be due to ecological exclusion by competing dinosaurs and non-dinosaur vertebrates, or as a secondary consequence of an inability to reduce body temperature like modern mammals or other anatomical or physiological constraints (see Kemp, 2005, pp. 185-186, for a discussion). The lineage that would eventually give rise to humans and all other placental animals was no exception to this

[1] Mesozoic refers the Triassic, Jurassic, and Cretaceous periods collectively, and corresponds to the common notion of the ‘Age of the Dinosaurs.’

diminutive stature. Indeed, the earliest stem **eutherians** (which appeared in the early Cretaceous period 146 – 99 Ma and includes all placental mammals) were very small, in the range of 5 – 20 g in overall body mass (Kielan-Jaworowska, et al., 2004).

Modern mammals are dominated by two main groups: placental mammals, which make up the vast majority of modern mammal species, and the **marsupials**, that make-up the large-part of the minority of living mammals. The split between these two main groups occurred somewhere between 104 and 218 Ma ago according to molecular data (105 Ma, Murphy, Pringle, Crider, Springer, & Miller, 2007), which is in line with the earliest known placental and marsupial mammals, 125 Ma ago (Kemp, 2005). Important to later discussion, the Mesozoic was not a time where mammals remained as static forms, despite all types remaining small in stature. Extant mammals represent only three surviving mammalian clades of ~25 distinct clades known to have evolved and gone extinct since the Mesozoic (Kielan-Jaworowska, et al., 2004; Luo, et al., 2002).

Of this great expansion in diversity, there were three groups which persist into the present: **Eutheria**, **Metatheria**, and **Monotremata**. Monotremata persist into the present in two forms, platypus and echidna (4 species); they are the only mammals to lay eggs and are defined by the presence of only a single duct for reproduction, urination, and defecation. Metatheria, which unites all extant marsupials and their extinct relatives, persist into the present with a notable diversification in Australia. Metatheria are defined by unique development which includes very short gestation followed most often by further development in an external pouch or marsupium of the mother; fossils are largely identified as Metatheria by their distinct dentition patterns. Finally, the Eutherian mammals, defined by unique reproductive physiology and often considered synonymously with Placentalia, are of particular interest to the present discussion as primates and humans are included within this group.

By at least ~65.5 Ma placental mammals had dispersed to all continents except Antarctica and Australia and currently comprise more than 1000 genera and more than

~5400 species (Luo, 2007; Wilson & Reeder, 2005). There was much supraordinal diversification within placental mammals during the Cretaceous period, shortly after the K-Pg event, and throughout the early Paleogene. The period between 100-85 Ma saw the origination of the many of extant mammalian orders and coincides with the origin of flowering plants (angiosperms) (Bininda-Emonds et al., 2007; Gingerich, 1977). The orders that diverged prior to the K-Pg boundary event (~5 – 12 million years prior) include Rodentia, Primates (~90 Ma) (Murphy, et al., 2007; Springer, Murphy, Eizirik, & O'Brien, 2003), Eulipotyphla (hedgehogs and moles), and Xenarthra (sloths and anteaters). Afrosoricida (tenrecs and golden moles), Chiroptera (all bats), and Cetartiodactyla (whales, pigs, and llamas) diverged approximately at the K-Pg boundary. Carnivora (cats, dogs, *etc.*), Lagomorpha (rabbits and pika), and Perissodactyla (rhinoceros and horses) diverged within the first 10 – 15 million years into the Paleocene[2].

Cretaceous – Paleogene Boundary

The Cretaceous period ended abruptly ~65.5 Ma when an asteroid, approximately 10 km in diameter impacted in the Yucatan peninsula, Mexico, leaving the ~180-200 km diameter Chicxulub crater and a worldwide layer of rock enriched in iridium from the impactor (Alvarez, Alvarez, Asaro, & Michel, 1980; Hildebrand, Penfield, Kring, Pilkington, & Camargo, 1991; Schulte et al., 2010). This impact had devastating effects on the environment and the habitats of the dinosaurs, mammals, and other flora and fauna both from the physical trauma of the impact itself and the impact on global climate as a result of short- and long-term consequences of the meteorite ejecta. The amount of debris thrown into the atmosphere led to a reduction of light levels shutting down photosynthesis. This lead to the destruction of food chains dependent on primary

[2] Divergence dates for the remaining mammalian orders are not adequately estimated given the small numbers of species in these families studied (Springer, et al., 2003).

production from plants, whereas the food chains relying on detritus (non-living organic material) were affected to a lesser degree (Schulte, et al., 2010; Sheehan, Coorough, & Fastovsky, 1996).

The Cretaceous – Paleogene (K-Pg) boundary event saw the extinction of all non-avian dinosaurs and the majority of all terrestrial vertebrates; 88% of terrestrial species went extinct (Sheehan & Fastovsky, 1992). Many vertebrate groups did survive, obviously, including fish, amphibians, lizards, snakes, turtles, crocodilians, birds, and mammals (monotreme, marsupial, and placental in addition to other now extinct types) (Robertson, McKenna, Toon, Hope, & Lillegraven, 2004). The mechanism of the extinction of the dominant land animals and the selective sparing of species was most likely a multifactorial combination of short- and long-term consequences of the Chicxulub impact. Immediately following the impact, reentry of ejecta sent into suborbital trajectories back into the atmosphere would have created a intense pulse of infra-red radiation that would have lasted hours (Robertson, et al., 2004), possibly resulting in energies similar to that of an oven on broil, igniting widespread wildfires in areas of sufficient fuel and literally roasting animals unable to escape the heat. The large amount of dust remaining in the atmosphere as well as the large quantities of sulphur released by the impact would have led to global cooling (~10^{o} C) (Schulte, et al., 2010) and global shutdown of photosynthesis as noted above. It appears that only animals capable of hiding underground or underwater from the heat pulse and those species that could adapt to abruptly cooler temperatures that followed could have survived the K-Pg extinction event.

The ecological niches and physiological **preadaptations**, including the improved homeostatic mechanisms of mammals as well as their small size, allowed them to survive this catastrophic event. At least 20 mammalian lineages with extant descendants survived the K-Pg event (Springer, et al., 2003), though most mammal radiations existing during the Mesozoic went extinct including two thirds of mammal species known from

the fossil record (Rose, 2006). The increase in diversity in mammalian orders may not be directly caused by the extinction event. In fact diversity was drastically curtailed. Rather, increased diversity occurred in the presence of niches that suddenly became vacant following the dinosaur extinction (Luo, 2007), though it occurred in lineages that had already diverged (Easteal, 1999).

Major Mammalian Adaptations

Among the myriad adaptations shared by all extant mammals, sensory adaptations merit special attention as they are vital to both day-to-day survival and may have shaped subsequent evolution and adaptations. Mass extinctions and relegation to tiny, nocturnal niches left an indelible mark on the mammalian brain leading to enhanced processing of the world. The evolution of enhanced auditory processing, whereby skull bones were converted into inner ear ossicles as mentioned above, characterizes all mammals. The evolutionary enhancement of the chemical senses likely had a profound impact on mammal evolution.

The key to the survival of any species is reproduction, and this requires finding a suitable mate. Early mammals needed to locate conspecifics in low-light conditions, without alerting potential predators. Chemical signalling in early mammalian ancestors was adapted or exapted as a likely means to communicate between conspecifics covertly. The adaptation of conspecific chemosignalling is not a mammal-specific adaptation as it is common in out-group reptiles; however there was obvious positive selective pressure maintaining and elaborating this trait among mammals, given the prevalence among extant species and the often extensive neural architecture supporting olfaction. In contrast, extant species of birds rely more heavily on visual information likely reflecting adaptations to diurnal living during the same evolutionary time. The adaptation of conspecific chemical communication in mammalian ancestors may have evolved out of the need to find and advertise fitness to mates without alerting predators. Airborne

(volatile) odourants may be one way to achieve this (*e.g.,* many species of moths communicate over distances of up to many miles this way). However, volatile odourants may be easily intercepted and may not persist long enough in a restricted area to signal location accurately. Fortunately for our mammalian ancestors, non-volatile[3] substances, such as components found in urine, sweat, and other bodily secretions, can also be used to communicate. The vomeronasal organ (VNO) evolved in mammalian ancestors as well as many reptiles[4] to detect these non-volatile odourants. By utilizing non-volatile odourants, mammalian ancestors evolved a mechanism of covert social communication. The essential components of this covert communication system include: sensory structures, adapted to efficiently sample the environment; a functional sensory transduction mechanism, to convert environmental signals into neural impulses; sensory processing apparatus in the brain, such that incoming information can be processed and biologically relevant information can be extracted; and lastly this system must interact with other brain systems such that sensory information can affect behaviour. The processing requirements of this sensory apparatus (the VNO and accompanying brain structures) has likely shaped the evolution of the mammalian brain, putting systems in place that have been largely co-opted, expanded, or otherwise utilized and altered by the evolution of primates and the human species.

Primate Evolution

Of the small-bodied mammals that coexisted and evolved in the shadows of the dinosaurs, the present discussion is ultimately concerned with the lineage that gave rise to Primates and among the primate linage that which evolved into *Homo sapiens*. Over a

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3 "Non-volatile" more accurately means low volatility such that these chemicals are in the liquid state at standard temperature and pressure.

4 For example, snakes whose forked tongue whips out, picks up odourants, and then retracts and places these chemicals directly in the openings of the VNO, or in some turtles which use it to smell underwater where chemicals are obviously not airborne.

period of time spanning more than 300 million years and surviving multiple mass extinctions, mammals and their ancestors evolved the sensory apparatus to sample from multiple distinct modalities, and the bodies and behaviours capable of surviving and thriving in their respective ecological niches. The evolution of Primates from small, placental mammals occurred sometime between 104 and 218 Ma. Molecular evidence suggests that the Primate-Rodent split occurred ~96 Ma (Nei & Glazko, 2002). Despite having diverged from other modern groups of mammals within the Mesozoic, it was not until the early Paleogene period that Primates greatly diversified.

Primates includes all apes, monkeys, tarsiers, lemurs, and humans as well as closely related fossil taxa (Rose, 2006). Characteristic primate traits include: opposable big toes and thumbs, flat fingernails as opposed to claws, forward-facing eyes and other cranial adaptations related to the orbits, brain enlargement, reduction in olfaction, and enlargement in vision (Preuss, 2007).

Archaic primate ancestors, **Plesiadapiformes**, flourished in the early Cenozoic[5] and ranged from the very small *Picromymus* (10 g) to the small *Plesiadapis* (5 kg). The plesiadapiformes lacked several primate characters including opposable toes and fingernails (Rose, 2006). The ecological niche of plesiadapiformes spanned at least the three northern continents, where specimens have been found, and approximated that of future rodents and true primates though they would be extinct by the Eocene likely from competition with these groups (Rose, 2006). **Euprimates**, or true primates, fall into two broad categories that exclude the archaic plesiadapiformes, the first fossil evidence of true primates comes from ~ 55 – 60 Ma (Miller, Gunnell, & Martin, 2005). Among the euprimates, the **strepsirrhine** primates include modern lemurs, lorises, and galagos. Second, the **haplorhine** primates include tarsiers, monkeys, apes, and humans.

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[5] The Cenozoic contains the Paleogene and Neogene periods and has lasted from 65.5 Ma to the present. It is often referred to as the 'Age of Mammals.'

Molecular sequence data suggest that the strepsirrhine – haplorhine split occurred shortly after the split between Primates and Rodentia ~77.5 Ma (Siepel, 2009; Steiper & Young, 2006). See figure 2 for a graphical representation of primate relationships and nomenclature.

The euprimate skeleton retains many primitive eutherian traits, including five digits on both the hands and feet, but also many adaptations to arboreal life. A major adaptation is large, anteriorly-facing orbits and a distinct and complete postorbital bar which provides a bony shield to the lateral aspect of the eye. Relevant to the present discussion, the euprimate braincase is enlarged particularly due to enlargement of the cerebrum at the expense of a shorter, broader snout (Rose, 2006). The postcranial skeleton of euprimates has evolved to be highly flexible at the shoulder, elbow, hip, and ankle joints, allowing a broad range of motion in their arboreal environment. The strepsirrhine primates tend to be nocturnal, solitary, and omnivorous, with the exception of the larger lemurs in Madagascar, which tend to be diurnal, social, and herbivorous. Tarsiers, among the haplorhines tend to be nocturnal, solitary, and insectivorous and have characteristically huge eyes.

The remaining splits within these two main primate groups all postdate the K-Pg boundary. Within the haplorhine primates, New World Monkeys, or **platyrrhine** primates, split from the other primates as they radiated into South American habitats approximately 42.9 Ma (Steiper & Young, 2006). The platyrrhines split from the rest of the primates, the **catarrhines**, approximately 42.9 Ma (Steiper & Young, 2006) during the mid Eocene. Together the platyrrhine and catarrhine primates are referred to as the **anthropoids**.[6] The anthropoids are diurnal (excluding the platyrrhine *Aotus*), social, and herbivorous, **frugivorous**, or insectivorous (humans being a clear exception of omnivory)

[6] Some researchers include Tarsiiformes in Anthropoidea and others do not, though where exactly tarsiers fall is somewhat irrelevant to the present discussion

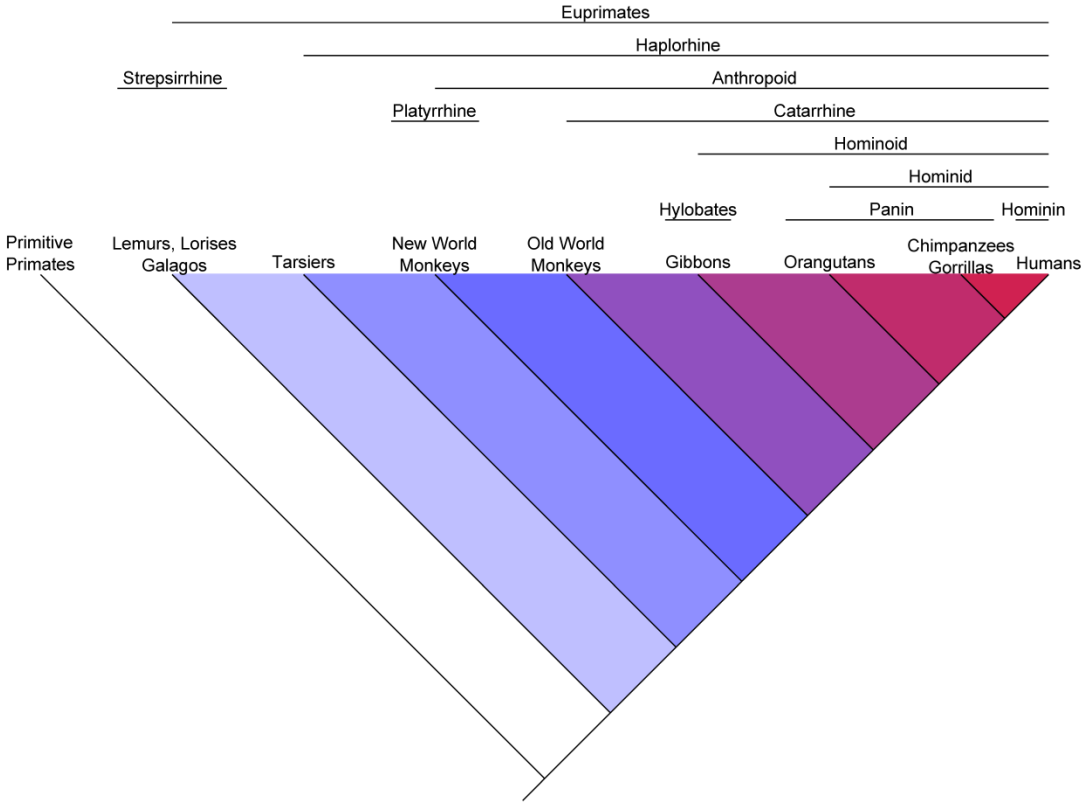

Figure 2 – Primate relationships and nomenclature. Species and groups of species are listed from left to right in order of closer relatedness to primitive primates to humans. Terminology above the species depicts the species and groups of species when referring to higher-order groups.

and probably originated early in the history of primates separate from strepsirrhine and **tarsiiforme** primates (Miller, et al., 2005). Approximately 30.5 Ma the **hominoids** split from the **cercopithecines**, where the latter consist of all Old World Monkeys including baboons and macaques (Steiper & Young, 2006). Within the hominoids, the **hylobates**, the gibbons, split from the great apes approximately 20 Ma (Siepel, 2009). The remaining hominoids, commonly known as the great apes and referred to as the **hominids**, consist of three groups: the orangutans, which split from the other hominids 18.3 Ma; the gorillas which split off 8.6 Ma; the chimpanzees (**panins**), which split 6.6 Ma, and the remaining primates which consists of humans and all species more closely related to us than other extant primates, the **hominins**.

Primates as a group are exquisitely adapted to life in the trees, and they evolved and flourished at a peculiar time in Earth's history when this arboreal ecological niche practically spanned the globe. To aid in understanding how primates evolved, an understanding of their world and the factors influencing their evolution (and the evolution of all other mammals alive at the time) is beneficial.

Paleogene Radiation

Following the K-Pg event and the demise of the dinosaurs ~65.5 Ma ago, an evolutionary radiation of mammals began leading eventually to the terrestrial domination by mammals observed today. Within ~10 Ma of the K-Pg extinction during the Paleocene epoch, mammals had reached hundreds of kilograms in body mass by the Eocene epoch (~56 Ma) and occupied all possible niches from bats in the skies to whales in the seas (Kielan-Jaworowska, et al., 2004). Following a sharp decline in mammal diversity following the K-Pg event, diversity at the family level of mammals increased steadily into the mid-Eocene epoch (48.6 – 40.4 Ma), declined somewhat in the Oligocene epoch (33.9 – 23.03 Ma) before reaching an all time high in the middle Miocene (15.97 – 11.61 Ma) (Rose, 2006).

The climate during the Paleocene epoch (65.5 – 55.8 Ma) and Eocene epoch (55.8 – 33.9 Ma) was much warmer than any other time during the Cenozoic period (including today), with little seasonal or latitudinal variation (Greenwood & Wing, 1995; Rose, 2006). These early Cenozoic epochs saw an unprecedented diversification in mammalian species (Alroy, 1999). 44 new families appear within a few million years of the K-Pg boundary, an additional 41 families by the end of the Paleocene (55.8 Ma) and a further 61 new families in the early Eocene (48.6 Ma) (Rose, 2006). Within these orders, the oldest split is within Primates ~77 Ma, where molecular data even suggest that the subordinal split between haplorhine from strepsirrhine primates occurred within the late Cretaceous (Rose, 2006).

The Paleocene epoch was marked by extreme environmental change in its beginning following the K-Pg boundary event and the Paleocene-Eocene Thermal Maximum that marked its end. At this thermal maximum the mean annual temperature at 45^{o} latitude was at least 27^{o}C.[7] These warm temperatures coupled with low seasonal or latitudinal variability likely resulted in almost global forestation from tropical rainforests up to 50^{o} from the equator, and other forests extending past 70^{o} from the equator essentially to the pole. This situation of low environmental variability probable made it relatively easier for mammals to migrate across available land routes (Rose, 2006) and provided huge areas of primate-suitable habitat. The mid-Eocene (48.6 – 37.2 Ma) was an important era of mammalian diversification, not least for the evolution of the earliest recognizable relatives of monkeys and apes (Beard, 2006; Prothero, 2006). By the late Eocene however, primates were extinct in Europe and much of North America and Asia, though they flourished in Africa (Prothero, 2006) where suitable forest habitat persisted.

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[7] compare this to the average temperature in Iowa City (41^{o}38' N 91^{o}33' W) in 2009 was 16.4^{o}C (Calculated using data available at http://www.weather.com/weather/wxclimatology/monthly/graph/52240?from=tenDay_bottomnav_undeclared)

Following the climatic optimum of the early Eocene, a long-term trend of global cooling began that continues into the present. Earth became substantially cooler around the Eocene-Oligocene transition (33.9 Ma) which corresponds to the appearance of permanent ice sheets. This change in global temperatures is punctuated by a decrease of ~12^{o}C at the transition between the mid- to late-Eocene (37.2 Ma) and perhaps led to the largest faunal change in the Cenozoic (Prothero, 2006). The late Eocene (37.2 – 33.9 Ma) saw a rebound in global temperature (~2^{o}C), however this did not persist. Rather, another bout of rapid global cooling, referred to as the Terminal Eocene Event (33.9 Ma, at the boundary of the Eocene and Oligocene) occurred. In the case of the Eocene – Oligocene boundary, massive global cooling, ~13^{o}C (review: Prothero, 1994), resulted from changes in ocean currents that in turn resulted in latitudinal stratification of temperatures such that ice sheets began to form at higher latitudes which further compounded cooling effects by reflecting more sunlight (Cavelier et al., 1981; Eldrett, Harding, Wilson, Butler, & Roberts, 2007; Lear, Bailey, Pearson, Coxall, & Rosenthal, 2008). Other researchers have suggested that increased seasonal variation in temperatures, particularly a 4^{o}C cooler winter, not overall climate cooling drove extinctions at the end of the Eocene (Ivany, Patterson, & Lohmann, 2000). The transition from the 'greenhouse' conditions extending from the Cretaceous through to the mid-Eocene was a marked change to 'ice house' conditions, with at least polar glaciation, that extend from the Oligocene to the present (JC Zachos, Shackleton, Revenaugh, Palike, & Flower, 2001). The Terminal Eocene Event resulted in the extinction of the extremely large browsing mammals, changes in turnover in carnivoran mammals (Van Valkenburgh, 2003), and extinction of 82% of placental mammals in Europe (Blois & Hadly, 2009). Present day mammal families are represented in the Oligocene, however they were not necessarily in their modern 'ecomorphological' roles (Janis, 1993). For example members of the bear family filled fox- or raccoon-like roles and canids (*e.g.*, dogs, foxes, and wolves) were small omnivores rather than large predators. By the late

Eocene, primates had spread to South America, leading eventually to the radiation of the New World monkeys (Prothero, 2006). However the large floral changes from vast expanses of tropical forest to latitudinally stratified **biomes** reduced the availability of the ancestral primate ecological niche.

Major Primate Adaptations

The first undisputed primate specimens are found from around the Paleocene – Eocene boundary (~55 Ma) (Martin, Soligo, & Tavaré, 2007) having evolved from a last common ancestor during the Cretaceous period (80 – 90 Ma) (Kumar & Hedges, 1998; Martin, et al., 2007). Primates are characterized by enlarged cranial capacity, **prehensile** hands and feet (and in some cases tails), optical convergence and stereopsis, regression of the snout and olfaction as well as other derived features (Radhakrishna, 2006). The selective pressures that resulted in primate evolution are a matter of intense debate and there is no clear consensus. There are several theories, each suggesting a specific selective pressure that resulted in the suite of primate adaptations.

1. *The Visual Predation Hypothesis* (Cartmill, 2002): The last common ancestor to all extant primates was an insectivorous predator that utilized vision to locate prey in the canopy and undergrowth of tropical forests. However additional research suggests that the primitive primate condition was omnivory, as ~95% of extant primates are omnivores (Harding, 1981)[8].
2. *The Angiosperm-Coevolutionary Hypothesis* (Chapman & Onderdonk, 1998; Sussman, 1991): The Paleocene-Eocene transition is remarkable for the shift in dominate terrestrial flora, in which angiosperms (flowering plants) became the dominate plant species on Earth. The fact that

[8] Cannot find this original work. Cited information is taken from (Sussman, 1991).

angiosperm radiation and primate evolution coincide in time and space has led to the suggestion that coevolutionary forces were the significant factors in the evolution of both groups. Basically, primates evolved to take advantage of the rich food stuffs provided by angiosperms on their terminal branches. In return, the primates served as seed dispersal agents for the angiosperms.

3. *The Leaping-Grasping Hypothesis* (Bloch & Boyer, 2002; R. Crompton, 1995; R. Crompton & Sellers, 2006): Primate adaptations are primarily needed for efficient and accurate locomotion in the forest canopy. This includes prehensile limbs and binocular convergence for stereopsis and breaking through camouflage.
4. *The Frugivory/Nectivory Hypothesis* (Barton, 1998; Osorio, Smith, Vorobyev, & Buchanan-Smith, 2004; Osorio & Vorobyev, 1996): Primate specializations are best-suited for visually-guided reaching and manual manipulation of fruits, leaves, and flowers that are distinguishable from a green leafy background or non-ripe (and less nutritious) plant foods via trichromatic vision, particularly those found at the terminal branches of trees.
5. *The Snake Detection Hypothesis* (Isbell, 2006): Co-evolution with snakes, first constricting then venomous, drove primate evolution to minimize mortality from snake contact. Increased orbital convergence enhances primate abilities to 'break through' camouflage under conditions of invariant trichromacy, which ironically is less effective than dichromacy at breaking through camouflage (Morgan, Adam, & Mollon, 1992).

The problem with each of these hypotheses is not necessarily that any of them are incorrect in the details. Each points to a potentially valid selective pressure that led to the evolution of Primates. However, looking for a single selective pressure that gave rise to a

specific clade is probably too narrow. Rather, the entire suite of selective pressures that constitute an ecological niche shape the problem-space that an organism must solve in order to survive and thrive.[9] All of the hypotheses overlap in explaining distinct aspects of early primates' environment that it needed to be adapted to in order to survive. Early primates likely needed an omnivorous diet rich in energy dense fruit and nectar, though these food sources are potentially low in protein which may likely be supplemented by insects. These food stuffs are found in the terminal branches of angiosperm trees, which require adept skill at leaping and grasping to reach them and to avoid plummeting to the forest floor. Furthermore, leaping and grasping require accurate positioning of target branches in three-dimensional space as well as accurate identification and discrimination between safe branches and branch-like snakes. What is certain, regardless of the ultimate cause, is that the ancestral primate condition led to the adaptations of enlarged brains, enhanced visual processing (including an avascular fovea), decreased chemosensory processing, prehensile limbs, omnivorous diets, and enhanced sociality (Cartmill, 2002). It is important to note that although the mammalian ancestors of primates were small, arboreal and nocturnal, the primates that would diverge to become the haplorhine primates were diurnal, which probably increased the importance of vision as a remote sensor of the environment (C. Ross, Hall, & Heesy, 2005).

The great apes (hominoids) had split from the Old World monkeys (cercopithecines) between ~19 and 30.5 Ma (Kumar & Hedges, 1998; Nei & Glazko, 2002; Pilbeam & Young, 2004; Siepel, 2009; Steiper & Young, 2006). This divergence is marked by striking contrasts in feeding, locomotion, reproduction, and development. It appears as though hominoids evolved more efficient means of locomotion, dominated by forelimb-suspension, to relocate between scarce high-quality food patches, whereas the

[9] This concept is similar to the concept of *mosaic evolution* by which species arise through acquisition of characters in stages, not all at once.

cercopithecoids retained the less efficient quadrupedal style of arboreal locomotion but adapted their dentition to more abundant but lower quality food (Temerin & Cant, 1983). Further locomotor adaptations within the human lineage have occurred leading to the unique upright, bipedal locomotion observed in the genus *Homo.*

Hominin Evolution

The evolution of hominins is of great interest and has received a great deal of attention and perhaps as a by-product of this attention, there is not necessarily any consensus on how to define and label hominin species. For simplicity, I will stick to a less speciose hominin taxonomy, similar to that of de Sousa and Wood (2007), with the exception of maintaining a strict categorization of *Homo sapiens* as anatomically modern humans, and grouping *Homo antecessor, heidelbergensis,* and *neanderthalensis* as archaic humans referring to this group as *Homo neanderthalensis s. l.* The species name for those that are not strictly defined will be followed by *s. l.* (*senso lato, i.e.,* in a broad sense) to refer to this looser definition.

The earliest hominins *Ardipithecus ramidus s.l.*[10] existed between 7.0 and 4.4 Ma (de Sousa & Wood, 2007), which is consistent with the molecular data for human-chimpanzee divergence between 4.98 and 7.02 Ma (Kumar, Filipski, Swarna, Walker, & Hedges, 2005). The hominins that would immediately follow the ardipithes were the australopithes, including *Australopithecus afarensis s. l.,*[11] which existed between 4.5 and 3.0 Ma, and *Australopithecus africanus,* which existed between 3.0 and 2.4 Ma (de Sousa & Wood, 2007). The australopithes appear to have given rise to at least two distinct lineages. One of these, the 'robust' australopithes, consisted of *Paranthropus*

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[10] *Ardipithecus ramidus s. l.* consists of *Ardipithecus ramidus*, and *kadabba*, *Sahelanthropus tchadensis*, and *Orroron tugenensis.*

[11] *Australopithecus afarensis s. l.* consists of *Australopithecus afarensis, anamensis,* and *bahrelghazali*, and *Kenyanthropus platyops.*

boisei s. l.,[12] which is known to have lived from at least 2.5 – 1.3 Ma and *Paranthropus robustus*, which existed between 2.0 and 1.3 Ma (de Sousa & Wood, 2007). The robust australopithes had more robustly built jaws and faces compared to the 'gracile' australopithes. The 'gracile' branch extending from the australopithes gave rise to the genus *Homo*.

The earliest members of the *Homo* genus was *Homo habilus s. l.*[13] existing between 2.4 and 1.6 Ma (de Sousa & Wood, 2007). Partially overlapping with *Homo habilus* was *Homo erectus*, probably the longest living hominin having existed from 1.9 to 0.2 Ma (de Sousa & Wood, 2007). An offshoot of *Homo erectus* that has received a fairly large amount of recent media attention is the diminutive *Homo floresiensis*, which appears to have existed between 90 and 12 thousand years ago (Ka) (de Sousa & Wood, 2007). Also stemming from *Homo erectus*, archaic humans *Homo neanderthalensis s. l.* evolved and inhabited the Earth between 0.7 Ma and 30 Ka (de Sousa & Wood, 2007). *Homo sapiens* appeared about 190 Ka in anatomically modern form (de Sousa & Wood, 2007).

Hominins evolved from arboreal hominid ancestors into its bipedal modern form in a fairly short period of time. It is important to point out that the evolution of *Homo sapiens* was far from a linear progression, rather a bushy, speciose conglomeration of evolutionary experiments. The adaptations of hominins appear to be a result of rapid and dramatic climate changes (Ash & Gallup, 2007). Hominins were the only hominoids to have adapted to the opening of the forests into grassland savannahs that resulted from increased latitudinal and seasonal stratification of climate. Rather than being adapted to one particular climate or habitat, environmental variability in the later Neogene period

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[12] *Paranthropus boisei s. l.* consists of *Paranthropus boisei* and *aethiopicus,* as well as *Australopithecus garhii*.

[13] *Homo habilus s. l.* consists of *Homo habilis* and *rudolfensis*.

may have been an important factor in the evolution of behavioural flexibility characteristic of *Homo*.

Neogene Adaptation

Global cooling and increased seasonal changes in temperature had a profound influence on mammalian evolution during the Neogene period (23.03 Ma – present) (Blois & Hadly, 2009). For example, following the evolution of C4 grasses[14] in the Oligocene, temperate grasslands, resistant to large seasonal differences in rainfall and decreased carbon dioxide levels, expanded and resulted in turnover of species favouring grazers over browsers (Cerling, Ehleringer, & Harris, 1998; Cerling et al., 1997; Janis, Damuth, & Theodor, 2000; Osborne, 2008). The massive change in flora from closed forest ecosystems to open grassland ecosystems favoured species adapted to this open environment. Indeed many of the larger Oligocene mammals went extinct, though smaller members of the same order were more likely to persist and fill these vacant niches (Janis, 1993). The early Miocene epoch (23-03 – 15.97 Ma) was still relatively warm up until the mid-Miocene Climatic Optimum (17 – 15 Ma) (J Zachos, Pagani, Sloan, Thomas, & Billups, 2001), but there were larger temperature differences by latitude from the equator to polar regions. A combination of the uplift of large mountain ranges including the Himalayas, Rockies, and Andes, which exposed carbon dioxide absorbing minerals, as well as the opening and expansion of oceanic passages between continents, particularly the opening of Drake's Passage leading to the cold circumpolar current around Antarctica, are the likely causes of this global climate change (Cerling, et al., 1998; Cerling, et al., 1997; Janis, 1993; Osborne, 2008). Global temperatures continued to drop following the mid-Miocene Climatic Optimum, marked by the return

[14] C4 photosynthesis as opposed to C3, is an adaptation to arid conditions whereby sugars are more efficiently created at higher temperatures and water is used more efficiently. Corn is an example of a C4 plant.

of vast ice sheets in Antarctica by 10 Ma in the late Miocene and ice in the Arctic by the early Pliocene (5.33 Ma) (Alroy, Koch, & Zachos, 2000).

The Neogene was not characterized by mass extinctions anywhere near the scale of previous events, although there was massive turnover of species and changes in levels of species diversity. Massive animal migration occurred during the early Miocene, perhaps due to warmer conditions that opened up passage along the Bering Strait (Prothero, 2006). Primates began emigrating from Africa by the middle Miocene and later diversified into the hominoids, adapted to woodland environments. Moreover, in the late Miocene, continued opening of habitats into savannahs and grasslands led to the diversification of hominoids, bipedalism, and eventually humans (Janis, 1993). The radiations of Primates in Europe that began around 16 Ma as they migrated from Africa ended by about ~9 Ma. Primates did not disappear from Africa; instead they diversified into Old World monkeys, numerous genera of apes including the first members of the Hominidae family (Prothero, 2006).

Interestingly, in the Neogene period, environments became less productive and more variable, in fact modern types of desert and other arid landscapes are largely limited to the past 5.33 Ma (Janis, 1993; Singh, 1988). The Pliocene epoch (5.33 – 1.81 Ma) represents the last of the warm periods to Northern Hemisphere glaciation, a continuation of the global cooling trend. By the late-Pliocene hominins were very diverse, including *Ardipithecus*, *Australopithecus*, and *Homo* (Prothero, 2006). At the same time as the diversification of the human lineage, the Old World monkeys were gradually replacing the apes, where only extant lineages survived. The diversification of baboons and hominins is likely a result of ground-dwelling adaptations being favoured in grassland ecosystems (Prothero, 2006). By the beginning of the late Pliocene (3.60 Ma), the Earth had cooled to ice age conditions, and for the first time an Arctic ice cap appeared (Kennett, 1995). Increased glaciation lowered sea levels such that intercontinental migration was again possible, particularly in the form of North American animals

invading South America displacing its endemic species (referred to as the Great American Interchange) (Prothero, 2006; S. Webb & Opdyke, 1995).

Pleistocene Origins

The Pleistocene epoch (beginning 1.81 Ma) is characterized by periodic episodes of glaciation and relatively warm interglacial periods. At glacial maxima, occurring at ~100 000 year intervals, ice sheets covered much of northern latitudes including much of the northern United States and all of Canada. The last glacial period lasted from 75 to 17 thousand years ago (Ka) (Prothero, 2006). By 1.9 Ma, *Homo erectu*s had appeared, and *Homo neanderthalensis* and early *Homo sapiens* were predators in the late Pleistocene. The current Holocene era (beginning ~10 Ka, makes up the most recent interglacial period of the Pleistocene), is marked by another extinction probably driven in part by climate change and the spread of modern humans, hunting (Barnosky, Koch, Feranec, Wing, & Shabel, 2004), and undoubtedly human-driven habitat change and loss. Humans are now overwhelming the geological and climatic forces of nature, and it is argued that we have recently entered a new geological epoch reflecting human domination. The controversially defined Anthropocene (beginning in 1784 CE) coincides with increased carbon dioxide and methane trapped in polar ice and coincides with the advent of the steam engine (Crutzen, 2002; Steffen, Crutzen, & McNeill, 2007). Humans currently add more nitrogen to the biosphere than all natural sources, move more soil than natural forces including erosion (Wilkinson & McElroy, 2007), and are responsible for possibly the largest and fastest mass extinction ever (compare 30 000 species per year at the current rate to not much more than 10 species every four years for the other major extinctions) (Prothero, 2006). Though it seems that mammals are superbly adapted to change, it remains to be seen whether or not mammalian adaptations will allow them to survive the unprecedented, rapid human-induced changes.

Major Hominin Adaptations

Hominins evolved several important features that have allowed humans to exploit almost every niche on Earth. Important and obvious adaptations include bipedal locomotion, improved manual dexterity and tool use, and an extremely large brain.

The traditional view is that hominins and bipedal locomotion evolved when climate change led to the opening of large stretches of savannah, however recently published data on *Ardipithecus ramidus* suggests that bipedalism evolved in a woodland environment (Isbell & Young, 1996; Louchart et al., 2009; Lovejoy, Suwa, Spurlock, Asfaw, & White, 2009; WoldeGabriel et al., 2009). *Ardipithecus ramidus* is close to the last common ancestor of humans and chimpanzees, which suggests that both humans and chimpanzees have many derived features. For chimpanzees these include knuckle-walking and a relatively large face including enlarged canines. The derived features that make up *Homo sapiens* were acquired in a mosaic fashion during hominin evolution. Despite having evolved facultative bipedalism (Lovejoy, et al., 2009), *Ardipithecus* retained adaptations to an arboreal lifestyle as well as a relatively small cranial capacity, ~300 – 350 cm^3 (Suwa et al., 2009).

Australopithecus (of which there are many known species in this genus, including *Australopithecus afarensis*) had further adaptations toward bipedalism, though maintained longer forelimbs compared to hind limbs than observed in modern humans suggesting an arboreal aspect to their way of life (Aiello & Andrews, 2000). Additionally, *Australopithecus* had evolved a larger brain than *Ardipithecus*, ~400 – 550 cm^3 (Suwa, et al., 2009). It seems that australopithes had evolved an ability to exploit both closed forest and relatively open woodland-savannah habitats, a flexibility that few mammal species share (Aiello & Andrews, 2000), perhaps indicating an early example of the increased behavioural flexibility observed in humans. Additionally there is evidence for an increasingly varied diet, including not only fruits from the forest but grasses, sedges, and possibly meat (Aiello & Andrews, 2000).

Within the genus *Homo,* there is a clear enlargement of cranial capacity when comparing modern to ancestral forms (though *Homo neanderthalensis* may have had an absolutely larger brain than modern *Homo sapiens* (Ruff, Trinkaus, & Holliday, 1997)). A portion of this increase in brain size is immediately attributable to the increase in overall body mass of members of *Homo* compared to earlier hominins (Aiello & Wells, 2002). Interestingly this increase in overall body mass is more pronounced in females than in males, resulting in a reduction in sexual dimorphism (Aiello & Key, 2002). In addition, obligate bipedalism evolved in *Homo,* which appears to coincide with continued opening of woodlands into savannah. Within the *Homo* genus the ability to use and create complex tools, the ability to communicate using complex syntactic language, and complex social structure and culture evolved. Where, when, and how these profoundly human traits evolved are a matter of intense debate and there is no clear consensus on the proximate or ultimate causes.

Key to the present discussion is the observed decline in importance of chemosensation throughout primate – hominin evolution, coinciding with enhanced visual processing particularly in the domain of colour vision (Gilad, Wiebe, Przeworski, Lancet, & Pääbo, 2004). Potentially, a shift in the dominant sensory apparatus in Primates, especially humans, has been an important driving force in the evolution of enhanced cognitive abilities.

CHAPTER 2

BRAIN EVOLUTION

Vertebrate Brains

The brains of all vertebrates can be subdivided into 3 components: rhombencephalon (medulla, pons, and cerebellum), mesencephalon (midbrain), and prosencephalon (telencephalon and diencephalon). All of the major senses, including chemical (olfactory and taste), visual, auditory, mechanosensory, vestibular senses were all established in early vertebrates, though not all at once (Butler & Hodos, 1996). In early vertebrates it is likely that the entire dorsal telencephalon (pallium) was olfactory. Additionally a striatal area in the telencephalon is likely **plesiomorphic** for vertebrates. The vertebrate diencephalon consists of several regions unique to vertebrates, including asymmetrical habenulae, and regions plesiomorphic to vertebrates and other chordates, including the retina. The sensory regions in the tectum (roof) of the midbrain may be unique to vertebrates, including the superior and inferior colliculi.

The last common ancestor to reptiles and mammals may be assumed to have had a brain very similar to that of modern reptiles. To understand what is unique to the mammalian brain one must have some idea of what the ancestral form was like, for instance, what structures are present in the reptilian brain. The reptilian telencephalon can be divided into two main subdivisions: the pallium and subpallium. The pallium can be divided into medial, dorsal, and lateral components each made up of three-layered cortex. The medial pallial component corresponds to hippocampal cortex, the dorsal component corresponds to isocortex, and the lateral component corresponds to piriform cortex. Subpallial regions include the basal ganglia which are highly conserved in all vertebrates though there may be important differences in input and output targets.

Birds have independently evolved a columnar-like organization in their hyperpallium (potentially homologous to mammalian isocortex discussed below)

(Medina, 2004). Additionally, there is a periventricular structure, called the dorsal ventricular ridge (DVR), which is the largest component of the telencephalon of reptiles (and birds) and serves as a main region of receiving input from non-olfactory senses (Aboitiz et al., 2003). The DVR can be divided further into 2 subcomponents an anterior portion (ADVR) which receives sensory input and projects to subpallial regions and the posterior/basal portion (PDVR) which in turn projects mainly to the hypothalamus. The ADVR most closely resembles the sensory, lateral amygdala of mammals (discussed below) (Bruce, 2007).

Mammalian Brains

The mammalian brain evolved uniquely compared to the brains of birds and reptiles. Mammals possess unique, derived structures in the telencephalon, namely isocortex (also known as neocortex, however since there are homologues in all amniote brains, the term 'neo' is not necessarily accurate). Isocortex is a six-layered section of the cerebral cortex in contrast to the other portions of cerebral cortex, medial cortex (essentially the hippocampal formation) and lateral cortex (essentially olfactory cortex),[15] which have fewer cortical layers (Northcutt & Kaas, 1995). Isocortex appears to have undergone dramatic expansion across all mammalian taxa, and is especially pronounced in humans (Jerison, 2007). Isocortex is unique in mammals both for its expansion in overall size in addition to its unique six-layered structure.

The pallium or cerebrum of mammals is made up mainly of cerebral cortex, including isocortex, hippocampal cortex, and piriform cortex (Aboitiz, Montiel, Morales, & Concha, 2002). These regions correspond to dorsal, medial, and lateral cortices in

15 Older terms for non-isocortical regions of cerebral cortex include archicortex for the medial division and paleocortex for the lateral division, though the idea that these terms reflect a progression from older to newer forms is incorrect.

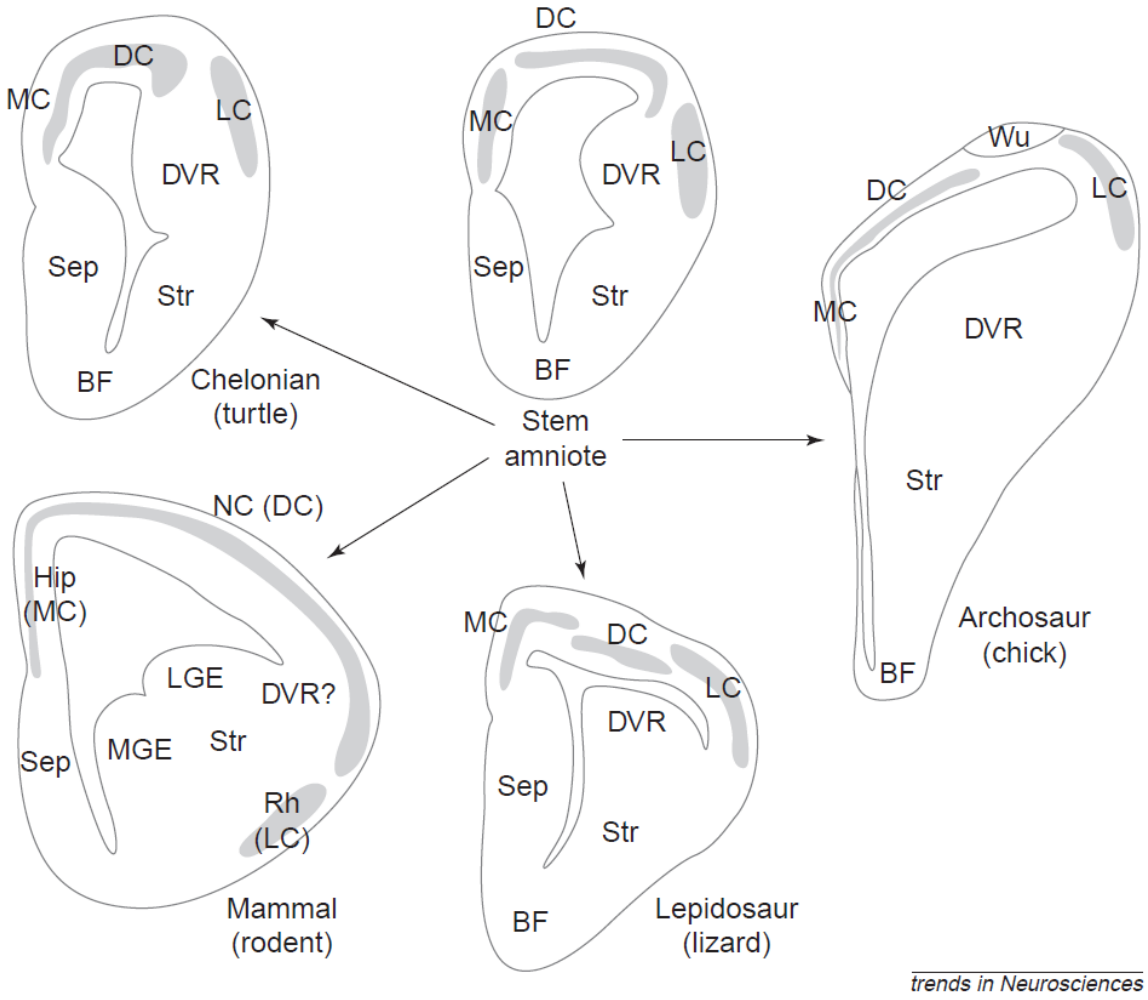

Figure 3 – Schematic coronal sections of dorsal embryonic telencephalon of stem amniotes, turtles, lizards, birds and mammals. BF=Basal forebrain, DC=Dorsal Cortex, DVR=Dorsal ventricular Ridge, Hip=Hippocampus, LC=Lateral Cortex, LGE=Lateral Ganglionic Eminence, MC=Medial Cortex, MGE=Medial Ganglionic Eminence, NC=Neocortex, Rh=Rhinencephalon, Sep=Septal Nuclei, Str=Striatum, and Wu=Avian Wulst. Reprinted from Trends in Neurosciences, 23 (12), Bar, I., Lambert de Rouvroit, C., & Goffinet, A.M., The evolution of cortical development. An hypothesis based on the role of the Reelin signalling pathway, p.634, copyright 2000, with permission from Elsevier.

reptiles, respectively and are likely common to all vertebrates (Bruce, 2007; Northcutt & Kaas, 1995). There are also some structures that have both pallial and subpallial components, namely the amygdalar nuclear complex (referred to as simply the amygdala). Broadly speaking, sensory inputs are relayed from the thalamus to the isocortex, though chemosensory information is an important exception, lacking an early thalamic relay. Isocortex then projects to other cortical and non-cortical brain regions, including hippocampus, amygdala, basal ganglia, and as motor output via the spinal cord.

There is active debate about which structures in the reptilian brain are homologous to the isocortex in the mammalian brain. Some researchers suggest that isocortex evolved from a DVR like structure, given the similarities of sensory projections, whereas other researchers favour an evolutionary relationship between isocortex and dorsal cortex of the pallium of reptiles, focusing on developmental similarities (Aboitiz, et al., 2002; Aboitiz, et al., 2003; Bar, Lambert de Rouvroit, & Goffinet, 2000; Bruce, 2007). Aboitiz and colleagues (2002) suggest that isocortex evolved from the use of olfactory-based representations of space and objects, that became elaborated to include the associative networks of other modalities in dorsal cortex. Further selection on these multisensorial maps led to the evolution of isocortex. Regardless of the actual reptilian homologue(s), the mammalian isocortex evolved uniquely in mammals and has undergone recurrent bouts of expansion in the phylogenetic history leading to primates and humans.

Aboitiz and colleagues (2003) suggest that emphasizing differential information processing strategies drove the divergent evolution of reptilian and mammalian brains. Reptiles and birds evolved a pair of distinct systems for analyzing sensory information; where sensory information from thalamic and mesencephalic relays have distinct targets and processing regions. Moreover, in sauropsids (non-mammals) mesencephalic sensory processing systems are the dominant exteroceptive processors similar to the ancestral vertebrate condition. In contrast, synapsid sensory processing involves convergence of

both of these sensory pathways. Aboitiz and colleagues (2003) suggest that mammals may have originally had an 'olfactory-based' brain, where mental maps were essentially odour-labeled routes, places and objects. In other words, early mammal reliance on olfaction, which conspicuously lacks an early thalamic relay, may have been a precursor to integration of sensory processing from thalamic and mesencephalic systems in the dorsal pallium which would eventually evolve into the mammalian isocortex. This is an interesting possibility, and places centre-stage one of the key features of the mammalian brain, the chemosensory systems.

Isocortex

There are several important conserved areas of isocortex that all mammals possess, including primary visual, auditory and somatosensory cortex. A primary motor area has been identified in all placental mammals that have been studied, though the evidence in marsupials and monotremes is not clear. In addition to primary sensory areas of isocortex, all mammals likely have 4 to 5 somatosensory areas; 4 to 6 visual areas, including V2 and temporal visual area; and 3 to 5 auditory areas, including a belt of secondary areas surrounding primary auditory cortex. In addition there were likely insular regions for taste sensation (dysgranular insular cortex) and an orbitofrontal area to evaluate the hedonistic properties associated with tastes. Other insular regions are likely present that relate to nociception, pain and temperature sensation. Limbic cortex is present in all mammals including anterior, middle, and posterior cingulate cortex and a retrosplenial region all highly linked to memory given their extensive connections with the hippocampus. Perirhinal cortex appears to be common among mammals, preserving its memory-related role. Finally, prefrontal cortex with 2 to 4 subdivisions, including orbitofrontal cortex (OFC), appears common to all mammals (see Kaas, 2007b; Karlen & Krubitzer, 2006; Krubitzer, 2007; Krubitzer & Kaas, 2005; Northcutt & Kaas, 1995). Though all mammals possess these brain regions or cortical fields, there may be

considerable variation in the organization and intrinsic and extrinsic connectivity of these brain regions (Krubitzer & Hunt, 2007). Furthermore, there are known differences between mammalian clades in terms of overall brain size that appear to be mainly driven by expansion of isocortex (Kruska, 2005).

There are several reasons why isocortex has been important in mammal evolution. First, isocortical structure allows modifications that can enhance processing capabilities and create new ones. Second, isocortex can form modules that create and maintain functional segregation of inputs (Kaas, 2007b; Karlen & Krubitzer, 2006; Krubitzer, 2007; Krubitzer & Hunt, 2007; Krubitzer & Kaas, 2005). As a good example, primary visual cortex is segregated into functional columns responding to different aspects of incoming visual stimulation. Additionally, distinct inputs can be segregated into different sub-layers rather than in modules, providing another mechanism of diversity in isocortical circuitry (Kaas, 2007b). It has been proposed that the increased layering in isocortex compared to allocortex enhances processing ability by allowing better simultaneous resolution of positional and identity information (Montagnini & Treves, 2003). On a larger scale, the distribution of number of functional columns devoted to particular functions can be specific to the specialized adaptations of an organism, for example, the enlarged foveal representation of the visual field in primates. Overall, the evolution of isocortex allows a substrate on which evolution can act in order to tune the behaviour and cognition of a given mammal to satisfy the requirements of their ecological niche.

It has been suggested that the evolutionary expansion of isocortex mammals is due to a series of fortuitous and irreversible adaptations, where evolution to nocturnal life early in mammal evolution favoured elaboration of olfactory systems, thus expanding the telencephalon, which were later **preadapted** to receive thalamic inputs from other senses (Aboitiz, 1992). In contrast, reptiles expanded visual systems, *i.e.*, the colliculi, which

led to the DVR structure and not their diminished cortex, preadapted to receive thalamic inputs.

Sensory Systems

Auditory System

In vertebrates the auditory sensory organs synapse first in the cochlear nuclei in the medulla/pons, then to the superior olives in the pons, the auditory areas in the midbrain, then the thalamus, and then finally to the telencephalon (Bruce, 2007). In mammals, the auditory sensory apparatus is housed in the spiral-shaped cochlea, where sounds are transduced into neural signals by the basilar membrane that winds its way through the cochlea. Mammals have exceptionally keen hearing aided in part by the translocation of three cranial bones (malleus, incus, stapes) that play important roles in amplifying ambient sound. There are also differences in intrinsic connectivity and non-cochlear inputs in the cochlear nuclei in mammals for which there are no known homologues in non-mammals and may be related to mobile, external ears and improved high-frequency range (Grothe, Carr, Casseday, Fritzsch, & Köppl, 2004).

The auditory midbrain in mammals is referred to as the inferior colluculi. The inferior colluculi project to two thalamic groups. The medial geniculate nucleus of the thalamus receives auditory information and relays it to isocortex in the temporal lobe. The perigeniculate thalamic group (consisting of the medial division of the medial geniculate nucleus, posterior intralaminar, and suprageniculate nuclei) projects auditory information to the lateral amygdalar nucleus (Bruce, 2007; Doron & Ledoux, 1999). The thalamic nuclei and temporal lobe regions have undergone considerable expansion and parcellation in mammals compared to non-mammals (Bruce, 2007).

Visual System

There are numerous **plesiomorphies** in the visual systems of all tetrapods, including a retina that projects to the hypothalamus, ventral thalamus, dorsal thalamus, midbrain tectum and tegmentum (Bruce, 2007). There are at least three conserved pathways: a thalamocortical pathway from retina to thalamus then dorsomedial pallium (e.g., Retina -> LGN -> V1 in humans), a tecto-thalamo-cortical pathway from retina to midbrain tectum to thalamus to dorsomedial pallium, and a tecto-thalamo-amygdalar pathway from retina to midbrain tectum to distinct thalamic regions to the striatum and ventrolateral pallium (DVR in reptiles, lateral amygdala in mammals) (Bruce, 2007). Like the auditory system, increases in size and complexity in the thalamic and cortical components accompany the transition from reptiles to mammals.

In mammals the hypothalamic target of the retina is the suprachiasmatic nucleus, implicated in circadian rhythms. Visual information has multiple relays to isocortex and midbrain tectum in mammals. One of these pathways projects from the retina to dorsal lateral geniculate nucleus (LGN) to primary visual (striate) cortex. The role of visual cortex in complex form discrimination and binocularity likely evolved independently in birds and mammals, and the cortical role in colour perception appears specific to mammals (Medina, 2007). Another pathway projects from, the retina to the superior colliculi; to multiple thalamic groups, notably the lateral posterior (pulvinar in primates) nuclei, but also including perigeniculate, midline, and intralaminar nuclei; and then to extrastriate (non-primary) visual cortex. A third pathway projects to the striatum and lateral amygdala from supragenicular nucleus (and other perigeniculate nuclei) of the thalamus which in turn received input from the superior colliculi (Bruce, 2007; Doron & Ledoux, 1999).

Somatosensory System

All tetrapods have similar projection pathways from the spinal cord and dorsal column nuclei to thalamic nuclei to the telencephalon. In addition somatosensory information projects from the spinal cord and dorsal column nuclei to regions in the midbrain before being routed to the thalamus and telencephalon. All tetrapods have three common thalamic nuclei for somatosensory information: ventral thalamic nuclei, nuclei that project to cortical targets, and nuclei that project to the striatum and ventrolateral pallium.

In mammals spinothalamic, dorsal columnar, and trigeminal pathways project to an intercollicular area in the midbrain and four thalamic areas: ventral thalamus, ventrobasal and posterior thalamic nuclei, a perigeniculate region at the ventromedial edge of the medial geniculate nuclei, and the central lateral intralaminar nucleus (and other intralaminar nuclei) (Bruce, 2007). The ventral thalamic nucleus does not project to the telencephalon. The ventrobasal and posterior nuclei project to somatosensory cortex. Somatosensory regions in the pallium of birds and mammals appears to have evolved independently in these groups as it was not present in their common ancestor (Medina, 2004). A limbic thalamic area projects to the striatum and basolateral amygdaloid complex (a derivative of ventrolateral pallium). Intralaminar nuclei project to the striatum and frontal motor cortex.

It appears that the presence of multiple somatosensory areas, association cortex, and functional and anatomical somatosensory specializations were present early in mammal evolution, at least in the common ancestor of placental, marsupial and monotreme mammals, including primary and secondary somatosensory areas (Krubitzer, Manger, Pettigrew, & Calford, 1995).

Chemosensory Systems

The chemosensory systems will be outlined in detail in a later chapter (Chapter 5). Briefly, the vertebrate neural plan includes both main and accessory (or vomeronasal) olfactory systems. The projections from these systems are largely conserved across vertebrates. The vomeronasal system has been subsequently lost independently in many vertebrate taxa including birds, crocodiles, cetaceans and some primates. In reptiles the main olfactory bulb (MOB) projects to the olfactory tubercle, lateral cortex, rostral septum, nucleus of the diagonal band, and amygdalar nuclei (Bruce, 2007). These fibres continue caudally in the stria medullaris, cross at the habenular commissure and contact similar regions in the contralateral hemisphere. The accessory olfactory bulb (AOB) of reptiles, which is part of the vomeronasal system, projects to the amygdala and the bed nucleus of the stria terminalis (BNST).

In mammals the two olfactory systems have lost contralateral projections remaining entirely ipsilateral. Targets of the MOB lack an early thalamic relay and include the olfactory tubercle, piriform cortex, entorhinal cortex, nucleus of the diagonal band, anterior amygdalar nucleus, anterior cortical amygdalar nucleus, posterior cortical amygdalar nucleus, and the ventral anterior part of the medial amygdala (Bruce, 2007; de Olmos, Hardy, & Heimer, 1978). The AOB projects to most of the medial amygdala, the medial BNST, and posteromedial cortical amygdalar nucleus.

Prefrontal Cortex

The prefrontal cortex (PFC) does not have a unitary definition across all mammalian species. Kolb (2007) suggests that the best definition of PFC is a region of cortex that has extensive projections from the mediodorsal nucleus of the thalamus (MDT) and/or amygdala and has extensive projections to the basal ganglia and the rest of the cortex. Within mammalian prefrontal cortex there are regions that correspond to primate anterior cingulate cortex, dorsolateral and orbital prefrontal cortices (Reep, 1984;

Uylings, Groenewegen, & Kolb, 2003). In rats, prefrontal cortex may include medial and lateral frontopolar regions; lateral, ventrolateral, ventral and medial orbital regions; an infralimbic region, a prelimbic region, anterior cingulate region, and a medial agranular region (Uylings, et al., 2003).

PFC Inputs

The prefrontal cortex receives input from virtually all cortical regions, including primary and secondary sensory areas for visual, auditory, and somatosensory modalities. In addition PFC receives input from primary olfactory regions of piriform cortex; visceral and gustatory sensory regions in the insula; several regions of the hypothalamus; and brainstem nuclei, including the major dopaminergic, serotonergic, noradrenergic, and cholinergic systems. Thalamic inputs to the PFC include a significant and potentially unique input from the MDT as mentioned above, however many other thalamic nuclei project to PFC, where lateral and medial geniculate nuclei are notable exceptions. The PFC also receives extensive input from all regions in the basal forebrain as well as from many amygdalar nuclei, especially the basolateral nuclear complex. To say that PFC is multimodal cortex is a drastic understatement, though not all regions of the cerebrum project to all regions of PFC nor are all inputs equally dense. Unfortunately a comprehensive review is well beyond the scope of this section, it should suffice to implicate the PFC as a connection hub within the cerebral cortex.

PFC Outputs

Like PFC inputs, PFC outputs are too numerous to review in their entirety here. It may be sufficient to say that connections are in general reciprocal, with the potential exception of primary sensory regions. Connections of note include PFC outputs to the hypothalamus that play a role in controlling the internal state of the organism. Additionally, projections to the amygdalar nuclei may be particularly important in

regulating and evaluating affect. Outputs to the basal forebrain may be involved in reward-related cognition and behaviour.

PFC Functions

The basic function of the prefrontal has been suggested to essentially possess the cognitive functions to organize behaviour in time, including broadly construed memory, attention, decision-making, monitoring, and flexibility (Kolb, 2007). An important and often neglected role of the PFC is the prominent role that it plays in chemosensation (e.g., Gottfried & Zald, 2005), which will be discussed in more detail in later chapters. It has been suggested that the PFC plays a role in coordinating cognition and emotion, to control behaviour and impulses in socially acceptable ways (e.g., Ardila, 2008).

Amygdala

The amygdala is a perplexing structure with diverse functions and complex afferent and efferent connections. Though the amygdala is commonly referred to as a whole, it is hardly a unitary structure. Rather it is made up of numerous distinct and interconnected nuclei that come from different embryological origins. Portions of the amygdalar nuclear complex develop from pallial regions of the embryo and others develop from subpallial regions. This is in contrast to other cortical regions (including hippocampal, isocortical, and piriform cortex), which are by definition pallial derivatives, and basal ganglia, which are subpallial derivatives. Regions of the amygdala that derive from the subpallium include: medial (mAMG) and central (cAMG) nuclei of the amygdala as well as the bed nucleus of the stria terminals (BNST) (Martinez-Garcia, Novejarque, & Lanuza, 2007). Pallial derivatives include the remaining nuclei: all cortical amygdalar nuclei (coAMG), the amygdalohippocampal area (posterior nucleus), and the entire basolateral division of the amygdala (blAMG), which includes lateral (lAMG), basal (bAMG), or basolateral and accessory basal (abAMG) nuclei (Martinez-Garcia, et al., 2007).

Within the pallial subdivision of the amygdala, the cortical nuclei have a layered organization, whereas the basolateral nuclei have a nuclear organization. The cortical amygdala includes the nucleus of the accessory olfactory tract (AOT), nucleus of the lateral olfactory tract (LOT), anterior coAMG, medial and lateral posterior coAMG (sometimes referred to as periamygdaloid cortex), and rostral and caudal transition areas (Martinez-Garcia, et al., 2007). LOT, anterior and lateral posterior coAMG receive inputs from the MOB, where medial posterior coAMG and AOT receive input from the AOB (Martinez-Garcia, et al., 2007; McDonald, 1998).

Within the subpallial subdivision of the amygdala, the cAMG is made up of three subnuclei, medial, lateral and paracapsular central nuclei (Martinez-Garcia, et al., 2007). Some authors consider a portion of the paracapsular cAMG to be a ventral continuation of the caudate called the amygadalostriatal transition (Cassell, Freedman, & Shi, 1999). The mAMG has two main subdivisions, anterior and posterior. The posterior subdivision can be further divided into dorsal and ventral components (Martinez-Garcia, et al., 2007). The BNST has two main subdivisions: anterior, which surrounds the anterior limb of the anterior commissure, and posterior, which is caudal to the anterior commissure possibly impinging on the hypothalamus.

Roughly speaking, the blAMG projects to the cAMG and mAMG and these project to the BNST. Some authors refer to a conglomeration of regions as the extended amygdala (EA). The mAMG and the portions of the BNST connected to it and few nearby cell groups in the sublenticular substantia innominata that make up the medial EA (mEA). The central EA (cEA) consists of cAMG, anterior BNST, and a ring of cell groups above and below the internal capsule (Martinez-Garcia, et al., 2007).

Amygdalar Inputs

Please note that the information on inputs to the amygdala are conglomerated mainly from Martinez-Garcia, et al. (2007) and McDonald (1998) unless otherwise noted.

The amygdala receives direct sensory information from the olfactory and vomeronasal systems, relatively direct sensory input from brainstem centres, unimodal and multimodal information from the dorsal thalamus, and highly processed information from cortical areas. Particularly germane to this discussion are the chemosensory connections of the amygdala expanded below.

Olfactory information is sent directly from the main olfactory bulbs to periamygdaloid cortex, mAMG, anterior and posterior coAMG, and the anterior amygdaloid area. In addition, secondary olfactory information is relayed from primary olfactory cortex to virtually all areas of the amygdala except the intercalated nucleus, the mAMG, the amygdalohippocampal area (AHA), and the posterior coAMG. Tertiary olfactory information is sent bilaterally from the nucleus of the LOT to the bAMG. The amygdala has many intrinsic connections that convey olfactory information between amygdalar areas, including: projections from the lateral posterior coAMG to the anterior abAMG), posterior bAMG, lAMG, as well as medial coAMG.

The accessory olfactory bulb projects to the AOT, medial posterior coAMG, mAMG, and BNST. Within the amygdala, intrinsic connections conveying information from the accessory olfactory system include: projections from mAMG to portions of cAMG, medial BNST, the posterior abAMG, AHA, and portions of the lAMG. The medial posterior coAMG projects to mAMG, BNST, abAMG, and posterior bAMG. The AHA area receives input from AOT.

Amygdalar Outputs

The information in this section is taken from (Martinez-Garcia, et al., 2007; McDonald, 1998; Reardon & Mitrofanis, 2000) unless otherwise noted.

The amygdala not only receives information from virtually all brain areas but sends widespread projections throughout the brain, including major outputs to brainstem nuclei, diencephalon (both thalamic and hypothalamic components), basal forebrain

(including nucleus accumbens, caudatoputamen, septum, *etc.*), and the cortex. As a rule, the amygdala connects reciprocally with the cortex, *i.e.*, if a given area of cortex projects to a particular region of the amygdala, that region projects back to that area of cortex. The main amygdalacortical terminations are in prefrontal (infralimbic, prelimbic, and anterior insular cortices), posterior insular, perirhinal, and entorhinal cortices. The bAMG has bilateral connections to the cortex and the AHA appears to be the main interface with the hippocampal formation.

The brainstem receives amygdalar projections from the subpallial components of the amygdala. The mAMG projects to periaqueductal gray, ventral tegmental area (VTA), and the midbrain raphe, allowing the amygdala to exert an effect on dopaminergic and serotonergic systems. The cAMG projects to VTA, median raphe, substantia nigra, locus coerulus, nucleus of the solitary tract, parabrachial nucleus, and laterodorsal tegmental nucleus (excluding the paracapsular nucleus of the cAMG). This allows the cAMG to influence dopaminergic, serotonergic, noradrenergic, and cholinergic systems as well as visceral and taste sensory systems (via the nucleus of the solitary tract and parabrachial nucleus), and activating systems (via laterodorsal tegmental nucleus). The BNST also projects to the laterodorsal tegmental nucleus influencing attention and activity levels.

The hypothalamus receives input from subpallial and lateral pallial regions of the amygdala. The mAMG projects to ventromedial, anterior, medial/lateral preoptic, ventral premammillary hypothalamic nuclei. The cAMG projects to posterolateral and paraventricular hypothalamic nuclei, and the lateral and medial subcomponents of cAMG (not the paracapsular cAMG) project to anterior and lateral hypothalamic nuclei. The BNST projects extensively to the hypothalamus, including, ventromedial, anterior, medial/lateral preoptic, lateral, ventral premammillary, posterolateral and paraventricular hypothalamic nuclei. Within the pallial component of the amygdala, the anterior coAMG and anterior abAMG project to the lateral hypothalamic nucleus. The posterior abAMG

projects to the ventromedial hypothalamic nucleus. Finally, the AHA projects to ventromedial, anterior, medial/lateral preoptic, ventral lateral and ventral premammillary hypothalamic nuclei.

The basal forebrain receives amygdalar inputs from lateral and ventral pallial and subpallial amygdalar regions. The ventral striatum, which includes the nucleus accumbens, receives amygdalar inputs from bAMG, anterior and posterior abAMG, AHA, BNST, and mAMG. In contrast, the dorsal striatum, which includes caudate and putamen, receives input from bAMG, lAMG, and abAMG. The AHA sends additional projections to ventral lateral septum, the olfactory tubercle, and substantia innominata. The BNST and mAMG project to ventral lateral septum and the olfactory tubercle.

Inputs from the amygdala to the thalamus indicate that cortical regions not only receive information directly from the amygdala but also secondary connections relayed through the thalamus as well. The abAMG projects to mediodorsal, paraventricular, reuniens, subparafascicular, parafasicular, interanteromedial thalamic nuclei, as well as to the zona incerta in the subthalamus. In contrast the posterior bAMG projects to largely the same areas including the zona incerta but excluding the reuniens nucleus of the thalamus, instead projecting to the rhomboid nucleus. The only component of the ventral pallial amygdala to project to the thalamus is the AHA, which sends axons to mediodorsal, reuniens, subparafascicular, reticular, medial geniculate, parafasicular, rhomboid, interanteromedial, and paratenial nuclei of the thalamus. The cAMG projects to mediodorsal, gustatory, paraventricular, and reuniens nuclei of the thalamus and the zona incerta. The mAMG projects to reuniens, posterior, subparafascicular, paracentral, ventromedial, and reticular nuclei, as well as zona incerta.

Amygdalar Functions

The functions of the amygdala may be broadly construed as evaluating incoming environmental stimuli and internal of the organism to provide a motivating force on

behaviour. Classically, the amygdala is known to be involved in the expression and acquisition of fear, aversion, and negative emotions. In addition, the amygdala is also known to be involved in expression of positive emotions as well, including reward learning and appetitive behaviours. The broadly construed expression and acquisition of positive and negative affect largely involves the cEA given its connections to the parabrachial area and posterior intralaminar thalamus in relation to nociceptive input and connections to nucleus accumbens and prefrontal cortex.

In contrast to the cEA, the mEA plays an evaluative role of incoming stimuli that have specific relevance to 'social' stimuli. These social stimuli include not only conspecifics but also predator and prey relationships as well. Given that the mEA is a main target of olfactory and vomeronasal afferents and that it in turn projects heavily to hypothalamic targets, it is no surprise that the mEA is involved in reproductive function and defensive behaviours. The respective roles of the cEA and mEA obviously interact and are indeed interconnected as noted above. For example, vomeronasal information from the mAMG can influence and cause fear reactions. Moreover, both areas interact to produce appetitive behaviours in response to chemicals such as sex pheromones. Martinez-Garcia and colleagues (2007) suggest that the amygdala may indeed have these two separate subsystems for emotional responses and social responses, however they also point out that these systems must interact to accomplish these functions.

Primate Brains

One of the most noticeable aspects of the primate brain is the fact that the primate brain is generally much larger than that of average mammals, being about twice the expected size in anthropoid primates (Jerison, 1973; Preuss, 2007). Within this enlarged primate brain, certain regions are enlarged more than others, including preferential expansion of isocortex compared to other gross brain regions. Even within isocortex, certain brain regions expanded preferentially, particularly visual cortex, including

expansion of primary visual cortex and the addition of new visual areas (Preuss, 2007). Likewise, refinements of the somatosensory and motor systems are observed in primates, particularly an increase in the relative importance of the corticospinal tract, related to fine motor control. In contrast to regional expansion of the visual and somatosensory systems, chemosensory systems experienced reductions in size and importance.

Visual Expansion

The visual system in Primates has many derived features compared to the ancestral mammalian condition. Moreover, within Primates characteristics of the visual system are acquired in a mosaic fashion. For instance, haplorhine primates have a retinal fovea and lack the reflective layer in the posterior retina, the tapetum lucidum, where strepsirrhine primates retain these mammalian traits.

All primates, compared to other mammals, have a distinct pattern of connections to the superior colliculus (homologous to the midbrain optic tectum in most vertebrates). The superior colliculus of primates receives strong input from regions of the retina in both eyes that represent the contralateral visual field. This configuration results in a representation of only the contralateral visual field in primate superior colliculi, where mammalian superior colliculi represent both contralateral and ipsilateral visual space (Preuss, 2007). In addition the superior colliculi of primates receive massive input from dorsolateral prefrontal cortex (Preuss, 2007).

Like most mammals, cortical visual projections mainly arise from the LGN and the pulvinar nucleus of the thalamus. The LGN itself possesses some uniquely primate traits, including complete segregation of magnocellular and parvocellular regions. The primate LGN projects almost exclusively to primary visual cortex (only koniocellular layers project to extrastriate regions), where in non-primate mammals these extrastriate connections are relatively major (Preuss, 2007). Within primary visual cortex cytochrome oxydase staining blobs are unique to primates and some carnivores (where

they likely represent convergent evolution). Primary visual cortex in primates is also characterized by ocular dominance columns (Sherwood & Hof, 2007), and again these are absent in other animals except for carnivores.

Primate extrastriate visual cortex is marked for the proliferation of retinotopically organized visual areas in two broad categories corresponding to a dorsal stream to the posterior parietal cortex and a ventral stream to inferior temporal cortex. These streams classically referred to as the 'where' and the 'what' systems respectively are uniquely primate (Preuss, 2007). This proliferation differs markedly from non-primate mammals; where primates have at least 15 additional visual areas, non-primate mammals have perhaps 5 (again **carnivorans** are an exception due to convergent evolution) (Preuss, 2007). The dorsal stream is a massive source of input to premotor cortex, facilitating primate abilities related to locomotion and manual manipulation.

Colour vision varies across primate groups. Catarrhine primates likely share similar trichromatic vision, whereas in platyrrhine primates only individuals with heterozygous alleles are trichromatic and strepsirrhines appear to be either monochromatic or dichromatic (Jacobs, 2007).

Motor and Somatosensory Refinement

Primates have intriguing specializations to the limbs that relate to grasping, including opposable digits and hairless, dermatoglyph[16] skin on the hands and feet (and sometimes tail). Grasping ability varies across primate species where strepsirrhine and most New World monkeys have little if any independent digit control compared to apes and humans with precision grip (Preuss, 2007). In the realm of touch sensation, Meisner corpuscles[17] are unique to primates, though similar structures have evolved convergently

[16] Regions of hairless skin with complex patterns of ridges, *i.e.*, fingerprints.

[17] Meisner corpuscles are specialized sensory cells in the skin. Presumably for fine touch abilities.

in other species with fine touch abilities (Preuss, 2007). The primate specializations for touch sensation are apparent even in the spinal cord where the dorsal horns conveying this information to the brain are enlarged and more is dedicated to the digits and palm (Kaas, 2007a). The somatotopic representation of touch sensation in the spinal cord is reversed in New World monkeys compared to Old World monkeys, apes, and non-primate mammals where the digit tips are ventrally located (Kaas, 2007a).

Like visual cortex, primate somatosensory cortex has several additional areas compared to that of the somatosensory cortex of other mammals. In addition to multiple somatic representations within primary and secondary somatosensory areas, primates possess additional representations in the lateral central sulcus anterior and posterior to secondary somatosensory cortex, posterior insular cortex, and additional parietal areas (Preuss, 2007). Most eutherian mammals and some strepsirrhine primates have direct thalamic projections to both primary and secondary somatosensory regions, whereas in anthropoid primates secondary somatosensory cortex does not receive thalamic input, instead receives input from primary somatosensory cortex (Kaas, 2007a; Preuss, 2007). Additionally, primates have a differentiated ventroposterior inferior thalamic nucleus where this is not recognized as a distinct nucleus in non-primates.[18] The anterior pulvinar nucleus of the thalamus appears to have no known homologue in non-primates (Kaas, 2007a). An interesting consequence of the setup of primate somatosensory cortex is that somatosensory information is sent to parietal regions that control the limbs in space, probably related to the enhanced tactile and grasping abilities in primates. Anterior parietal cortex in anthropoids has four distinct contralateral somatic representations, where non-anthropoids do not (Kaas, 2007a).

[18] Raccoons, known for their manual dexterity share this specialization likely having evolve convergently.

Primate cortical motor regions have additional divisions compared to non-primate mammals. Where non-primate mammals have primary motor cortex and maybe a very tiny region of premotor cortex, primates possess distinct subdivisions within primary motor cortex as well as seven or more non-primary motor areas (Preuss, 2007). All primates have a rostral subdivision of dorsal premotor cortex that is heavily connected to prefrontal cortex and less densely with primary motor cortex, as well as a caudal region of dorsal premotor cortex with dense primary motor cortex connections (Kaas, 2007a). Additionally, all primates have frontal eye fields, a supplementary motor area, a pre-supplementary motor area, and rostral and caudal cingulate motor areas (Kaas, 2007a). One particular region in primate motor cortex, a ventral premotor subdivision of primary motor cortex, contains discrete corticospinal projections and represents the face and forelimbs exclusively. This region in conjunction with the corticospinal tract likely evolved to organize and implement the complex visually guided reaching and grasping (Preuss, 2007; Wise, 2007). Interestingly, anthropoid primates have distinct rostral and caudal subdivisions in this ventral premotor area (Kaas, 2007a).

The corticospinal tract is very important for primate locomotion. Lesions to the corticospinal tract create profound, detrimental effects on movement of the contralateral side of the body. In contrast similar lesions in many mammal species produce minimal effects (Preuss, 2007). Claims have been advanced that the corticospinal tract extends to deeper levels of the spinal cord in primates compared to other mammal species and also invades and innervates greater territory of the motor neuron pools in the ventral horn of the spinal cord (Preuss, 2007).

Higher-order Systems

Superior Temporal Sulcus

The cortical regions in the superior temporal sulcus receive multimodal input including both visual streams, and neurons in this region respond to biological motion

where some are even responsive to particular actions (Preuss, 2007). Within Primates some strepsirrhines have only a single architectonic zone, where most other primates have multiple zones. Moreover there is no evidence that a homologous region exists in non-primate mammals (Preuss, 2007).

Prefrontal Cortex

There are several generally defined regions in primate prefrontal cortex, including dorsolateral, orbital, and medial regions. Unique to Primates is a well developed granular layer in the dorsolateral area, and is particularly enlarged in anthropoids (for a review see Preuss, 2007). This region has strong connections with higher-order parietal and temporal regions and in humans is often associated with attention and working memory. All non-primate mammals possess homologues to dorsolateral prefrontal cortex, which receives input from the mediodorsal thalamus, though they do not have a distinct granular cell layer. In Primates mediodorsal thalamus projects not only to dorsolateral prefrontal cortex but also orbital and anterior cingulate areas (for a review see Preuss, 2007). The observation that orbital and medial prefrontal cortices more closely resemble the purported dorsolateral homologue in mammals has led to the suggestion that the dorsolateral region of primates may indeed be entirely unique to the primate brain (for a review see Preuss, 2007).

Posterior Parietal Cortex

The posterior parietal cortex in primates has undergone expansion and reorganization (Hinkley, Padberg, & Krubitzer, 2007). The rostral portion of posterior parietal cortex is part of the somatosensory cortex given its connections with other somatosensory areas. However, given its dense projections to motor cortex and further inputs from dorsal stream visual areas presage the involvement of this region in mediating visually-guided movements such as reaching, retrieving, and defensive movements (Kaas, 2007a). In macaque monkeys, area 5 in the rostral parietal lobe

represents somatic and visual information of the hands and forelimbs during intentional movement in a body- rather than a visually-centred frame (Hinkley, et al., 2007). In catarrhine primates, the area of cortex in and around the intraparietal sulcus has undergone expansion and increased differentiation. The lateral intraparietal area appears specialized for directing saccadic eye movements, the medial intraparietal area is involved in visually guided reaching, the ventral intraparietal area is involved in visually guided locomotion, and the anterior intraparietal area is involved in guiding grasping and manipulation movements (Kaas, 2007a).

Chemosensory Reduction

Within Primates, the chemosensory apparatus appears to have dwindled in importance among the haplorhines, particularly the anthropoids. Strepsirrhines have likely retained more of the ancestral mammalian chemosensory systems, where haplorhines exhibit reductions in both main and accessory olfactory systems (Preuss, 2007). Indeed, all strepsirrhine species studied, where all families are represented, have demonstrably functional vomeronasal organs (Bhatnagar & Smith, 2007). Comparisons between strepsirrhine and haplorhine primates show that the olfactory bulbs are relatively smaller in the latter group (the size difference has been called “enormous” (Preuss, 2007)) (Stephan & Andy, 1969). Moreover, in all catarrhine species a functional accessory olfactory bulb is completely absent, though it is present in platyrrhine primates and tarsiers (Bhatnagar & Smith, 2007). This deficit extends to include the sensory apparatus, where strepsirrhine primates possess chemosensory vomeronasal organs, no catarrhine primates have functional VNOs as adults, and platyrrhine primates have all of the components but functional studies are inconclusive (Bhatnagar & Smith, 2007). This issue of reduced chemosensory abilities in haplorhine primates will be returned to in more detail in Chapter 5, however one peculiar aspect of the reduction of chemosensory systems is that the reductions in main and accessory olfactory bulb volumes are not

necessarily accompanied by reductions in cortical regions related to olfactory processing, though this may be an artifact of the difficulty in defining and identifying these regions.

Hominin Brains

Overall, there may not be many features or abilities of the human brain that are entirely unique; indeed many of the features that are assumed to be "uniquely" human have obvious precursors in the primate and non-primate mammalian world. The human brain, instead of being a unique entity, is an exaggeration and continuation of many of the trends evident in the evolution of primate and mammalian brains.

Gross Morphological Features

From the fossil record one can infer that some aspects of gross human brain morphology are present in earlier forms,[19] though the gestalt of the modern human brain is only present in fully modern humans. Early in hominin descent, primary visual cortex decreased in relative size (de Sousa & Wood, 2007), as demonstrated by a comparatively posterior position of the lunate sulcus, which leaves its mark on fossil **endocasts**. This feature appears to be somewhat variable in *Au. afarensis*, though this may be an artifact of small sample size; given that it is more clearly visible in *Au. africanus* (de Sousa & Wood, 2007). Modern humans have an expanded and rostrally blunted OFC, and this appears to extend back to *Au. africanus.* This feature is absent in the paranthropes and *Au. afarensis*, which retain the chimpanzee-like beak-shaped OFC probably present in the human-chimpanzee last common ancestor (de Sousa & Wood, 2007). Early hominins exhibited the gross hemispheric organization whereby the left occipital pole is broader and extends farther posteriorly than the right, and the right frontal pole is broader and extends farther anteriorly than the left. This feature, known as the left-occipital right-

[19] These similarities are at least in the modern human direction, though not necessarily as pronounced (de Sousa & Wood, 2007).

frontal petalial pattern, has been observed in almost all hominins, excluding *H. habilis* which retains the chimpanzee-like pattern.[20] Asymmetrical Broca's regions in the frontal lobe are present in *Au. africanus* as it is in modern humans, likely in all of the *Homo* genus, but not in *Au. afarensis s. l.* (de Sousa & Wood, 2007). These asymmetrical morphologies that began to be evident in human ancestors are consistent with language ability and right handedness, and intriguingly the earliest known stone tools that appeared at a similar time were apparently made by right-handed hominins (de Sousa & Wood, 2007).

The temporal poles are expanded anteriorly in *Au. africanus* as it is in modern humans, where paranthropes have rounded temporal poles that are not expanded anteriorly as in chimpanzees (de Sousa & Wood, 2007). *H. rudolfensis*, but not *H. habilis* (both mentioned above under *H. habilis s.l.*), shows the first example of the modern orbitofrontal sulcus pattern (de Sousa & Wood, 2007). An expanded thoracic vertebral canal as well as increased relative size of the cerebellum are apparent only as early as *H. neanderthalensis* (de Sousa & Wood, 2007). Finally, a globular cranium due to expansion of the parietal lobes is only seen in anatomically modern humans (Bruner, Manzi, & Arsuaga, 2003; de Sousa & Wood, 2007).

Brain Enlargement

The average chimpanzee brain weighs approximately 405.6 g for males and 368.1 g for females (Herndon, Tigges, Anderson, Klumpp, & McClure, 1999). The modern human brain mass is more than three times larger, the mean highest value across the lifespan is 1450 g in men and 1340 g in women (Dekaban & Sadowsky, 1978). Early hominins had a brain of similar size to that of the modern chimpanzee, though as hominins evolved the brain got steadily larger toward the human grade. *A. ramidus s.l.*

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[20] Many earlier species including the ardipithes, and *Au. afarensis s. l.* lack sufficient information or specimens to address this asymmetry.

had a brain mass between 300 and 363 g (de Sousa & Wood, 2007; Suwa, et al., 2009).[21] Other early hominins had brain weights closer to the chimpanzee grade: *Au. afarensis* 385 – 542 g, *Au. africanus* 424 – 508 g, *P. boisei s. l.* 397 – 537 g, and *P. robustus* 446 – 638 g (Aiello, 1992; de Sousa & Wood, 2007). Within the *Homo* genus, brain size continues this trend toward larger brain size; *H. habilis s. l.* 503 – 805 g, *H. erectus s. l.* 580 – 1218 g,[22] *H. heidelbergensis* 858 – 1397 g,[23] *H. neanderthalensis* proper 1135 – 1669 g, and *H. sapiens* 1057 – 1799 g (de Sousa & Wood, 2007) (see Figure 4).

In addition to the absolute enlargement of the brain, it is potentially meaningful to estimate the changes in brain size relative to differences in body size. Typically this is given as an encephalization quotient (EQ). In the same manner as absolute brain size, early hominins had a chimpanzee-like EQ grade and progressed toward a modern human EQ; *A. ramidus s. l.* ~1.6,[24] *Au. afarensis s. l.* 2.5, *Au. africanus* 2.8, *P. boisei s. l.* 2.5, *P. robustus* 3.1, *H. habilis s. l.* 3.5, *H. erectus s. l.* 3.1 – 3.9, *H. heidelbergensis* 4.2, *H. neanderthalensis* 4.7, and *H. sapiens* 5.3 (de Sousa & Wood, 2007). Encephalization in the hominin lineage likely began with the appearance of *Au. afarensis*, where earlier hominins retained relatively smaller brains (see Figure 5).

Given the overall trend towards larger brains, some researchers have suggested that different hominin lineages may have increased brain size by different changes in morphology. Bruner , Manzi, & Arsuaga (2003) point out that archaic and Neanderthal

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[21] Following the method in de Sousa & Wood (de Sousa & Wood, 2007) brain mass was calculated using the methodology from Ruff and colleagues (Ruff, et al., 1997), where brain mass = 1.147 x cranial capacity$^{0.976}$.

[22] *H. ergaster* specimens range from 590 – 877 g and *H. erectus* proper specimens range from 712 – 1218 g. The wide range given in the text is due to the large differences between these species.

[23] Previously grouped under *H. neanderthalensis s.l.* however data for H. antecessor is missing and H. floresiensis with its diminutive stature would distort these estimates away from that representative of this species.

[24] Similar to the chimpanzee male minimum.

specimens share a broadening of the frontal lobe and a reduction in the occipital lobe. In contrast, they point out that modern humans have additional parietal enlargement, resulting in a more globular cranial structure.

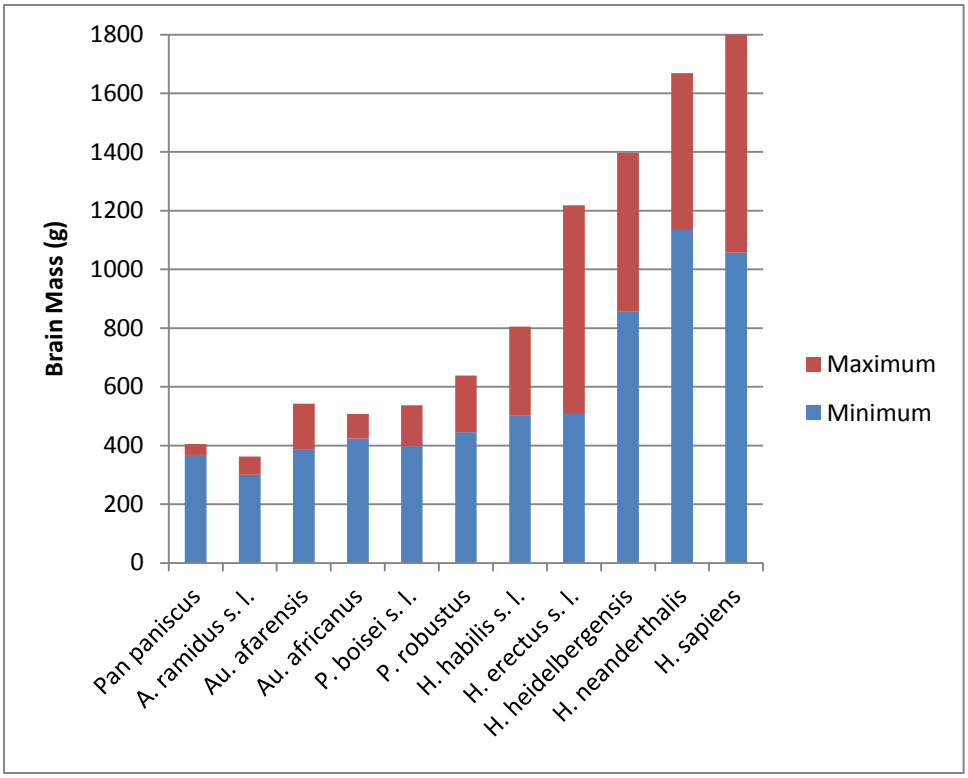

Figure 4 – Hominin Brain Mass. This chart represents the changes in brain weight from early hominins to modern *Homo sapiens*. Chimpanzees (*Pan paniscus*) is included as a reference. It is interesting to note that the initial encephalization in the hominin lineage beyond the panin grade is relatively modest compared to the much larger encephalization observed in modern humans. Data are taken from de Sousa & Wood (2007).

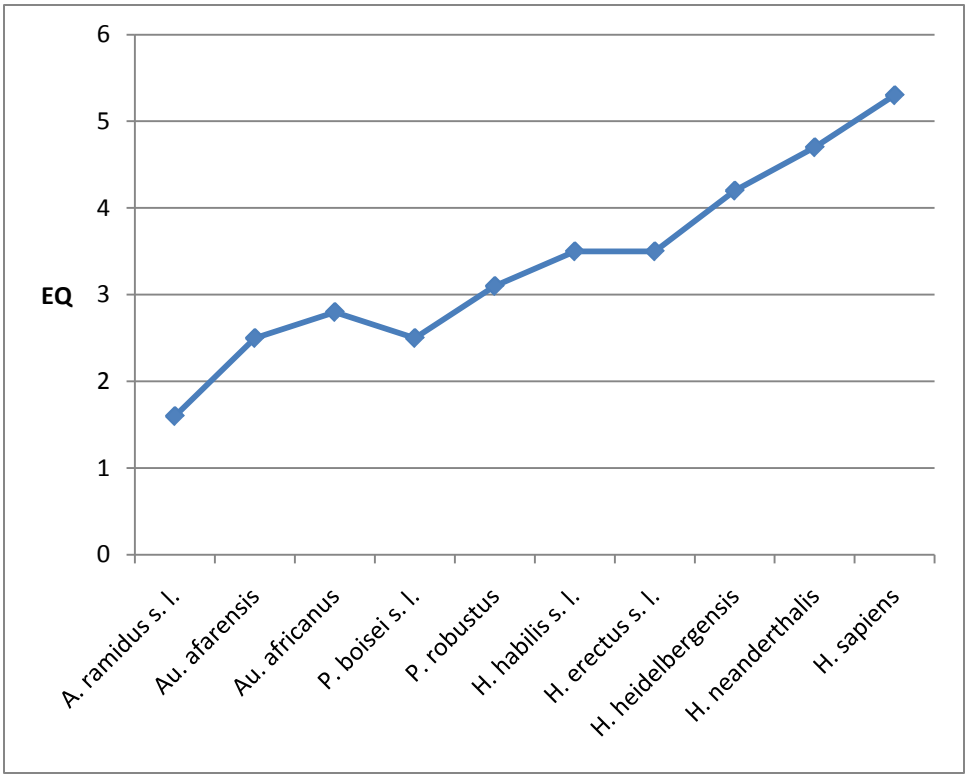

Figure 5 – Hominin Encephalization Quotients. Data are taken from de Sousa & Wood (2007)

Regional Changes to the Human Brain

Sensory Cortex

Visual cortex in humans is larger than that in any other primate in absolute terms, however, in proportion to an overall larger brain, visual cortex takes up a smaller amount of the cortex. Indeed, visual cortex is only ~60% of the size predicted from primates but is ~1.5 times larger in absolute terms compared to a chimpanzee brain (Schoenemann, 2006). The human olfactory bulb is only 30% as large as would predicted for our brain size, however the olfactory bulbs are 1.6 times larger than what would be predicted based on our body size (Schoenemann, 2006).

Motor Processing

Although the frontal lobes of humans are close to the predictions from other primates for our overall brain size, human frontal lobes are 3 times larger than that of primates in absolute terms (Schoenemann, 2006). There may be hominin specific changes to gray/white matter ratios, where white matter of human frontal lobes has been disproportionately expanded (Schoenemann, 2006). Within the frontal cortex, primary motor cortex appears to have kept pace with growth in body size, however this means that it is only ~33 % of the expected value for our brain size. Likewise, premotor cortex in humans is smaller than what is predicted for our brain size, but at ~60 % of the expected value, it has not lagged as far behind, possibly suggesting an elaboration of motor planning but not motor control *per se* (Schoenemann, 2006).

The posterior parietal cortex in humans is expanded compared to that of primates. There appear to be additional regions to the putative homologues (Hinkley, et al., 2007). These new areas are likely related to the hand and the precision of manual manipulation present in humans.

The human cerebellum is ~2.9 times as large as expected from primate data (Schoenemann, 2006). Given the role of the cerebellum in refining motor movements,

this expansion of the cerebellum in humans may be related to enhanced manual dexterity characteristic of humans and perhaps a similar role on refining human cognitive function.

Prefrontal Cortex

Despite the somewhat lackluster expansion of frontal motor regions in the human brain, prefrontal regions have expanded more dramatically to ~ 2 to 4 times the larger than that of nonhuman great apes (Schoenemann, 2006). Moreover, the prefrontal cortex of humans exhibits a greater degree of gyrification than nonhuman primates (Rilling & Insel, 1999). Despite an increase in the size of the prefrontal cortex, the frontal cortex, as a whole, does not show increased relative size compared to that of hominids. Moreover, regions within the frontal lobe including dorsal, medial and orbital sectors retain relative sizes compare to other hominids (Semendeferi, Damasio, Frank, & Van Hoesen, 1997). In absolute terms the human frontal lobe is much larger than that of chimpanzees, such that the frontal lobe of humans is roughly the same size as the entire cerebral hemisphere in chimpanzees (Semendeferi, et al., 1997).

Parietal Cortex

In humans, the cortex in and around the intraparietal sulcus (IPS) contains more functional regions than in monkeys (*Macaca mulatta*) (Orban et al., 2006). There are four regions in ventral IPS which are sensitive to motion as well as structure from three dimensional motion, where monkeys have only one region which is relatively insensitive to three dimensional structure. There are also four regions sensitive to object shape and three regions which represent foveal vision, where monkeys have only two shape sensitive regions and one for foveal vision. Orban and colleagues (2006) conclude that a portion of the anterior IPS is unique to humans.

Hemispheric Specialization

Bilateral symmetry evolved at least 900 Ma in the lineage that would eventually lead to all vertebrates including humans, possibly with the need for directional movement (for a brief review see Corballis, 2007). There is a trade-off in all bilaterally organized species between bilateral symmetry, which is beneficial for many aspects of life such as efficient locomotion, and asymmetry, which would be beneficial in providing specializations of structures that could offer unique functions. Even though asymmetries are present in possibly all bilaterally organized species, it appears that the evolution of hominins benefitted by capitalizing on these asymmetries.

Approximately 90 % of humans are right-handed, whereas 65% of chimpanzees appear to be right handed, suggesting that asymmetry is stronger in humans (for a brief review see Corballis, 2007). Consistent with human right-handedness, human brains show a greater proportional amount of gray matter in the left hemisphere primary motor cortex (Sherwood & Hof, 2007). Similarly, left-hemisphere asymmetries for vocalizations are common to most species from amphibians, birds, and mammals. Furthermore, the left-hemisphere bias for human language may reflect this bias across species (for a brief review see Corballis, 2007).

Ventromedial Prefrontal Cortex

Within OFC, area 13 [25] is common to all primates, however it is not without interspecific differences (Sherwood & Hof, 2007). This region of cortex receives input from all of the senses as well as motor and parahippocampal cortex. Area 13 in humans and bonobos (*Pan pygmaeus*) is proportionally small and there are more cytoarchitectonic subdivisions in adjacent OFC (Sherwood & Hof, 2007). This reduction of area 13 is likely due to the expansion of adjacent area 11 and area 47.

[25] Area 13 is probably more accurately described as anterior insular cortex, however it is the portion that is continuous with the orbitofrontal aspect of the prefrontal cortex.

The anterior cingulate cortex (ACC) also appears to display differences in the great apes and these differences may be exaggerated in humans. The ACC of hominids contains unique, large spindle-shaped cells (Von Economo neurons) and other pyramidal neurons that have a unique calcium binding signature (Nimchinsky et al., 1999; Sherwood & Hof, 2007; Watson & Allman, 2007). Von Economo neurons are also found in frontoinsular cortex of great apes and humans (Watson & Allman, 2007). Unique to humans, the pyramidal cells with the unique calcium binding signature are concentrated in area 32 of ACC (Sherwood & Hof, 2007). Von Economo neurons are hypothesized to be critical for fast decision-making based on 'gut feelings' as opposed to reasoning common in social situations (Watson & Allman, 2007). It has also been suggested that the Von Economo neurons in relation to an extremely expanded area 10 at the frontal pole is a unique human adaptation, possibly related to planning under changing circumstances (Allman, Hakeem, & Watson, 2002).

Are Bigger Brains Better?

Much of the literature on brain evolution is focused on size differences between brains of different species and classes. The basic idea is that bigger brains have greater processing power than smaller brains (Northcutt, 2002), much like a computer that has a billion transistors has more potential processing power than a computer with a million transistors. A long-standing body of research indicates that mammalian brains have become larger over geological timescales (Jerison, 1961, 1970)-(review: Hofman, 1989; Jerison, 1961, 1970; Karlen & Krubitzer, 2006). Indeed, brain size has increased independently in some members of all vertebrate groups (Northcutt, 2002); this does not imply that evolution is progressive toward larger-brained, intelligent animals (Deacon, 1990). From the study of fossil endocasts, which are essentially molds of intracranial space (for an excellent example see Macrini, Rougier, & Rowe, 2007), an increase in brain size, particularly isocortex, in all mammals has occurred at least since the

Paleocene, ranging from 30% in koalas to 80% in humans (Jerison, 2007). Brain enlargement may date back to early mammal-like reptiles, where endocasts indicate that brain-size increased gradually from the reptilian grade to the larger mammalian grade, where transitional forms are in between or even on the lower end of what is presently observed in mammals (Quiroga, 1979, 1980). Primates tend to have large amounts of isocortex compared to insectivores, where haplorhine primates have the largest brains within Primates (Barton & Harvey, 2000).

In reality, it is *not only* the sheer number of neurons in a brain or transistors in a computer that determine processing power, rather the distribution and properties of individual processing units as well as the connections and relationships between units are integral determinants of processing capacity. Moreover, despite the increased complexity observed in larger brains, there are not necessarily correlations with enhanced behavioural repertoires (Changizi, 2007; Chittka & Niven, 2009; Deacon, 1990; Kruska, 2005), though they can be (Jerison, 1975; Karlen & Krubitzer, 2006). Indeed the larger brains of Mesozoic mammals conferred no advantage over the smaller brained dinosaurs (Jerison, 1971). In addition to the general trend that larger bodies have larger brains, there are potentially grade shifts across taxa where certain species of animals have larger brains than others. For example, an opossum has a brain about four times larger than a reptile of similar size (Jerison, 1975).

Larger species tend to have larger brains, that is brain size scales with body size (though a measure of lean body weight excluding fat weight may be more appropriate, (Schoenemann, 2000)). Indeed, selection experiments suggest that selecting for body size results in concomitant increases in brain size (e.g., Atchley, 1984). As a counter example, domesticated animals have smaller brains in general than their feral counterparts, yet score higher on tests of memory, social cognition, *etc.*; they often prove adaptable and survivable when returned to the wild; and feral animals retain large brains over generations in captivity not subject to domesticative selection (Kruska, 2005, 2007).

However, domestication resulting in distinct increases in body size particularly in animals bred for human consumption, actually results in decreases in brain size (Kruska, 2007). To be fair, domestication by artificial selection may differ significantly from laboratory controlled selection experiments, not least for duration of the selection process.

Larger brains probably mean greater intelligence when looking across species though it is not necessarily easy to say how or why this may be the case. Unfortunately, fossil endocasts do not reveal much more than general size measurements and proportions of only major lobes and regions. Comparisons of specific functional systems is perhaps ultimately more fruitful but limited by the inferential nature of comparative neuroanatomy.

CHAPTER 3

THEORETICAL PERSPECTIVES ON BRAIN SELECTION

There are many theories concerning how and why the human brain evolved into the exquisite piece of machinery that is its modern form. These theories can be grouped into three classes: climatological, ecological, and sociological (Bailey & Geary, 2009). The common feature across all of these theories is the idea that the human brain evolved to cope with variation and change.

Climatological Hypotheses

Savannah Adaptation Hypothesis

The Savannah Adaptation Hypothesis states that humans evolved by adaptation to the drier, cooler, and more open savannah grasslands that displaced woodlands, forests, and jungles during the Late Miocene through the Pleistocene and the present. From 6 Ma to the present there has been a long term cooling trend as shown from oxygen isotope records from deep sea cores (Potts, 1998).

The simplest version of the Savannah Adaptation Hypothesis is the Cold Climate Hypothesis. Simply put, colder habitats are potentially more demanding of cognitive resources to solve the problems of gathering and storing food and finding shelter compounded during prolonged winters (e.g., Rushton, 2010). However, colder climates may have an effect on brain size such that the insulating properties of greater tissue volume cause increases in brain size without increasing processing power (Manger, 2006). Moreover, scores on psychometric tests may vary systematically across cultures due to sociocultural factors such as education and other factors such as the language of test design and potentially inadequate and culturally-insensitive norming procedures. This could possibly result in biases against the African and Latino populations that just happen to live nearer to the equator.

A slightly more complex version of the Savannah Adaption Hypothesis suggests that it is not colder climates per se that have driven the evolution of the large hominin brain, rather it is the evolutionary novelty of a given habit that increases cognitive demands and thus selects for brain size (Kanazawa, 2008). Kanazawa (2008) argues that general intelligence evolved as a domain-specific adaptation to solve evolutionarily novel problems. Essentially, the farther that a given habitat diverged from the hypothetical ancestral habitat, the greater the cognitive demand and thus selective pressure on brain size and cognitive ability.

Variability Selection Hypothesis

The Variability Selection Hypothesis states that wide environmental fluctuations over time created a large disparity in available niches. This led to inconsistency in selection pressures, which in turn reduced adaptations to any specific habitat and replaced them with adaptations that are responsive to change (Potts, 1998). An important feature of the Variable Selection Hypothesis is the lack of directional consistency in selective processes, instead selective pressures are variable.

Contrary to the Savannah Adaptation Hypothesis, the spread of savannah habitats apparently postdates the evolution of the first hominins. Indeed, *Ardipithecus ramidus* existed in a woodland environment (T. D. White, Ambrose, et al., 2009; T. D. White, Asfaw, et al., 2009; WoldeGabriel, et al., 2009), and *Australopithecus africanus* retained limb proportions that would have assisted in moving through treed environments (Aiello & Andrews, 2000). Records of paleoclimate indicate that climate change became more extreme from the Miocene to the present, including extremes of glaciations and warm interglacial periods as well as arid and moist cycles (reviewed in Potts, 1998).[26] Although, as mentioned above, there has been a long term trend toward a cooler climates,

[26] Some of this apparent shorter term climate variation may be due to the higher fidelity associated with measuring more recent climates.

this trend is punctuated by short term reversals and increasingly large fluctuations in climate (reviewed in Potts, 1998). Likewise, European pollen sequences indicate shifts from dense, moist forests and cold, dry steppes occurring repeatedly over the past million years (reviewed in Potts, 1998).

One way that organisms can adapt to these abrupt climate changes is by migrating and/or dispersing. In essence, the ability to move from less suitable habitats to more suitable ones allows organisms capable of doing so to be less susceptible to the pressures associated with variable environments. The second approach is for the organism to expand the range of conditions in which it can survive. Some organisms may do this through genetic polymorphism, where one allele confers and advantage is adaptive under certain environmental conditions and another allele is adaptive under alternate conditions. The proportion of these alleles in a population is then altered by the appropriate conditions. Phenotypic plasticity, the range of phenotypic response to environmental conditions, is another way a population can respond genetically to environmental change. Third, organisms may evolve mechanisms including complex structures and behaviours that respond to novel and unpredictable environments; this is variability selection (Potts, 1998). The mechanisms that arise through variability selection are strikingly uniform within a species, yet they mediate diverse responses to novelty.

Examples of mechanisms produced by variability selection in humans include: bipedalism, which may allow a wide repertoire of movement; a dental structure that can handle diverse food stuffs; and a large brain and brain structures capable of processing novelty to generate complex solutions (Potts, 1998). Probably the most profound consequence of the Variability Selection Hypothesis is the suggestion that the human brain is not adapted to specific ancestral conditions. The idea, common in evolutionary psychology, that human cognition bears the indelible mark of the environment of evolutionary adaptedness, may not reflect the reality of an irregular environment and unpredictable ecological niche. It would then be erroneous to assume that the human

brain and human mental life is dominated by cognition specifically designed to deal with recurrent Pleistocene problems (Potts, 1998).

A recent study has tested the relative contributions of both the Savannah Adaptation hypotheses and the Variability Selection hypotheses. By correlating brain volumes of hominin fossil specimens with the paleoclimate variations, it appears that both long-term climate trends as well as the amount of climatic variation contribute to an increase in brain size (Ash & Gallup, 2007). Climatic trends throughout the past 6 Ma, and in 200 thousand and 100 thousand year intervals, all correlate with increased brain size. Interestingly, birds with larger brains tend to be able to establish themselves in novel environments through innovative behaviours rather than through morphological or physiological mechanisms (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005).

Ecological Hypotheses

Ecological models of human brain evolution focus on the selective advantages that a complex human brain provides that allow more efficient exploitation and extraction of biological resources.

Foraging – Hunting Hypotheses

It has been suggested that human ecology is unique in that humans are adept at exploiting rich but difficult to use resources. Particularly, hominins have shifted from a diet that exploited the primary trophic level, plant products such as leaves, seeds, and fruits, to the second trophic level including increasing amounts of animal products. Primate cognitive abilities allow the exploitation of plant foods in tropical forests despite their complex distribution in space and time. The shift to a diet with greater dependence on animal protein created an intensification of a preexisting primate trend of using cognitive solutions to foraging, to adapt and exploit a potentially difficult to access second trophic level (Milton, 1981).

Miller (1981) suggests the lack of teeth and claws, characteristic of virtually all other predatory groups, predisposed hominins to utilize cognitive and behavioural solutions to hunting and scavenging. The niche associated with exploiting animal resources brought added complexity by increasing home-range size, requiring a consistent water source despite movement away from single sources, defense from other predators, and the abilities to both kill and extract nutrients from other animals.

Kaplan, Hill, Lancaster, and Hurtado (2000) propose that extreme human intelligence co-evolved with an exceptionally long lifespan, extended juvenile dependence, support from post-reproductive adults, and paternal care . These features evolved as responses to a shift toward nutrient-dense but difficult to acquire resources. First, knowledge, skill, coordination and strength are required to exploit resources that are difficult to acquire, such as hunting large game. Second, these traits, necessary for acquiring these resources, require a large developmental commitment. Productivity increases with age, thus selecting for lowered mortality rates and greater longevity. Third, these specializations and age-based stratification of productivity promote food sharing and provisioning of juveniles. Finally, men play a large role in group provisioning, lowering mortality risk during development (for both juveniles and mothers) as well as investing in future group productivity. This hypothesis is largely dependent upon observations of modern hunter-gatherer societies. Though the predictions bear out within these groups (Kaplan, et al., 2000), these extant groups may not necessarily reflect the ancestral condition.

Tool Use – Innovation Hypotheses

Potentially, one of the unique human capacities is that of complex tool use. Stone tools appear for the first time in the fossil record 2.5 Ma (Semaw et al., 1997), which roughly corresponds with the appearance of early *Homo* (see references Chapter 1). Tool use in the animal kingdom is fairly widespread, however, the human ability to use a tool

to fashion another tool is potentially unique (Stout & Chaminade, 2007). The manufacture of stone tools using the knapping technique activates premotor cortex and regions in the IPS, as well as functional areas in the parietal lobe unique to humans in the dorsal IPS (Stout & Chaminade, 2007). Only hominins are thought to possess the manual dexterity to manufacture early stone tools, in part due to a very flexible wrist not possessed by chimpanzees (Ambrose, 2001). It is intriguing that the first appearance of simple stone tools corresponds to the appearance of *Homo erectus*, and the appearance of more complex tools correlates with the transition to archaic *Homo sapiens* (Wynn, 2002). Interestingly the transition from the relatively simple stone tools of *Homo erectus*, to the more sophisticated tools of *Homo heidelbergensis* appears to be concomitant to the increase in encephalization from ~3.1 – 3.9 in *H. erectus* to 4.2 in *H. heidelbergensis* (Rightmire, 2004). In a related manner, innovation rate, where tool use is undoubtedly innovative, is positively correlated with relative isocortical size in primates and potential homologues in birds (Lefebvre, Reader, & Sol, 2004).

Killing-at-a-Distance Hypothesis

Some authors have argued that the development and deployment of projectile weapons was a driving force in human evolution. The capability to "kill-at-a-distance" allowed Paleolithic hominins to diversify their types of prey, allowed hunting in new environments with new tactics, and reduced the risk of injury and death from hunting (Churchill & Rhodes, 2009). It appears that projectile weapons arose with modern humans and spread as they migrated out of Africa (Churchill & Rhodes, 2009). It has been suggested that the human brain has evolved neural machinery to rapidly sequence movements, where throwing was the first and fastest application and language may be an application of this sequencing machinery to social communication (Calvin, 1983).

Bingham has proposed that human uniqueness can be explained by his "theory-of-everything" (Bingham, 2000, p. 248). He argues that unique human attributes are all due

to cooperation among non-kin conspecifics particularly for coalitional violence against other conspecifics. The immediate ancestors to the *Homo* genus gained the capacity to kill or injure adult conspecifics from a distance. Bingham argues that, "coalitional enforcement of kinship-independent social cooperation is the fundamental thing humans do, in the same sense that flight is the fundamental thing birds do" (Bingham, 2000, p. 249). Remote killing allows animals to attack others simultaneously, thus the risk associated with punishing non-cooperators can be spread across all social enforcers. If a lack of cooperation would need to be enforced in one-on-one scenarios, similarly-sized conspecifics would have to accept a 50 % chance of losing the engagement, thus limiting the advantage to cooperative enforcement. Coalitional enforcement, made possible by remote killing, reduces enforcement risk by n^2 (Bingham, 2000). This reduction in risk works in the favour of an individual's self-interest, however only under circumstances where this self-interest is congruent with the interests of the majority of surrounding individuals, regardless of kinship.

Despite the grandiose[27] claims of these Killing-at-a-Distance hypotheses, they may be based on stereotypes and exaggerations of the fossil record. As Whittaker and McCall (2001) demonstrate, the majority of stone hand-axes that are found are not suitable for throwing. They do not show the wear or impact damage expected from having been thrown, and the sharp-edge would have made throwing difficult and inaccurate (Whittaker & McCall, 2001). It may be that Killing at a Distance theories apply only to later hominins and perhaps only to *Homo sapiens*, thus influencing our evolution from a later point. However, this may preclude killing-at-a-distance from being a driving force in early hominin evolution and may not have driven the evolution of

[27] The term grandiose may seem like a relatively harsh assessment of these theories, the authors, particularly Bingham claim to purport to explain not only human evolution but all of human history as well. This is what I mean by grandiose.

larger brains at all, rather coalitionary enforcement of social norms via advanced weaponry may be a consequence of already possessing a large brain.

Expensive Tissue Hypothesis

The Expensive Tissue Hypothesis, put forward by Aiello and Wheeler (1995), suggests that the energy-demands of a large brain were offset by a reduction in the energy consuming tissues of the digestive tract. These authors argue that a relatively large brain cannot be achieved without either an increase in metabolic rate or an increased reliance on high-quality foods. The addition of greater quantities of animal products was essential to the evolution of the human brain.

There is no evidence for an increased basal metabolic rate in humans, in fact humans fit predictions for primates and for eutherian mammals of a given body weight (Aiello & Wheeler, 1995; B. McNab & Eisenberg, 1989). On the other hand, human brain mass is ~4 times greater than that would be predicted from the brains of other mammals (Aiello & Wheeler, 1995). It seems as though whatever was selecting for brain size increase in primates and humans was also driving a reduction in digestive tract size. It is not likely that other energy-demanding organs could reduce in size to maintain a steady metabolic rate; the heart is needed to pump oxygenated blood and the liver titrates blood glucose levels, both of which are vital for the moment to moment function of the brain. The digestive tract is potentially the only tissue that could be reduced as it is only partially dependent on body size and also dependent on diet (Aiello & Wheeler, 1995).

The Expensive Tissue Hypothesis raises the question of what factors allowed the development of a diminished digestive tract. A smaller digestive tract implies more nutritious food sources, indeed, primates with relatively nutrient-poor diets have larger digestive tracts, including in some cases expanded stomachs (Aiello & Wheeler, 1995). In addition, relative gut size is inversely correlated with relative brain size (Aiello & Wheeler, 1995). “A high-quality diet relaxes the metabolic constraints on

encephalization by permitting relatively smaller guts, thereby reducing the considerable metabolic cost of this tissue" (Aiello & Wheeler, 1995, p. 209). Reduction of digestive tract size and a shift to higher quality foods was likely a prime releaser to human encephalization.

Sociological Hypotheses

The third class of theoretical explanations for the evolution of humans emphasizes the influence of human sociality as the driving force behind the evolution of the human brain. The complexity of human society is surely unique in the animal kingdom, and it seems logical to assume that the complex human brain is somehow linked.

Ecological Dominance Hypothesis

Humans dominate the planet; there are virtually no habitats or ecosystems that are free from human influence. Moreover, there is not a single organism that routinely preys upon human beings despite the fact that some species benefit from the niches created by humans. Ecological dominance is much more than simply not having active predators, instead, ecological dominance has been defined as the diminishment of selection by extrinsic factors compared to the increased importance of selection from competition and interactions with members of the same species (Alexander, 1990; Flinn, Geary, & Ward, 2005).

Anderson (1990) and more recent advocates such as Flinn and colleagues (2005) suggest that the coupling of ecological dominance with increasingly important conspecific interaction was the key factor in human evolution. They argue that humans uniquely link social success to competition between social coalitions, rather than to individual competition within social groups. "The nature of this within-species competition appears to have involved an evolutionary arms race among ever-more effective coalitions. Both the success of one's coalitions and of individuals within their coalitions depended, in part, on sociocognitive competencies… which required new and

expanded brain structures" (Flinn, et al., 2005, p. 15). The increasing competition between individuals of the same species led to linguistic and social cognitive abilities that allowed better anticipation and understanding of social interactions. Moreover, extended childhood periods are useful to acquire social skills and to build coalitional relationships necessary in later life.

Machiavellian Intelligence Hypothesis

The Machiavellian Intelligence (Byrne, 1996; Byrne & Bates, 2007) Hypothesis suggests that other individuals use their intelligence to gain resources and benefit from group living. It is the dynamic of continually changing behaviour of others that corresponds to an individual's own behaviour that comprises the largest intellectual challenge. Thus a larger brain with greater processing capacity is needed to successfully reap the benefits of permanent social living. To differentiate the Machiavellian Intelligence Hypothesis from other incarnations of sociological hypotheses, this hypothesis may put more emphasis on the ability of individuals to manipulate and deceive others, though cooperative processes are undoubtedly important as well.

Social Brain Hypothesis

The most recent incarnation of sociological hypotheses rests on a potentially obvious assumption "that information-processing demands can be expected to increase as the number of relationships involved increases" (Dunbar, 1998, p. 180). Several cognitive factors potentially constrain group size, such as the ability to identify and remember others which likely increase in difficulty with the number individuals. Moreover, the ability to extract social information from others is presumed to increase in difficulty and become increasingly cognitively demanding as group size increases. Despite the potential perceptual and mnemonic constraints on social group size, Dunbar (1998) suggests that the ability to manipulate information about social relationships is the key factor.

Proponents of the Social Brain Hypothesis suggest that as social groups became increasingly complex from monkeys to apes to humans, there are observed grade shifts in the relationship between neocortical[28] size and group size (Dunbar, 1998). As would be expected from the closely related Machiavellian Intelligence Hypothesis, increased cerebral cortex is related to increased use of tactical deception. Moreover, cerebral cortex ratio correlates with clique size in humans and other primates (Dunbar, 1998).

Problems with the Social Brain Hypothesis

The Social Brain Hypothesis has gained increasingly popular among researchers as well as mainstream media. Despite its popularity, the Social Brain Hypothesis rests on several potentially unwarranted assumptions and evidence that has not held up in light of recent evidence.

Dunbar (Dunbar, 1998; Dunbar & Shultz, 2007a) suggests that adult cerebral cortex size correlates with length of the juvenile period in humans. However, this claim is based on an analysis by Joffe (1997), which contains several errors and unfounded assumptions. Despite being cited at least 110 times,[29] there has been no acknowledgment of these problems nor have corrections been made. A close examination of the data presented in table 1 of this article, suggests that something is very wrong in reporting the data. The values given for gestation period and for weaning age are incorrect. In fact, the values for weaning age are actually those of the gestation period (compare to the values given in the cited reference Harvey & Clutton-Brock, 1985). Also, the values given for age at sexual maturity in months are grossly off, and are actually values for age of weaning in days. For example, according to the data

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[28] Dunbar (1998) refers to neocortex, however what is actually meant is cerebral cortex including hippocampal, isocortical, and piriform cortices.

[29] Using a Google Scholar search on Oct. 14, 2010; this has increased by 27 citations over the past year when a similar search was performed.

presented in Joffe (1997) gorillas become sexual mature at an astonishing age of 1583 months or ~131 years old, which exceeds their reported lifespan of 39.3 years. If accurate, this would create an overwhelming dilemma detrimental to the reproductive success of this species; no wonder they are on the endangered species list! These errors do not appear to be included in Joffe's calculations, though they are manifest in the reported data. Joffe also includes an estimate of maximum lifespan for primates in the analysis, using a value of 60 years for the maximum age of humans, which is probably not reasonable given that among hunter-gatherer societies ~15 % of individuals live into their 7^{th} decade (Kaplan et al., 2007).

Using a more or less accurate value of 124 years of age for the maximum recorded human lifespan (though this may vary depending on how it is calculated, for argument sake I am sticking to a literal interpretation of maximum recorded lifespan) and corrected values for primate life history, the apparent extension of the human juvenile period is none existent. Joffe reports that 24.2% of the lifespan is reserved for the juvenile period, however using a more realistic estimate of maximum lifespan a value of ~11.7 % is observed. This is shorter than that observed for chimpanzees at 13.1 % of the lifespan reserved for the juvenile period. Moreover, if you use these values to examine the correlation between neocortex size and juvenile period, the relationship disappears for the larger bodied primates more closely related to humans. If you examine how the t-values change with estimates of the maximum human lifespan, the correlation between juvenile period and non-visual cortex ratio is only significant for estimates of maximum human lifespan of < 70 years of age. With realistic estimates of human life expectancy, only the proportion of the lifespan in adulthood (negatively) correlates with neocortex size.

Sociological theories concerning brain evolution cannot account for several observable phenomena. First, the brain size of prey animals has increased through geological time and is followed by increases in predator brains. Second these changes

occurred in both social and solitary animals, such as bears, small cats and musteloids which are primarily solitary (Finarelli & Flynn, 2009; Holekamp, Byrne, & Bates, 2007). Third the brains of bears are larger than that of social carnivores and bears show more flexible behaviour (Holekamp, et al., 2007). Social Brain hypotheses rely heavily on an apparent correlation between social group complexity (where group size is often used as a proxy measurement) and brain size (e.g., Dunbar, 1998). Given that social taxa are not more encephalized than related solitary taxa and groups that show greater encephalization do not necessarily have increases in sociality, this casts doubt on one of the key pieces of evidence for the Social Brain Hypothesis (Finarelli & Flynn, 2009). Fourth, tool use, innovation, and frequency of social learning are not correlated with groups, none of which are consistent with Social Brain hypotheses (Reader & Laland, 2002). Fifth, despite living in larger groups, macaques and baboons cannot match the cooperative behaviour and tool use in capuchins (Mendres & de Waal, 2000; Moura & Lee, 2004).

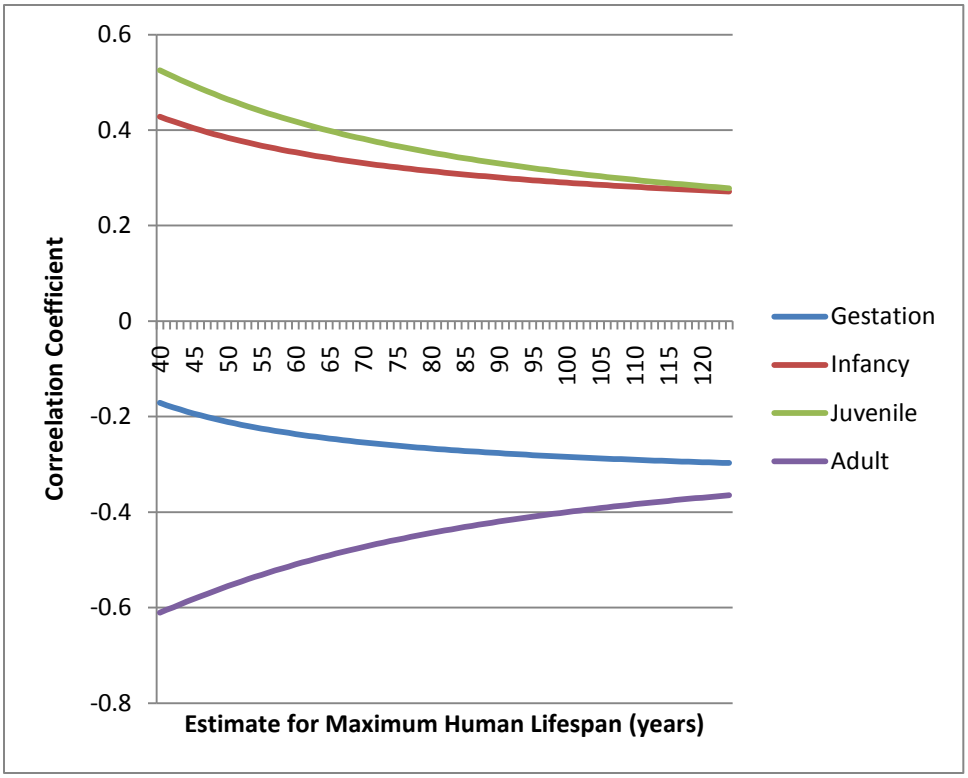

Figure 6 – Expected correlation coefficients for varying estimates of Maximum Human Lifespan. This graph depicts the correlation coefficients that are generated by the data in Joffe using different estimates of Maximum Human Lifespan. The correlations are calculated by relating the estimates of the proportion of the lifespan spent in a given stage, either gestation period, infancy, juvenile, and adult stages with non-visual cortex size.

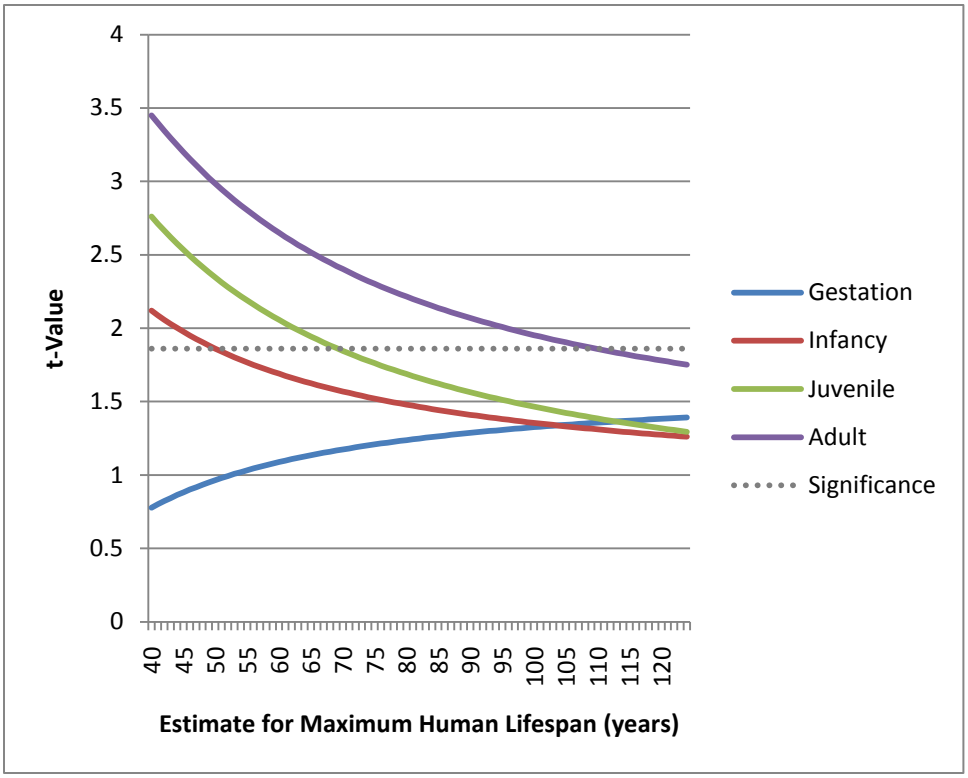

Figure 7 – Estimated t-values for expected correlation coefficients for varying estimates of Maximum Human Lifespan. This graph represents the t-values for correlation coefficients given Joffe's data with varying estimates of Maximum Human Lifespan. It is important to note, that only estimates of maximum human lifespan that are less than 70 years are the only values that result in significant correlations between the proportion of the lifespan spent in the juvenile period and non-visual cortex size. The dotted line represents the t-value where $p = 0.05$.

CHAPTER 4

SMELL, SEX, AND SOCIAL INFERENCE

Chemosensation

Chemosensation is intriguing for its uniqueness among the senses. Unlike the other senses, olfactory information does not have an early thalamic relay. Furthermore, visual and aural sensory transduction are categorically different from chemotransduction. Both vision and audition respond to a change or transfer of energy where the chemical senses respond to physical matter. Visual and aural sensory transducers respond in a graded fashion to a single property of the stimulus. For example, photoreceptive pigments have a bell-shaped response distribution according to the wavelength of incoming photons. Likewise, hair cells in the inner ear respond in a graded fashion to the frequency of incoming pressure waves. In the case of chemosensation, the sensory apparatus must transduce signals from an enormous variety of chemicals that vary across many dimensions in a non-contiguous fashion. Moreover, the chemical senses must distinguish between similar chemicals accurately as opposed to having a graded response. For example, ammonia and ammonium chloride require very different responses though are very similar in structure.[30]

As mentioned above, chemical sensation is vitally important to mammals and can be grouped into two relatively distinct (though interacting) systems. The olfactory system, responsible for the sense of smell, responds to volatile chemicals present in the air that enters the nasal cavity. The vomeronasal system responds to non-volatile chemicals most often present in aqueous solution. The sensory apparatus associated with each of these systems is located in the nasal cavity. Olfactory cues are transduced in the

[30] This difference is striking. Ammonia (NH_3) is severely hazardous to health where ammonium chloride (NH_4Cl) tastes delicious to some northern European cultures as a key ingredient in salty licorice.

upper nasal mucosa and vomeronasal cues are transduced in two specialized pits located in the floor of the nasal cavity in most mammalian species. In some mammals (*e.g.*, in felids and ungulates), a narrow passage behind the upper teeth, the nasopalatine ducts, connects the oral cavity and the vomeronasal region of the nasal cavity.[31] Each of these systems has separate projection pathways in the brain, involving overlapping, but partially disjunct neural systems. The connections and regions in this system lay out an important portion of the basic mammalian brain design.

Neurobiology of the Olfactory System

The olfactory system begins with transduction of airborne chemicals into neuronal signals by the olfactory sensory neurons located in the main olfactory epithelium in the upper nasal cavity. These sensory neurons project to the main olfactory bulb through the cribiform plate (the portion of the skull separating the nasal cavity and cranium). Each sensory neuron expresses one olfactory receptor gene of which there are on the order of a thousand[32] (Buck & Axel, 1991; Mori, Nagao, & Yoshihara, 1999). The olfactory bulb projects to many brain areas including piriform cortex and nearby structures (including the amygdala) located near the uncus in the medial temporal lobe (Hadley, Orlandi, & Fong, 2004; Scalia & Winans, 1975; Scott, 1986). Other branches of the olfactory tract from the olfactory bulb send projections directly to a region of ventromedial prefrontal cortex, located ventral to the genu and rostrum of the corpus callosum (Afifi & Bergman, 2005). Primary olfactory cortex projects to secondary olfactory regions in the OFC, insula, dorsomedial nucleus of the thalamus, lateral hypothalamus, and hippocampus.

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[31] Species in which the nasopalatine ducts are is present exhibit what is known as "the flehmen response" or referred to as "flehming." Flehming is a characteristic movement of the upper lips in many mammals to facilitate the transfer of chemicals from the mouth to the vomeronasal organ.

[32] Making olfactory receptors the largest family of g-protein coupled receptors and perhaps the largest family of genes in the genome (Firestein, 2001).

Data from macaques (*Macaca irus*) suggest that orbitofrontal regions are critical for odour discrimination; however the homologous region in humans may be significantly more anterior and in a different cytoarchitectonic region (Gottfried & Zald, 2005).

Where the olfactory bulb and primary olfactory cortex are necessary for odour detection, other brain regions are most likely necessary for extracting more complex information from odourants. The human amygdala has been shown to be involved with the intensity, but not the valence of olfactory stimulation (A. Anderson et al., 2003; Gottfried, Deichmann, Winston, & Dolan, 2002). It has also been demonstrated that the amygdala is activated by highly aversive odours and is related to subjective ratings of aversiveness (Gottfried, et al., 2002; Royet, Plailly, Delon-Martin, Kareken, & Segebarth, 2003; Zald & Pardo, 1997). Likewise, the amygdala has been shown to be involved in encoding and retrieving olfactory information, from recordings made directly from the amygdala of people with epilepsy, independent of the hedonic properties of the odours (Jung et al., 2006). Temporal lobe resections, which often include the amygdala and likely many other olfactory related regions, result in deficits in odour discrimination but not detection (Jones-Gotman & Zatorre, 1988).

The OFC of humans has likewise been shown to be involved in higher-order olfactory processing (Gottfried, et al., 2002). OFC is activated more for the valence of olfactory stimuli than its intensity (A. Anderson, et al., 2003). Furthermore, the OFC has been shown to be involved in emotional olfactory processing (A. Anderson, et al., 2003; Royet, et al., 2003; Zald & Pardo, 1997) and odour discrimination and recognition but not odour detection (Jones-Gotman & Zatorre, 1988; Potter & Butters, 1980; Zatorre & Jones-Gotman, 1991). Pleasant odours have been found to activate dissociable brain regions from that of unpleasant odours, where medial OFC is activated for pleasant but not unpleasant odours, where more lateral OFC regions are activated for unpleasant odours (Rolls, Kringelbach, & De Araujo, 2003). Active olfactory exploration has been

shown to activate medial and posterior OFC, where passive smelling activated lateral and anterior OFC (Sobel et al., 1998).

Neurobiology of the Vomeronasal System

The vomeronasal system, often referred to as the accessory olfactory system, begins with transduction of chemicals with low volatility and often in an aqueous solution. These chemicals, often found in urine, sweat, or other excreted bodily fluids, enter the cigar-shaped vomeronasal organ (VNO; also referred to as Jacobson's Organ) through two pits located on the floor of the nasal cavity, distinct from the main olfactory epithelium. This location on the floor facilitates transfer of chemicals that can be picked up in the oral cavity and transferred through the nasopalatine ducts directly to the VNO. A few animals can create suction to directly uptake fluid into this organ, though this is not very common. Sensory cells in the VNO project to the accessory olfactory bulb, which in turn projects directly to the cortex like the main olfactory bulb. The accessory olfactory bulb has direct connections to the amygdala, particularly medial and posteromedial cortical amygdalar nuclei, as well as the bed nucleus of the stria terminalis and accessory tract (Halpern & Martinez-Marcos, 2003; Meredith, 1991; Scalia & Winans, 1975). From these first connections with the amygdala, VNO signals are sent to mainly to the hypothalamus (the medial preoptic area, ventromedial hypothalamic area and premammillary nucleus, where they affect hormone release) as well as reciprocally back to the accessory olfactory bulb (Halpern, 1987; Halpern & Martinez-Marcos, 2003; Meredith, 1991). The connection of the vomeronasal system to the amygdala is important as it is in this region where the olfactory and vomeronasal systems interact, particularly the posteromedial cortical amygdala. An interesting feature is that it appears that olfactory information is input to the regions of the amygdala receiving vomeronasal input, though vomeronasal input does not flow reciprocally to these olfactory regions (Halpern & Martinez-Marcos, 2003).

Social Function of the Chemosensory Systems

The functions of chemosensation in mammals are varied and diverse; however there are key elements of basic biological importance to all of them. The main olfactory system, essentially synonymous with the sense of smell, serves the function of alerting an organism to the airborne chemical constituents of the environment, revealing food sources, predatory dangers, and environmental hazards that are simultaneously invisible, silent, and out of reach. As mentioned above, this may have evolved out of a need to locomote and locate resources in low-light conditions. Furthermore, chemical signals from conspecifics may have been used to attract potential mates from a distance without alerting predators especially attuned to visual or aural signals. To this end, mammals have an additional system, the vomeronasal system. This system enhances the repertoire of chemical sensitivity of the main olfactory system to include chemicals that are not usually airborne, rather are found in aqueous solution.

The vomeronasal system allows mammalian conspecific chemical communication through urine, sweat, or other aqueous, bodily excretions. This ability to detect compounds within aqueous solution allows mammals to communicate biologically relevant information between individuals, including sex, reproductive status, social status, immunological status, *etc.* A functional vomeronasal system has been shown to be involved in sexual behaviour, parental behaviour, aggression, territorial marking, and individual discrimination (for a review see Brennan, 2004; Halpern & Martinez-Marcos, 2003). Together, the olfactory and vomeronasal systems allow location or avoidance of conspecifics, as well as evaluation of conspecifics once they are in close proximity. Moreover, these two systems work together to evaluate conspecifics and mediate social behaviour (for a review see Kelliher, 2007). It is clear that many, if not most species of mammals utilize both systems adaptively in their environments. However, within the lineage of Primates, there appears to be a decline in the importance of chemical sensation. This may correspond to the emergence of trichromatic vision in the ancestors of old

world monkeys and apes (Zhang & Webb, 2003). In humans, the vomeronasal system is likely vestigial, if it is present at all, though the need to fill its role in evaluating or inferring the value of conspecifics is surely present and necessary for normal function.

Given the complexity of human social behaviour, it is imperative for humans to evaluate one another in order to be successful. Social interaction is incredibly challenging and complex in humans; this is compounded by the absence of the basic systems that helped (and continue to help) mammalian ancestors solve similar problems. At the same time, human social behaviour is extremely fluid and adaptive and not subject to the same constraints imposed by these very same ancestral systems.

Disconnection of the Vomeronasal System

The vomeronasal system is largely vestigial in hominoid primates (Old World monkeys and the great apes), the Primates more closely related to *Homo sapiens*. Monkeys and apes lack the wet nose tip found in lower primates and many other mammals, which may facilitate non-volatile chemicals entering the nasal mucosa and vomeronasal organ (Cartmill, 2002). Additionally, the gene for the only transduction channel expressed in vomeronasal sensory neurons in mammals, the TRPC2 channel, contains several pseudogene mutations[33] in these primates (Zhang & Webb, 2003). These pseudogene mutations render the ion channel non-functional, which means sensory signals from the VNO cannot be transduced into neuronal signals. Researchers have suggested that this is indicative of decreased selective pressure on maintaining the functionality of the TRPC2 channel (Liman & Innan, 2003; Zhang & Webb, 2003), in other words the primates including and most closely related to humans do not seem to have a biological need for a functional VNO.

[33] Pseudogenes are genes that have lost their ability to code for proteins or are otherwise not expressed.

Mouse models of TRPC2 mutation provide a clue to what can happen when social cues are absent. TRPC2 -/- mutant (knockout) mice, which lack a functional copy of the TRPC2 gene, are unable to discriminate the sex of conspecifics (Leypold et al., 2002; Stowers, Holy, Meister, Dulac, & Koentges, 2002). Male TRPC2 -/- mutants mate indiscriminately; they attempt to mount other males almost as often as they do females. Mutant males invariably lose fights with wild-type males, and do not establish appropriate dominance hierarchies from confrontations with other mutant male mice. Furthermore, mutant females do not show normal maternal aggression to intruders as do wild-type females. Surgical removal of the rodent vomeronasal results in a loss of the preference for odourants from estrus females as opposed to males, however this did not affect mating preference, though sexual behaviour may be decreased but not eliminated (Pankevich, Baum, & Cherry, 2004; Saito & Moltz, 1986). A similar result is observed after surgical ablation to the VNO in at least one strepsirrhine primate (*Microcebus murinus*) where VNO removal reduces sniffing exploration, decreased sexual behaviour, and a lack of intermale aggression (Aujard, 1997). Without a functional VNO, these animals have lost the ability to acquire the biologically relevant information about conspecifics that is necessary for appropriate and adaptive social interaction (for a review of the effects of surgical and genetic VNO ablations see Brennan & Keverne, 2004).

As mentioned above, many primates do not have a functional transduction apparatus in the VNO. Most primates with one or more pseudogene mutations to TRPC2 have evolved other cues to signal reproductive fitness and social status. For example, vaginal swellings and colouration changes accompanying ovulation are observed in most primate species (orangutans and humans are notable exceptions of concealed ovulation) and likely serve as signals of reproductive susceptibility (Gilad, et al., 2004). Non-human primate species have developed other morphological differences, such as differences in gross facial morphology between dominant orangutans and subordinates, or the colouration of mandrills. Indeed, it has been proposed that the evolution of

trichromatic vision in Primates coincides with the decline in selective pressure on a functional TRPC2 gene in the VNO (Liman & Innan, 2003; Zhang & Webb, 2003). The coexistence of trichromatic vision and functional pheromone perception in howler monkeys may provide evidence to contradict the co-evolution of pheromonal loss and trichromacy (D. Webb, Cortés-Ortiz, & Zhang, 2004).

There is a great deal of discrepancy in the scientific community about whether or not humans possess a functional vomeronasal system. Some researchers claim that human adults have a functional vomeronasal system that detects chemicals and affects behaviour (for a review see Halpern & Martinez-Marcos, 2003). This extreme position may not be warranted. The VNO is not consistently present in adulthood, where 41.4% of adults have no visible vomeronasal pit, only 13.5% have a well-defined bilateral pits, 26.4 % have a unilateral vomeronasal pit, and the remaining 18.7% have putative pits (Trotier et al., 2000). Moreover, there are no demonstrable neural connections of the VNO to the central nervous system in humans, including a lack of the accessory olfactory bulb. There are no conclusive demonstrations that the effects of putative human pheromones are mediated via the vomeronasal system, instead they may be potentially mediated by the olfactory system or by other means of detection, such as direct entry into the bloodstream and crossing the blood-brain barrier. However these putative human pheromones do seem affect the hypothalamus in a sexually dimorphic manner (for a review see Halpern & Martinez-Marcos, 2003; Monti-Bloch, Jennings-White, & Berliner, 1998; but see Monti-Bloch, Jennings-White, Dolberg, & Berliner, 1994). In a study of 34 distinct VNO receptor genes, all were found to contain pseudogene mutations (Kouros-Mehr et al., 2001). Though there may be an active, putative pheromone receptor, V1RL1, present in human main olfactory mucosa, suggesting that any remaining conspecific chemosensory functions are mediated by the main olfactory system (Rodriguez, Greer, Mok, & Mombaerts, 2000). For example, putative pheromones, such as androstadienone, have been shown to result in changes in glucose metabolism in the

brain (Jacob, Kinnunen, Metz, Cooper, & McClintock, 2001) and may be capable of altering the menstrual cycles of women (Stern & McClintock, 1998; see Whitten, 1999 for a dissenting methodological review). A consensus is appearing to emerge from the literature that humans do not have a functional VNO though some remaining chemical signalling mediated by the main olfactory system is present in humans, however chemical signalling in humans has only a minor impact on human behaviour.

Humans must gather social information in order to survive in even the simplest human societies. However, humans must do so without the benefit of one of the key sensory systems used in other mammals, the VNO. Indeed, partial anosmia is common and a part of normal variance observed in humans; this is especially true of adult men and prepubescent boys and girls, but not adult women for certain 'musky' odourants (Le Magnen, 1952). Humans are left with a difficult problem to solve; there are no single cues that provide information about the social status or reproductive fitness of others. In other words, social status and reproductive status are relatively independent of visual, aural, and chemical appearance in *Homo sapiens*. Despite this sensory handicap, humans nonetheless navigate the complex social world and reproduce successfully.

Sex and Social Behaviour

Reproduction is essential to biology and may be one of the defining characteristics of life. The introduction of sexual reproduction to life on Earth immediately introduced a layer of complexity to the social interactions between organisms. In addition to inter-individual competition for resources and predation or avoidance thereof, sexual reproduction requires a minimal level of cooperative interaction. Not only is it necessary to identify others as predators, prey, or conspecifics, sexually-reproducing organisms need to identify the value or quality of potential mates to maximize fitness. This difference is significant in that the problem-space is increased from simple identification to include observed or inferred value. In addition, sexual

reproduction often creates two classes of conspecifics (the sexes), which have competing goals in terms of investment in offspring and mate selection. This system has led to sex differences in the biology and behaviour of males and females, which may in turn be reflected as differences in brain structure and function. Sexual reproduction seemingly sets the stage for increased social complexity; at the same time, sexual behaviour constitutes only a subset of social behaviours particularly for humans. Furthermore, successful sexual reproduction in humans and other species depends highly on successful navigation of one's social milieu.

Sex Differences and Hemispheric Specialization

Given that sexual reproduction is a potential driving force behind the evolution and refinement of social behaviour and that sexual behaviours in turn make up an integral subset of social behaviours, it is reasonable to expect that there are observable and significant differences between sexes[34]. Men and women are neither biologically nor behaviourally identical; for example, women bear children and men do not. These differences extend not only to physical appearance and reproductive behaviours, but include cognitive abilities and neuroanatomy. For example, researchers have found that men had better performance on a mental rotation task and that this was related to increased surface area in the right parietal lobe, on the other hand women had poorer performance on the same task and this was related to increased thickness in the left parietal lobe (Koscik, O'Leary, Moser, Andreasen, & Nopoulos, 2009). In relation to social behaviour and functional localization in the brain, it appears that right hemisphere structures are critical for men and left hemisphere structures are critical for women

[34] Sex is properly defined by differences in gamete size, the sex with the larger gamete being female, thus differences between the sexes are a defining feature of sex. In the context of the present work, the working definition of sex refers to self-reported values of male or female.

(Tranel & Bechara, 2009; Tranel, Damasio, Denburg, & Bechara, 2005).[35] It is likely that these cognitive and neural adaptations result from the selective pressures associated with sex-specific ecological and sociological niches of men and women.

The extent to which sex differences in the brain are products of biological or environmental factors is often under debate. Realistically brain structure and any individual differences therein are the products of the complex interaction between genes and experience. There are many examples of how training and brain injury can induce observable structural changes in the brain, including the adult brain (Butefisch, 2004; Draganski & May, 2008; Elbert & Rockstroh, 2004). Research in rats suggests that hormone-mediated changes in adult brain structure are themselves programmed by early developmental hormone exposure, providing a perfect example of how both biology and environment interact to determine brain structure (McEwen, 1999). In humans, sex differences in cell density in the planum temporale, where the distributions for men and women do not overlap (Witelson, Glezer, & Kigar, 1995), are difficult to explain without including some biological developmental factor (McEwen, 1999). Furthermore, gross morphological measures including cortical surface area and average cortical thickness are highly heritable (0.89 and 0.81 respectively) with distinct genetic components (Panizzon et al., 2009). In contrast, hormone therapies associated with transsexual operations can alter adult brain volumes toward the proportions of the sex to which they are changed

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[35] It is not the aim of the present discussion to include anything close to a review of this large body of literature on sex differences in the brain, cognition, and behaviour, however a there a few general predictions (or 'postdictions') that may be made at this point.

1. Sex differences exist due to the biological realities associated with sexual reproduction.
2. Sex differences are most likely to be observed in brain regions that are unique, highly developed, or expanded in humans compared to our relatives, and this likelihood will increase as phylogenetic distance increases.
    - For example, in parietal lobe regions associated with human-enhanced spatial manipulations associated with tool-making and wide territorial ranging.
    - In social brain regions, including ventromedial prefrontal cortex, amygdala, *etc.*, associated with the ubiquitous sociality of modern humans.
3. These differences are likely to be manifest as differences in hemispheric specialization, as unilateral alterations represent a no-cost solution to cognitive adaptation (see Gazzaniga, 2000, for a detailed discussion).

(Pol et al., 2006). It seems that both biology and environment have interacting roles in determining brain structure and that these effects are mediated by the actions of sex-related hormones. For the present discussion, sex differences in brain structure are assumed to be both biologically-programmed throughout life-long development and environmentally determined via individual experience and culture. Simultaneously, biological predispositions influence experience and narrow environmental constraints, while environment and experience modulate potential developmental trajectories.[36]

It is possible that sex-related functional asymmetry observed in the human brain resulted from divergent selection acting upon the capacity of homologous brain regions in each cerebral hemisphere to process information in different ways (for a brief discussion see Koscik, Bechara, & Tranel, 2010). Potentially, the left hemisphere 'dominance' observed in women reflects selective pressure for specialization in interpersonal relationships that are necessary for personally rearing children, soliciting resources and cooperation from others to rear children, to maintain in-group cohesion, *etc*. On the other hand, the right hemisphere 'dominance' observed in men may reflect selective pressures imposed by intergroup co-operation and warfare, out-group relations, leverage of critical resources, *etc*. For the purposes of the present work, sex-related differences in performance are expected to follow the basic pattern found in the literature, namely, left hemisphere structures are disproportionately important in women, and right hemisphere structures are disproportionately important in men.

Given that all sexually reproducing animals, including all mammals, have two sexes with distinct needs and demands that must be met in order to ensure successful reproduction, it is reasonable to expect sex differences in the brain regions that mediate reproductive and related behaviours. In rats, the VNO is larger in volume and contains

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[36] I appreciate the fact that taking such a broad approach to the nature-nurture debate does not help resolve the issue one way or another. This is however deliberate in that the solution that best fits all of the available data is such that both types of factors are integral and interacting.

more neurons in males. The VNO of rats also projects to sexually dimorphic regions including the medial preoptic area, the ventromedial hypothalamus, arcuate nucleus, and supraoptic nucleus. The accessory olfactory bulb in rats is also larger in volume, cell size, and has more dendritic branches than in females. The bed nuclei of the accessory olfactory tract and stria terminalis are also sexually dimorphic (for a review see Guillamón & Segovia, 1997).

Social Inference

One of *Homo sapiens'* biggest challenges is how to successfully navigate the social world. Human social groups are a highly complex, interwoven network of cliques, allies, and competitors, and there is an immense impetus to know the qualities and values associated with others. Having knowledge of these qualities is particularly important for the deep, long-lasting social interactions that are integral for success and personal fulfillment. Likewise, this knowledge of others and the ability to rapidly infer these values undoubtedly guide the cursory, ephemeral social interactions that humans encounter on a daily basis. There are cues to social value in others' appearance, for example, factors like symmetry, body-mass index, and waist-to-hip ratio may signal fertility; however, the correspondence between any morphologic characteristic and reproductive fitness is associated with a level of uncertainty. Additionally, there are cues to social value in behaviour. These cues signal personality, intelligence, mood, *etc.*, which all are relevant for social interaction. However, it is difficult to appropriately sample others' behaviours to infer values (if it were a simple endeavour to do so then progress in the field of psychology might be much quicker). It is clear that there is uncertainty in inferring the qualities and values of others, particularly in socially relevant domains. And one need not spend too much time in a crowded city, for example, to recognize the critical role of social navigation aptitude in the modern world.

Navigating the social world requires constructing and flexibly utilizing social hierarchies and knowing one's place within them. Furthermore, knowing with whom to interact and cooperate and who to avoid (and perhaps even shun) is important for success. Unfortunately for humans, as mentioned before, there is no single cue, olfactory or otherwise, that provides the necessary information. Instead humans must infer the qualities of others from observing their behaviour. In a sense, this makes each and every human individual a behaviourist observing others trying to infer the rules and laws that govern another individual.

Without the benefit of a functional VNO to detect chemical signals from conspecifics, or any other one-to-one signal of social value, humans must rely on much more subtle cues regarding reproductive fitness and must use more variable information to infer the qualities and social value of others. In contrast, female mice emit odourants by virtue of their ovulatory status; the female smells a certain way because she is that way. Dominant male mice leave obvious and specific scent patterns in their territory and can do so only if they are dominant or unchallenged. Assessing reproductive susceptibility (via ovulatory status) and social dominance constitute single pieces of information indicating overall reproductive fitness. Many signals of reproductive fitness hold whether or not the female is ovulating and of the individual's rank within a dominance hierarchy. For humans these signals may include physical signals of waist-to-hip ratio, body mass index, physique, facial symmetry, neoteny, *etc.*, as well as behavioural cues of personality, intelligence, sociability, aggression, *etc.* Since humans have no obvious cues to the fitness of others, humans have an inferential problem in that fitness must be deduced from observation of behaviours or other subtle signalling mechanisms. Unlike the vast majority of our mammalian ancestors, humans can only infer the social value of others from potentially variable cues including: behaviour, dress, carriage, general appearance, *etc.* An example of this is the observation that women may "try to look more attractive" in the fertile stage of their menstrual cycle (*e.g.*, Haselton,

Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007). A change in the amount or style of grooming or changes in the attractiveness of clothes that are worn are far more subtle cues compared a direct observation of a change in odour. Furthermore, these behavioural changes require a level of inference over and above a direct chemical, visual, or auditory cue.

Additionally, a signal for fitness in one situation depends on the context and combinations in which they occur, in other words, social cues are dependent on the situation and behavioural context in which they occur. Using the example above, a change in the attractiveness in dress may only be informative of fertility status if the context of the situation does not provide a more obvious reason for the change, *e.g.*, the change between work dress and dress for the bar scene.

Given that cues to social value are highly variable, difficult to detect, and dependent on situational and behavioural context, the probability that any given piece of information is associated with an honest signal of social value is significantly less than 1. As a byproduct of this probabilistic association between cues and actual values, it is often prudent to increase the number of observations that are made to reduce the uncertainty of inferences, and this may as a consequence lead to increased time spent among familiar others and neophobia.

CHAPTER 5

INFERENTIAL BRAIN HYPOTHESIS

I hypothesize that *Homo sapiens* are presented with an inferential problem that must be solved in order to maintain adaptive social relationships and ensure reproductive success of the species. The systems and sensory apparatus that have evolved to accomplish these goals in our mammalian lineage have become fundamentally altered in our close primate relatives and have undergone further modification in humans. These modifications may be responsible for our success as a social species and may have also set in motion a series of changes that necessitated enhanced cognitive abilities to solve increasingly difficult inferential problems.

Based on the evolutionary heritage of *Homo sapiens*, I predict that the functions of certain regions with the limbic brain, and certain closely related brain areas, are intimately involved in processing social information and ultimately are responsible for social behaviour due to their evolutionary roles in conspecific chemical communication. These brain regions, originally adapted for mate selection and relatively simple social behaviour, have been exapted for increasingly complex human social interaction. Specifically, the amygdala and the ventromedial prefrontal cortex (VMPC) are of key interest. Both of these regions are critical for chemical sensation, discrimination, and evaluation, and both are known to be integral components of social processing in the human brain (for reviews see Adolphs, 1999, 2003).

The roles of the VMPC and amygdala in human social interaction will reflect their roles in mammalian chemosensation. The amygdala is an important relay for both olfactory and vomeronasal systems, and potentially and important site for interaction of these sources information. VMPC (more accurately the orbitofrontal aspect) is the primary neocortical target of primary olfactory cortex (including the amygdala). Given the role of both the amygdala and the VMPC in integrating sensory information, I predict that damage to these regions will have similar and necessary roles in making social

inferences. Ultimately, the amygdala and VMPC make complimentary contributions to the processes in question, perhaps the amygdala is more specific for negative evaluations given its role in fear processing, where the VMPC plays a more important role in behavioural inhibition in response to social information given its role in adaptive social conduct. However, the present hypothesis aims to demonstrate that both of these brain regions are necessary for making social inferences in general and not to determine their specific role in the processing steps associated with social inference at this time.

As discussed in Chapter 3 there are other hypotheses about some of these issues. An important example is the 'Machiavellian Intelligence Hypothesis' (Byrne, 1996) and the 'Social Brain Hypothesis' (Dunbar, 1998) (these hypotheses will be collectively referred to as the Social Brain Hypothesis). This hypothesis suggests that increases in social group size, social complexity, and social competition are responsible for enhanced cognition (*e.g.*, memory for socially relevant information) and increased brain size. The hypothesis presented here, by contrast, suggests that social group size, social group complexity, and social competition are neither necessary nor sufficient to explain the evolution of the cognitive capacity of the human brain.[37]

I hypothesize that the amount of uncertainty associated with the inferential problem of deducing the qualities of others due to an overall lack of invariant cues, including chemical, visual, and auditory signals, has been the driving force behind the cognitive expansion observed in humans. Individual humans must infer the values associated with others from their observable behaviours; these inferences are associated with causal uncertainty and may be prone to dissimulation and deception. This inferential problem placed increasing demand on cognitive structures and drove brain evolution.

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[37] These hypotheses are not necessarily mutually exclusive; increased social group size may indeed be an important factor if this increased size leads to increased inferential complexity.

The Social Brain Hypothesis predicts that increasing group size predicts increased brain size. However, recent evidence suggests that this is not necessarily the case. Once species outside of Primates (*e.g.*, Carnivora) are taken into account, including a representative sample of extant clades and fossil taxa, the relationship between social group size and brain size disappears (Finarelli & Flynn, 2009). Finarelli and Flynn (2009) report that support for the Social Brain Hypothesis is entirely driven by Canidae (wolves, foxes, *etc.* but excluding domesticated relatives, dogs) in respect to Carnivora. Despite this finding, the Social Brain Hypothesis does seem to hold for certain clades, *e.g.*, Primates and perhaps among porpoises. However, it may be that in these taxa in which the Social Brain Hypothesis appears true, this may be a consequence rather than cause. The current hypothesis suggests that instead of social group size, the common feature driving brain size evolution may be the difficulty of inferring traits of others.

In defence of the Social Brain Hypothesis, proponents may argue that inferential complexity may in fact increase with social group size. I would argue that this is not necessarily the case. As groups get larger and larger it may be a simple matter of learning new social rules, though learning any given rule is only associated with a certain degree of difficulty. There is no reason to assume that signals and cues to social value become more difficult to detect or interpret simply because there are more of them. Where this may tax memory to hold and utilize all of the available information, if cues remain highly honest, invariable, and non-ambiguous, then there is no increase in inferential complexity. Rather it is when cues become associated with higher degrees of uncertainty for whatever reason, including difficulty of detection over time or vulnerability to deception, is when inferential complexity increases. In formulaic terms, if cue X always equals value Y, it does not matter how many times you encounter cue X. However if cue X sometimes equals value Y and sometimes equals value Z depending on cue W, this is inferentially more complex irrespective of the number of times it is encountered.

The Reinterpretation Hypothesis posits that for millions of years social animals have been under selective pressure to detect regularities in conspecifics. The Reinterpretation Hypothesis claims that hominins began to evolve to the ability to interpret these statistical regularities in terms of unobservable causal states (Subiaul, Barth, Okamoto-Barth, & Povinelli, 2007). This hypothesis is very similar to the current hypothesis, in that both posit the inference of characteristics, however, the present hypothesis posits social inference as a prime mover in human cognitive evolution. The Reinterpretation Hypothesis suggests that humans began to extract something fundamentally new from social information, i.e., unobservable mental states, where the current hypothesis suggests that this human ability to infer unobservables is a byproduct of a system for inferring social values that suddenly[38] became unobservable for human species only. The current hypothesis may be a subtle refinement of the Reinterpretation Hypothesis as it moves social inference from a process by which humans gained new abilities in evolutionary time to a process by which humans maintained biologically necessary abilities in the face of a sensory handicap, and this had the byproduct of setting the stage for unique human abilities.

Ultimately, the current hypothesis rests on several assumptions: 1. A better ability to infer the useful traits of others provides a fitness advantage. 2. The ability to better infer traits of others is itself transmitted to offspring. 3. This advantage was great enough to offset the cost of increased energy-demanding brain tissue. People who are better at inferring the values of others and utilizing this information should produce more or better quality offspring. There may however be differences in what is evolutionarily fit in modern society compared to what was fit in our evolutionary past. In the past, up until relatively recently, infant mortality was fairly high, and thus reproductive strategies that

[38] Suddenly in this sense may mean over a matter of a few million years, roughly corresponding to the length of time that it took for environments to shift from forest to savannah type habitats during the same period of history.

emphasized quantity of offspring were more likely to make larger genetic contributions to the next generation. On the other hand, in modern societies where infant mortality is relatively low, a reproductive strategy emphasizing 'higher quality' offspring may be more fit and result in the same number of survivable offspring overall. Either way, whoever makes the largest contribution to the subsequent generation is by definition the most fit. However, producing a large quantity of offspring that are themselves low in fitness would render this fitness boost irrelevant.[39] A conceptually simple test of the current hypothesis would be to test whether or not individuals with brain damage that leads to deficits in social inference produce fewer and less viable offspring. Unfortunately, reality makes this testing this possibility difficult, if not impossible. Brain lesions typically occur later in life, when people are well past their reproductive years. Certainly, cases of developmental defects and severe mental retardation result in profound decreases in evolutionary fitness in addition to deficits in activities of daily living. Instances of developmental damage from focal brain lesions do occur, however the data on these populations are generally scarce compared to that of older populations.

An interesting case may be advanced for instances of psychopathy. Psychopathy may be conceptually similar in many ways to the social conduct disorders observed following damage to the brain regions relevant to the current hypothesis. Indeed, similar neural substrates have been implicated, including OFC and the amygdala (for a review see Glenn & Raine, 2009).[40] The fact that psychopathy may be associated with more offspring rather than fewer appears to counter the current hypothesis. However, it is unclear that psychopathy is associated with deficits in inferring social values *per se*,

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[39] For example, a male donkey and female horse could produce many mule offspring, but this is ultimately unfit due to the infertility of the offspring.

[40] A notable exception to this similarity is a pronounced lack of instrumental aggression following focal brain injury to the target regions, but is potentially a defining feature of psychopathy.

which is in stark contrast to the obviously abnormal utilization of this information that characterizes psychopathy. There is a clear genetic component to psychopathy (for a review see Harris, Skilling, & Rice, 2001), though a greater number offspring does not necessarily mean greater fitness particularly in the absence of normal parental care. Furthermore, in a similar manner to predator-prey relationships, there is a finite number of psychopaths (predators) that can survive on a population of non-psychopaths (prey), depending on the costs and benefits from engaging psychopathic behaviour, as well as additional costs incurred from social sanctions imposed by the non-sociopaths.

The experiments outlined in this document aim to test predictions made by the current hypothesis. I will use a lesion approach to test the notion that the ventromedial prefrontal cortex and amygdala are involved in inferring the traits of others through observing behaviour reflecting their evolutionary involvement in conspecific chemical communication and evaluation of conspecifics in terms of biologically relevant social goals. I predict that the contributions of these areas to social processing will be independent of social group size; instead they will be related to the inferential complexity of the social decision. Finally, capacities in lower-order information processing domains that are necessary for social inference will be unaffected by damage to the VMPC or amygdala, suggesting that the deficits observed are specific to the social realm. In other words, the deficits observed in social inference (in patients with damage to VMPC or amygdala) may not be due to dysfunctional extraction of information from sensory signals in a general sense, instead the deficits are specific to extraction of social information from environmental stimuli and/or deploying this information in social settings.

As a starting point, social inference, in the context of biologically relevant decisions, is integral to the development and basis of the current hypothesis. Given that reproduction is an extremely important biological function and that mate choice is one of the largest and most consequential decisions made throughout the course of human lives,

the role of the VMPC and amygdala in inferring and utilizing information to guide mate choices is highly important. As a second target of inquiry, it is important to demonstrate that damage to the VMPC or amygdala interferes with inferring social information. Damage to the VMPC or amygdala is predicted to reduce the likelihood of the individual to make dispositional social attributions. As a third target of inquiry, the proponents of competing hypotheses, namely the Social Brain Hypothesis, have made some specific claims about the relationship between the ability to infer the thoughts of others and social clique size. The current hypothesis makes different predictions, as outlined below; potentially the current project can differentiate between these hypotheses. As a fourth and final area of inquiry, a critical component to social inference is the ability to infer values transitively. This ability exists ubiquitously in the animal kingdom and allows individual organisms to infer the relative value of itself and others without having to directly engage in potentially risky interactions with each other individual organism. Since transitive inference is a basic deductive reasoning process and has obvious benefits for safe, social interaction any deficit due to damage to the VMPC or amygdala may be at the root of defective social conduct.

SPECIFIC AIMS

SPECIFIC AIM #1: Mate Choice

To investigate whether the ventromedial prefrontal cortex (VMPC) and amygdala are necessary for making mate choices, reflecting their evolutionary role in reproduction.

> HYPOTHESIS #1: Damage to the target brain regions will result in diminished preference for biologically relevant information when making mate choices. In other words, the relative value associated with physical attractiveness and relative age for men, and socioeconomic status and paternal investment for women, will be decreased following damage to VMPC or amygdala.

SPECIFIC AIM #2: Social Attribution

To investigate whether the VMPC and amygdala are necessary for inferring the qualities of others. In other words, these brain regions are potentially necessary for extracting dispositional information from others' behaviour.

HYPOTHESIS #2: Target participants (patients with damage to VMPC or amygdala) will not exhibit the fundamental attribution error as normal, healthy comparisons and brain-damaged comparisons will. Specifically, target participants will not display the normal bias toward making dispositional attributions over situational ones. Furthermore, these target participants will be not display the correspondence bias when utilizing dispositional information instead of situational information while making economic decisions.

SPECIFIC AIM #3: Perspective-Taking

To investigate the relationship between complex perspective-taking and social group size and how these phenomena are affected by damage to the target brain regions.

HYPOTHESIS #3: The Social Brain Hypothesis predicts a strong relationship between higher-order perspective-taking (e.g., thinking about the thoughts of others, thinking about thoughts of others' thoughts of others' thoughts) and social group size, thus under this view damage to target regions will show correlated deficits on these tasks. However, another possibility is that higher-order perspective-taking is limited largely by memory capacity and is independent of social group size. In this view, perspective-taking complexity does not pose an inferential problem of increasing difficulty, thus target participants will not show deficits in higher-order perspective-taking or a relationship between their perspective-taking ability and social group size.

SPECIFIC AIM #4: Social Hierarchy

To investigate whether participants with damage to target brain regions can appropriately and effectively utilize transitive inference in an experimental paradigm as well as in a real-time, social simulation.

HYPOTHESIS #4: Damage to the target brain regions will interfere with the ability to utilize transitive inference, in both an experimental, non-social paradigm as well as when inferring a social hierarchy.

CHAPTER 6

GENERAL APPROACH AND METHOD

Participants

Participants consisted of 4 sample groups. There were two *target groups*: participants with focal VMPC lesions and participants with focal amygdala lesions (AMG). These target groups were subdivided by sex (men and women) and hemisphere of damage (unilateral left, unilateral right, or bilateral). In order to take into account various demographic variables (such as age, education, IQ, etc.), *comparison groups* were included. These consisted of one group of brain-damaged comparison (BDC) participants and a group of normal, healthy adult comparisons (NC). Both of these groups were matched as closely as possible to the participants in the target groups in terms of demographic factors. BDC participants have brain lesions that exclude VMPC or either amygdala, and that are of comparable size to other lesions in target regions. Certain areas of brain lesions have been excluded, for example bilateral hippocampal regions were not sampled as the memory deficits associated with this type of damage may be too severe in these patients to accurately test them on portions of the paradigms which require intact memory function. Comparison subjects were matched to the schedule of testing as given to the target participants, *i.e.*, all participants completed the tasks in the same order with similar time intervals between individual experiments, as best as possible, however the realities of scheduling based on participant volunteerism meant that the order of testing was not always consistent. There was not much attrition, as the majority of subjects who began the protocol finished it.

I recruited participants with brain damage from the Patient Registry in the Department of Neurology (see Tables 1 -5 for demographic data). For inclusion in the Patient Registry individuals must: 1) have no premorbid neurologic or psychiatric dysfunction (*e.g.*, mental retardation, dementia, psychiatric history, 2) no history of

alcohol or drug abuse prior to their lesion, 3) single, focal damage, 4) and only brain damage due to vascular accidents (strokes, aneurysms), herpes simplex encephalitis, surgical resection, and hypoxia/anoxia. Currently the Patient Registry includes approximately 500 active participants available for testing.

Bilateral lesions to structures distal to the midline, *e.g.*, the amygdala, are rare and thus the numbers in some of these groups was challenging to achieve, accordingly I was able to recruit only 1 of the possibly three available subjects with bilateral amygdala damage. Relatively circumscribed unilateral amygdala lesions due to temporal lobectomy on the other hand are relatively common in the Patient Registry, and consistent with prior experience working with these patients they were in general very willing to participate in research in our laboratory and the protocols laid out here. Regarding patients with VMPC damage, although these patients are fairly numerous and willing to participate, the demand for their time has been very high so access was somewhat limited in comparison to amygdala patients, however recruitment levels were only slightly short of predictions.

Participant's sexual orientation was not screened prior to testing, though it was directly relevant to the Mate Choice paradigm. Homosexuality is not common within the Patient Registry (I am aware of only a single individual). All participants, both brain-damaged participants and normal comparisons, completed all of the tasks as much as possible. Since homosexuality is not a reasonable exclusion criterion for 3 of the 4 experiments, it was not used as exclusion criteria for the mate choice paradigm. However, sexual orientation was queried and used to exclude or properly classify this data during analyses. Given the low rate of homosexuality in the Patient Registry as well as the low frequency in the normal comparisons recruited for unrelated studies, this problem did not present itself; all subjects reported being heterosexual.

To compare our groups in terms of demographic variables, a MANCOVA was calculated on the variables age, education, and estimated FSIQ, with brain damage group

and sex as fixed factors. The overall model revealed a significant effect of group (using Wilk's Lambda since there are more than two groups) ($F=3.253$, $p=0.001$), but no effect of sex ($F=0.357$, $p=0.784$) or group by sex interaction ($F=0.772$, $p=0.643$). Test of between subjects effects reveal that the groups significantly differed on all three variables; age ($F=1746.606$, $p<0.0005$), education ($F=3086.352$, $p<0.0005$), and estimated FSIQ ($F=10212.673$, $p<0.0005$). Pairwise comparisons suggest that participants with amygdala damage were 11.6 years younger than the participants with VMPC damage ($p=0.010$), 11.7 years younger than brain damaged comparison participants ($p=0.004$), and 13.5 years younger than normal healthy adults ($p<0.0005$).

All brain damaged groups had significantly fewer years of education than normal comparisons; VMPC 2.3 fewer years than NC ($p=0.002$), AMG 1.9 fewer years than NC ($p=0.010$), and a trend in BDC with 1.2 fewer years of education than NC ($p=0.054$). The brain damaged groups did not differ from each other (minimum $p=0.152$). Likewise NC estimated FSIQ is significantly higher than brain damaged groups, 8.8 points higher than VMPCs ($p=0.003$), 9.5 points higher than AMGs ($p=0.001$), and 5.153 points higher than BDCs ($p=0.033$). Years of education was highly correlated with estimated FSIQ in the entire group ($r=0.771$, $p<0.0005$) and within each of the groups (VMPC: $r=0.670$, $p=0.002$; AMG: $r=0.647$, $p=0.002$; BDC: $r=0.723$, <0.0005; NC: $r=0.753$, $p<0.0005$), for both sexes (Men: $r=0.825$, $p<0.0005$; Women: $r=0.681$, $p<0.0005$). Both education and estimated FSIQ are uncorrelated with age in the entire sample (education and age: $r=0.097$, $p=0.269$; estimated FSIQ and age: $r=0.125$, $p=0.190$).

A one-way ANOVA reveals no significant differences between groups in years since lesion onset ($F=0.557$, $p=0.575$).

Since there are age differences in age and education, these variables will be used as covariates in further analyses where appropriate. Estimated FSIQ will not be used as a covariate in further analyses since it is highly correlated with education and there are

more missing data points (21) for estimated FSIQ compared to years of education, for which all subjects have data collected.

Neuropsychological Data

All of the neurological patients in the Patient Registry have undergone extensive neuropsychological testing. Neuropsychological testing was completed in the chronic stage following brain injury, a minimum of 3 months post-lesion. These data were used to compare brain damage comparison to target participants. Ideally, all participants would not have underlying deficits in basic cognitive functions that might influence performance on the experimental battery. For example, target participants should have normal memory; likewise matched comparisons should have normal memory performance. Realistically, neurological damage is never completely and uniquely focused on the region of interest (which is one of the important reasons for including brain damage comparison participants) and this may result in cognitive dysfunction in other areas as well. Thus, having this extensive neuropsychological battery allowed psychometric variables to be included as covariates in our analyses to control for deficits in these other functions. The core test battery available for all patients in the registry includes:

1. Intellectual and Achievement Abilities, e.g., WAIS-III (recently testing has begun on WAIS-IV), WRAT-4;
2. Memory, e.g., WMS-IV, AVLT, Complex Figure Test;
3. Speech and Language, e.g., Boston Naming Test, MAE;
4. Perception and Attention, e.g., Facial Recognition Test, Judgement of Line Orientation;
5. Visuoconstruction, e.g., Complex Figure Test-Copy;
6. Psychomotor and Psychosensory Function, e.g., Purdue Grooved Pegboard Test, Smell Identification Test;

7. Executive Functions, e.g., Trail-making Test, Wisconsin Card Sorting Test, Tower of London/Hanoi Tests;
8. Personality and Affect, e.g., Beck Depression/Anxiety Inventories, Minnesota Multiphasic Personality Inventory-2, Iowa Scales of Personality Change;
9. Premorbid Status, e.g., National Adult Reading Test, Geschwind-Oldfield Handedness Questionnaire, Patient Biography Form (Patient and Relative versions).

A sample of the neuropsychological data from this core battery was collected, such that tests relevant to the specific aims of this study were compared for between groups differences. The variables selected were chosen to be the same variables that we have used in publications from our lab for tasks that are somewhat similar (e.g., Koscik & Tranel, 2010). The tests that were used, included, Wechsler Adult Intelligence Scale-III (WAIS), Full Scale (FSIQ), Verbal (VIQ), and Performance (PIQ) Intelligence Quotients; Beck Depression Inventory (BDI); Beck Anxiety Inventory (BAI); Rey Auditory Verbal Learning Test, 30-min recognition score, correct + correct rejections (AVLT); Wisconsin Card Sorting Test, number of categories completed (WCST), Facial Discrimination Test (Face Disc.), Controlled Oral Word Association Test (COWA), Boston Naming Test (BNT) (See Tables 6-13 for Neuropsychological data).

Most of the data, including neuropsychological, neuroanatomical, and experimental variables, were collected within 2 years of the date of testing the current protocol. In cases where larger periods of time separate measurements, the protocol of the Patient Registry from which these data were taken, indicates that these measures are stable across time. If there are suspected changes to any of these measures either new neuroanatomical scans are taken or neuropsychological tests are re-administered as needed (and where possible). In addition, the WTAR was administered to the subjects on the date of testing for this protocol, providing a contemporaneous measure of estimated

IQ to testing, moreover given the previously mentioned relationship to education level, this provides evidence that at least IQ measurements are stable across time.

A MANCOVA was run to test for between group differences on neuropsychological variables, with age and education included as covariates. There was no observed effect of group ($F=0.640$, $p=0.851$) or age ($F=0.757$, $p=0.666$), however there was a weak trend for education having an effect on neuropsychological variables. Tests for between subjects effects revealed that education significantly effects FSIQ ($F=14.009$, $p=0.001$), VIQ ($F=19.061$, $p<0.0005$), and PIQ ($F=4.962$, $p=0.035$) as expected given their highly correlated nature as noted above. There was potentially a trend toward a group difference on the Boston Naming Test ($F=2.718$, $p=0.086$), where amygdala subjects tended to score lower than BDCs. The reason for this potential singular difference is unclear (likely the result of anterior temporal lobectomy), though it's impact on the current studies should be minimal since none of the tasks are dependent on verbal fluency or naming abilities, and all subjects are made to understand the instructions before any given task begins. Importantly, the groups did not differ in terms of depression or anxiety as measured by the BDI ($F=0.493$, $p=0.617$) and BAI ($F=0.444$, $p=0.729$). Moreover, pairwise comparisons reveal no differences between groups for either BDI or BAI (all p's >0.331). Since the groups did not differ significantly, these variables were not included as covariates in further analyses, nor were they expected to affect results differentially for anyone group.

Table 1 – Demographics by Brain Damage Group

		Age (years)	Education (years)	Handedness		
	N	Mean (Std.Dev.)	Mean (Std.Dev.)	Right	Left	Mixed
VMPC	21	59.47 (13.53)	14.07 (2.09)	20	1	0
AMG	23	47.15 (11.94)	14.33 (2.22)	19	3	1
BDC	39	59.00 (10.81)	15.10 (3.11)	36	3	3
NC	46	60.84 (13.20)	16.13 (2.45)	43	3	0

Table 2 – Demographics by Group and Brain Damage Side

			Age (years)	Education (years)	Handedness		
		N	Mean (Std.Dev.)	Mean (Std.Dev.)	Right	Left	Mixed
VMPC	Right	7	52.15 (19.51)	13.93 (1.69)	7	0	0
	Left	4	60.87 (9.76)	15.25 (2.75)	4	0	0
	Bilateral	10	64.03 (7.45)	13.70 (2.11)	10	0	0
AMG	Right	9	47.34 (14.82)	15.78 (1.99)	9	0	0
	Left	13	47.23 (10.70)	13.46 (1.94)	13	0	0
	Bilateral	1	44.46 (.)	12.50 (.)	1	0	0
BDC	Right	13	56.04 (14.54)	15.62 (3.55)	12	0	1
	Left	21	60.87 (9.09)	15.29 (2.95)	17	2	2
	Bilateral	5	58.85 (3.80)	13.00 (2.00)	4	1	0

Table 3 – Demographics by Group, Sex, and Side of Brain Damage

				Age (years)	Education (years)	Handedness		
			N	Mean (Std.Dev.)	Mean (Std.Dev.)	Right	Left	Mixed
VMPC	Men	Overall	11	58.14 (14.40)	13.91 (2.59)	10	1	0
		Right	4	52.88 (23.41)	12.75 (0.96)	4	0	0
		Left	3	56.18 (3.30)	15.67 (3.21)	3	0	0
		Bilateral	4	64.85 (5.88)	13.75 (3.10)	3	1	0
	Women	Overall	10	60.94 (13.11)	14.25 (1.48)	10	0	0
		Right	3	51.18 (17.81)	15.50 (0.87)	3	0	0
		Left	1	74.95 (.)	14.00 (.)	1	0	0
		Bilateral	6	63.48 (8.85)	13.67 (1.51)	6	0	0
AMG		Overall	7	45.40 (11.78)	13.71 (1.25)	5	1	1
	Men	Right	3	47.37 (12.48)	14.67 (1.15)	1	1	1
		Left	4	43.92 (12.91)	13.00 (0.82)	4	0	0
		Overall	16	47.92 (12.32)	14.59 (2.52)	14	2	0
	Women	Right	6	47.32 (17.01)	16.33 (2.16)	5	1	0
		Left	9	48.70 (10.06)	13.67 (2.29)	8	1	0
		Bilateral	1	44.46 (.)	12.50 (.)	1	0	0
BDC		Overall	21	60.40 (8.35)	15.19 (3.27)	18	2	1
	Men	Right	8	58.15 (10.91)	16.88 (3.60)	7	0	1
		Left	8	63.60 (7.27)	14.88 (2.90)	7	1	0
		Bilateral	5	58.85 (3.80)	13.00 (2.00)	4	1	0
		Overall	18	57.37 (13.18)	15.00 (3.01)	15	1	2
	Women	Right	5	52.65 (20.07)	13.60 (2.61)	5	0	0
		Left	13	59.19 (9.95)	15.54 (3.07)	10	1	2
NC	Men		23	63.82 (12.10)	16.74 (2.68)	22	1	0
	Women		23	57.87 (13.84)	15.52 (2.06)	21	2	0

Table 4 – Lesion Onset and Etiology by Group and Side of Brain Damage

		Lesion Onset (years)	Etiology			
		Mean (Std.Dev.)	Resection	CVA	Tumor	Other
VMPC	Overall	14.07 (2.09)	1	10	9	1
	Right	13.93 (1.69)	1	3	3	0
	Left	15.25 (2.75)	0	3	1	0
	Bilateral	13.70 (2.11)	0	4	5	1
AMG	Overall	10.72 (10.29)	19	2	1	1
	Right	9.33 (10.51)	7	2	0	0
	Left	9.08 (4.61)	12	0	1	0
	Bilateral	44.46 (.)	0	0	0	1
BDC	Overall	13.18 (11.28)	2	30	7	0
	Right	12.62 (11.87)	1	11	1	0
	Left	14.10 (12.37)	1	17	3	0
	Bilateral	10.80 (2.95)	0	2	3	0

Table 5 – Lesion Onset and Etiology by Group, Sex, and Side of Brain Damage

			Lesion Onset (years)	Etiology			
			Mean (Std.Dev.)	Resection	CVA	Tumor	Other
VMPC	Men	Overall	13.91 (2.59)	0	7	4	0
		Right	12.75 (0.96)	0	2	2	0
		Left	15.67 (3.21)	0	3	0	0
		Bilateral	13.75 (3.10)	0	2	2	0
	Women	Overall	14.25 (1.48)	1	3	5	1
		Right	15.50 (0.87)	1	1	1	0
		Left	14.00 (.)	0	0	1	0
		Bilateral	13.67 (1.51)	0	2	3	1
AMG	Men	Overall	12.86 (10.99)	5	1	1	0
		Right	16.67 (16.77)	2	1	0	0
		Left	10.00 (5.35)	3	0	1	0
	Women	Overall	9.78 (10.19)	14	1	0	1
		Right	5.67 (3.98)	5	1	0	0
		Left	8.67 (4.53)	9	0	0	0
		Bilateral	44.46 (.)	0	0	0	1
BDC	Men	Overall	13.57 (10.70)	1	15	5	0
		Right	15.50 (14.55)	1	6	1	0
		Left	13.38 (10.03)	0	7	1	0
		Bilateral	10.80 (2.95)	0	2	3	0
	Women	Overall	12.72 (12.22)	1	15	2	0
		Right	8.00 (3.00)	0	5	0	0
		Left	14.54 (13.99)	1	10	2	0

Table 6 – Neurospychology – WTAR Estimated IQ and WAIS by Group and Brain Damage Side

		N	Estimated FSIQ	FSIQ	PIQ	VIQ
VMPC	Overall	21	102.89 (11.08)	106.40 (19.65)	105.30 (17.08)	105.80 (19.50)
	Right	7	103.17 (10.32)	101.33 (11.85)	100.67 (13.32)	101.33 (10.12)
	Left	4	107.25 (13.28)	118.33 (31.01)	119.33 (20.13)	113.67 (34.50)
	Bilateral	10	100.50 (11.35)	101.25 (14.86)	98.25 (14.22)	103.25 (13.72)
AMG	Overall	23	102.15 (11.34)	103.72 (11.30)	107.50 (10.68)	101.21 (14.24)
	Right	9	112.25 (5.44)	114.71 (5.19)	112.57 (8.89)	113.75 (7.55)
	Left	13	95.64 (9.32)	96.73 (7.91)	104.27 (10.83)	92.09 (10.38)
	Bilateral	1	93.00 (.)	. (.)	. (.)	. (.)
BDC	Overall	39	106.33 (10.27)	104.83 (13.86)	129.00 (122.31)	102.33 (23.03)
	Right	13	108.11 (11.45)	105.50 (9.23)	104.75 (15.10)	94.38 (33.88)
	Left	21	105.94 (10.36)	105.41 (15.17)	107.53 (13.04)	106.00 (18.46)
	Bilateral	5	104.40 (9.37)	101.80 (17.63)	240.80 (297.69)	102.60 (17.02)

Mean (Std. Dev.)

Table 7 – Neurospychology – WTAR Estimated IQ and WAIS by Group, Sex, and Brain Damage Side

				Estimated FSIQ	FSIQ	PIQ	VIQ
VMPC	Men	Overall	11	104.30 (12.70)	103.14 (22.97)	101.43 (18.83)	103.00(23.20)
		Right	4	104.00 (7.30)	94.50 (0.71)	93.00 (1.41)	95.50 (0.71)
		Left	3	108.33 (16.04)	118.00 (43.84)	118.00 (28.28)	113.50(48.79)
		Bilateral	4	100.67 (18.56)	99.00 (17.35)	96.00 (16.52)	101.00(15.87)
	Women	Overall	10	101.13 (9.17)	114.00 (5.57)	114.33 (8.62)	112.33 (2.08)
		Right	3	101.50 (19.09)	115.00 (.)	116.00 (.)	113.00 (.)
		Left	1	104.00 (.)	119.00 (.)	122.00 (.)	114.00 (.)
		Bilateral	6	100.40 (7.30)	108.00 (.)	105.00 (.)	110.00 (.)
AMG	Men	Overall	7	101.40 (11.22)	101.55 (12.50)	99.55 (13.18)	67.91 (48.19)
		Right	3	112.33 (6.51)	114.33 (8.08)	111.00 (9.54)	115.33 (7.37)
		Left	4	100.33 (9.50)	94.00 (9.76)	99.50 (11.70)	91.00 (12.36)
	Women	Overall	16	100.00 (10.46)	105.39 (9.95)	102.94 (12.89)	60.86 (48.85)
		Right	6	112.20 (5.54)	115.00 (3.16)	113.75 (9.64)	112.80 (8.35)
		Left	9	93.88 (9.23)	98.29 (6.99)	107.00 (10.15)	92.71 (10.09)
BDC	Men	Overall	21	106.93 (10.07)	104.94 (12.75)	144.06 (162.62)	107.29(14.02)
		Right	8	110.25 (11.15)	104.00 (10.24)	101.50 (16.13)	105.67 (9.61)
		Left	8	106.80 (11.39)	108.50 (11.86)	106.00 (13.97)	112.83(15.57)
		Bilateral	5	104.40 (9.37)	101.80 (17.63)	240.80 (297.69)	102.60(17.02)
	Women	Overall	18	105.81 (10.74)	104.69 (15.74)	109.31 (12.34)	95.85 (30.65)
		Right	5	106.40 (12.68)	110.00 (4.24)	114.50 (6.36)	60.50 (67.18)
		Left	13	105.55 (10.42)	103.73 (16.99)	108.36 (13.12)	102.27(19.51)
NC	Overall		46	111.55 (8.53)	. (.)	. (.)	. (.)
	Men		23	108.86 (8.03)	. (.)	. (.)	. (.)
	Women		23	114.23 (8.34)	. (.)	. (.)	. (.)

Mean (Std. Dev.)

Table 8 – Neuropsychology – Depression and Anxiety Inventories by Group and Brain Damage Side

			BDI	BAI
VMPC	Overall	21	6.09 (7.13)	5.33 (3.08)
	Right	7	2.60 (5.81)	3.75 (3.77)
	Left	4	16.00 (.)	6.50 (3.54)
	Bilateral	10	7.60 (7.13)	6.67 (1.15)
AMG	Overall	23	6.52 (6.36)	7.50 (5.68)
	Right	9	4.38 (7.35)	5.67 (5.09)
	Left	13	7.85 (5.57)	8.60 (5.99)
	Bilateral	1	. (.)	. (.)
BDC	Overall	39	10.47 (7.58)	5.74 (3.94)
	Right	13	8.00 (5.69)	7.14 (4.38)
	Left	21	11.94 (8.47)	5.20 (3.85)
	Bilateral	5	11.00 (8.29)	3.50 (2.12)

Mean (Std. Dev.)

Table 9 – Neuropsychology – Depression and Anxiety Inventories by Group, Sex, and Brain Damage Side

				BDI	BAI
VMPC	Men	Overall	11	8.43 (8.02)	3.20 (2.17)
		Right	4	4.33 (7.51)	2.00 (1.73)
		Left	3	16.00 (.)	4.00 (.)
		Bilateral	4	10.00 (8.89)	6.00 (.)
	Women	Overall	10	2.00 (2.45)	8.00 (1.41)
		Right	3	0.00 (0.00)	9.00 (.)
		Left	1	. (.)	9.00 (.)
		Bilateral	6	4.00 (1.41)	7.00 (1.41)
AMG	Men	Overall	7	7.64 (5.54)	9.40 (5.38)
		Right	3	2.00 (2.00)	4.50 (4.95)
		Left	4	9.25 (2.36)	10.25 (7.04)
	Women	Overall	16	6.95 (6.69)	8.47 (4.26)
		Right	6	5.80 (9.26)	6.25 (5.80)
		Left	9	7.22 (6.55)	7.50 (5.58)
BDC	Men	Overall	21	10.29 (7.04)	4.82 (3.71)
		Right	8	8.14 (5.08)	6.00 (4.74)
		Left	8	12.33 (8.64)	4.00 (3.16)
		Bilateral	5	11.00 (8.29)	3.50 (2.12)
	Women	Overall	18	10.67 (8.40)	7.00 (4.14)
		Right	5	7.75 (7.50)	10.00 (1.41)
		Left	13	11.73 (8.79)	6.00 (4.34)

Mean (Std. Dev.)

Table 10 – Neuropsychology – AVLT and WCST by Group and Brain Damage Side

		N	AVLT	WCST
VMPC	Overall	21	11.46 (3.23)	9.08 (3.17)
	Right	7	10.80 (3.19)	7.20 (1.79)
	Left	4	13.00 (3.46)	11.67 (4.16)
	Bilateral	10	11.20 (3.56)	9.40 (2.97)
AMG	Overall	23	11.50 (2.28)	7.86 (3.78)
	Right	9	13.11 (1.62)	10.00 (2.60)
	Left	13	10.38 (2.02)	6.38 (3.84)
	Bilateral	1	. (.)	. (.)
BDC	Overall	39	11.33 (2.53)	9.15 (3.37)
	Right	13	11.90 (1.73)	10.30 (3.23)
	Left	21	11.56 (2.99)	9.44 (3.33)
	Bilateral	5	9.40 (0.89)	5.80 (1.64)

Mean (Std. Dev.)

Table 11 – Neuropsychology – AVLT and WCST by Group, Sex, and Brain Damage Side

				AVLT	WCST
VMPC	Men	Overall	11	10.38 (3.02)	8.88 (3.31)
		Right	4	8.67 (1.53)	6.67 (1.15)
		Left	3	12.00 (4.24)	11.00 (5.66)
		Bilateral	4	11.00 (3.61)	9.67 (2.89)
	Women	Overall	10	13.20 (3.03)	9.40 (3.29)
		Right	3	14.00 (1.41)	8.00 (2.83)
		Left	1	15.00 (.)	13.00 (.)
		Bilateral	6	11.50 (4.95)	9.00 (4.24)
AMG	Men	Overall	7	10.64 (3.88)	12.18 (7.12)
		Right	3	13.33 (1.15)	9.67 (3.21)
		Left	4	11.00 (2.94)	8.25 (5.06)
	Women	Overall	16	9.13 (3.80)	9.58 (4.16)
		Right	6	13.00 (1.90)	10.17 (2.56)
		Left	9	10.11 (1.62)	5.56 (3.17)
BDC	Men	Overall	21	11.06 (1.89)	8.94 (3.08)
		Right	8	12.14 (1.86)	11.14 (3.08)
		Left	8	11.17 (1.72)	9.00 (1.41)
		Bilateral	5	9.40 (0.89)	5.80 (1.64)
	Women	Overall	18	11.67 (3.18)	9.40 (3.79)
		Right	5	11.33 (1.53)	8.33 (3.21)
		Left	13	11.75 (3.52)	9.67 (4.01)

Mean (Std. Dev.)

Table 12 – Neuropsychology – Facial Discrimination, COWA, and Boston Naming Test by Group and Brain Damage Side

			Face Disc.	COWA	BNT
VMPC	Overall	21	13.62 (2.26)	13.82 (1.89)	27.64 (4.13)
	Right	7	13.80 (1.10)	13.00 (1.83)	27.00 (2.94)
	Left	4	14.67 (0.58)	15.00 (0.00)	29.67 (0.58)
	Bilateral	10	12.80 (3.49)	13.75 (2.50)	26.75 (6.50)
AMG	Overall	23	14.59 (3.67)	10.73 (6.06)	25.32 (6.66)
	Right	9	14.44 (1.01)	10.11 (7.11)	24.56 (7.75)
	Left	13	14.69 (4.79)	11.15 (5.47)	25.85 (6.07)
	Bilateral	1	. (.)	. (.)	. (.)
BDC	Overall	39	13.53 (2.86)	13.09 (3.87)	26.62 (6.16)
	Right	13	14.60 (0.70)	14.10 (1.10)	28.70 (1.57)
	Left	21	13.26 (3.62)	12.42 (5.03)	25.68 (8.04)
	Bilateral	5	12.40 (1.67)	13.60 (1.52)	26.00 (1.00)

Mean (Std. Dev.)

Table 13– Neuropsychology – Facial Discrimination, COWA, and Boston Naming Test by Group, Sex, and Brain Damage Side

				Face Disc.	COWA	BNT
VMPC	Men	Overall	11	14.00 (1.20)	13.86 (1.68)	28.14 (2.54)
		Right	4	13.67 (1.15)	12.33 (1.53)	26.00 (2.65)
		Left	3	14.50 (0.71)	15.00 (0.00)	29.50 (0.71)
		Bilateral	4	14.00 (1.73)	15.00 (0.00)	30.00 (0.00)
	Women	Overall	10	13.00 (3.46)	13.75 (2.50)	26.75 (6.50)
		Right	3	14.00 (1.41)	15.00 (.)	30.00 (.)
		Left	1	15.00 (.)	15.00 (.)	30.00 (.)
		Bilateral	6	11.00 (5.66)	12.50 (3.54)	23.50 (9.19)
AMG	Men	Overall	7	13.64 (6.79)	16.82 (9.27)	19.91 (11.62)
		Right	3	14.67 (0.58)	15.00 (0.00)	29.67 (0.58)
		Left	4	18.00 (8.04)	8.50 (5.20)	26.50 (6.24)
	Women	Overall	16	13.17 (3.47)	16.13 (9.82)	17.43 (11.06)
		Right	6	14.33 (1.21)	7.67 (7.71)	22.00 (8.51)
		Left	9	13.22 (1.48)	12.33 (5.45)	25.56 (6.35)
BDC	Men	Overall	21	13.89 (1.37)	14.22 (1.06)	28.11 (1.60)
		Right	8	14.86 (0.38)	14.29 (0.95)	29.14 (0.90)
		Left	8	14.00 (0.63)	14.67 (0.52)	28.67 (0.82)
		Bilateral	5	12.40 (1.67)	13.60 (1.52)	26.00 (1.00)
	Women	Overall	18	13.13 (3.95)	11.81 (5.33)	24.94 (8.65)
		Right	5	14.00 (1.00)	13.67 (1.53)	27.67 (2.52)
		Left	13	12.92 (4.37)	11.38 (5.84)	24.31 (9.50)

Mean (Std. Dev.)

Neuroanatomical Data

Neuroanatomical data were available for every participant in the Patient Registry. All brain-damaged participants have structural magnetic resonance (MR) images, unless contraindicated for example due to aneurysm clips or other reasons. VMPC damage is not uncommonly due to an aneurysm in the vicinity of the anterior communicating artery, and thus many of these participants do not have MR images, though there are lower resolution CT images instead. Of the majority of patients who have an MR image available, these images are generally T1-weighted images obtained during the chronic epoch (at least 3 months post-lesion as noted above) via a General Electric Signa 1.5T scanner. More recently inducted patients have multi-spectral images via Siemens Trio 3T scanner including: T1, T2, and Flair images. Detailed MR (or CT) images allow careful neuroanatomical localization of brain lesions.

All lesions were visually inspected blind to the experimental results, lesion location, and lesion etiology. Participants were assigned to the VMPC group if this region was damaged. The VMPC consists of the medial portion of the orbitofrontal surface of the PFC as well as the ventral portion of the medial wall of the PFC, partial or complete damage to these regions resulted in inclusion in the VMPC group. Participants were assigned to the amygdala group for analysis if at least one of their amygdalae was clearly damaged or removed entirely or if the amygdala was clearly and completely undercut of surrounding tissue. Participants were included in the BDC group if both amygdalae were completely intact and not undercut, and if there was no damage to ventromedial prefrontal cortex or insular cortex.

General Approach to Data Analysis

Data analysis followed a general pattern for all experiments and hypotheses. Analyses were carried out to examine main effects of group (VMPC damage, amygdala damage, brain-damaged comparisons, and normal, healthy, adult comparisons) on the

dependent variables of each task (main contrast variables are outlined below with each experiment). For all contrasts, demographic and neuropsychological variables were included as covariates, namely age and education as group differences were observed.

Since the sex and hemisphere of damage are of particular interest and groups were being directly manipulated in terms of these variables, analyses were run to examine potential interaction effects between sex, hemisphere of damage, and group. Analyses consist of a main analysis where brain damage group is the main factor and age and education are included as covariates. Secondary analyses include 3 (lesion location: VMPC, amygdala, or BDC) x 3 (left-sided, right-sided, or bilateral lesions) and 4 (brain damage group) x 2 (men or women) factorial designs, where age and education are entered as covariates, to examine the effects of lesion side and sex respectively. A model include both sex and laterality was not utilized as there are too few participants to utilize this method. Effects of lesion side and sex were expected to follow the general pattern of deficits being most severe in men with right-sided VMPC or amygdala damage and women with left-sided VMPC or amygdala damage, men and women with damage to the opposite hemisphere would not differ from comparisons. Bilateral cases were predicted to resemble men with right-sided damage and women with left-sided damage. Where BDC participants provided a "negative control," *i.e.,* they are expected to show no deficit in comparison to target participants, bilateral VMPC and amygdala cases provided a "positive control" in terms of effects of side, *i.e.*, they should show a deficit regardless of lateralized effects.

Social versus Cognitive Processes

An important distinction may benefit further discussion, that of whether or not brain processes can be considered social processes or cognitive processes. It may be argued that certain functions of the brain are specifically social and that others are not, i.e., they are cognitive processes. The view taken here does not reflect such a dichotomy,

rather social processes are better thought of as a subset of cognitive processes that are applied to social domains. Given a modular view of the human brain, certain regions process incoming information in a specific way. Moreover the processing steps, or the algorithms implemented by the given brain region, are independent of the type of information that are input into the module. In other words, whether or not the input information has or has not any social content is irrelevant to the process implemented by the given brain region. Certain processes and brain modules may be more or less likely to be implemented in the analysis of social information. In this sense these modules and processes that are more often implemented in the analysis of social information could be considered social processes. However, there is nothing intrinsically social about any brain processes as the modules could process any input information in a similar manner. Thus, differentiating between so-called social processes and cognitive processes is actually concerned with the informational content of processing rather than the processing itself. In the remainder of this document, tasks are thus considered social in content if social information is being processed. This includes all tasks that specifically involve other agents as sources of information. Tasks are considered non-social if the information involves no other agents.

CHAPTER 7

MATE CHOICE

Logic

If the evolutionary role of ventromedial prefrontal cortex and the amygdala in reproductive function is conserved (or even elaborated) in humans, albeit in the absence of chemical cues, then these target brain regions might be expected to be involved in human reproductive decisions. Since, no organism mates indiscriminately under normal conditions and a relatively large amount of resources are expended locating and courting mates as well as rearing offspring, cognition should be optimized to facilitate the best possible mate choice. Focal brain damage to regions including the VMPC and amygdala have been linked to changes in sexual-social conduct (S. Anderson, Bechara, Damasio, Tranel, & Damasio, 1999) and changes in ratings of sexual awareness and risky sexual behaviour (Koscik & Tranel, unpublished). Surprisingly there is a dearth of literature on mate choice in humans in relation to the brain, beyond involvement of reward-related areas in the brain (*e.g.*, ventral tegmental area) (Fisher, Aron, & Brown, 2006).

According to evolutionary models of human mate selection, people should prefer honest signals of mate value. It has been suggested that men should look for cues of fertility (*e.g.*, physical attractiveness and relative youth) whereas women should look for socioeconomic status or paternal care cues to maximize reproductive fitness (Bereczkei & Csanaky, 1996). There is a great deal of debate surrounding which cues are used, whether or not these cues are honest, and whether or not preferences for certain cues varies across cultures. As an example, the potential cue of waist-to-hip ratio (WHR) has received a great deal of attention in the literature. Research suggests that a low WHR (0.6 – 0.8) is an honest cue of female reproductive potential (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004). It has also been suggested that a lower WHR specifically reflects the availability of "neurodevelopmental resources" (Lassek &

Gaulin, 2008) which may reflect how WHR depends heavily on body mass, particularly in relation to additional body fat.

Given that a low WHR is an honest signal for some measures of mate value, it is no surprise that men prefer women with a lower WHR (Dixson, Dixson, Bishop, & Parish, 2009; Dixson, Dixson, Morgan, & Anderson, 2007; Marlowe, Apicella, & Reed, 2005; Streeter & McBurney, 2003; Swami, Jones, Einon, & Furnham, 2009). Some authors have argued that the preference observed for a low WHR is specific to Western men and not present in foraging populations, such as the Hadza of Tanzania (Wetsman & Marlowe, 1999). Some researchers have argued that weight (body mass index) is a more significant factor than WHR influencing mate preferences (Swami, Neto, Tovée, & Furnham, 2007; Swami & Tovée, 2007). However, it is not possible to entirely dissociate WHR and body mass index as one influences the other. Further examination of the preferences of the Hadza foragers in Tanzania, reveals that they too prefer low WHRs however only when stimuli are viewed in profile (Marlowe, et al., 2005). These results suggest that there is little cultural variability in the real-life preferred WHR, however the preferred distribution of body mass, *e.g.,* wide hips or protruding buttocks, appears sensitive to cultural variation. Likewise women show similar relatively culturally invariant preferences for male attractiveness, though preferences for resource potential and interpersonal factors have been shown to very between geographical regions (McGraw, 2002). Recent research suggests that attractiveness is more important in settings in which personal choice and multiple options are available, such as urban versus rural areas (Plaut, Adams, & Anderson, 2009). Personal attributes are important mediating factors of individual differences in mate preferences; highly attractive individuals place more emphasis on attractive mates (McGraw, 2002) and physical attractiveness and body mass estimations depend on observer's body mass index (Tovée, Emery, & Cohen-Tovée, 2000). Overall, there appears to be somewhat culturally

invariant preferences for fit and attractive individuals; however culture, geographic, and situational circumstances constrain choices and emphasize different attributes.

If the VMPC or amygdala is necessary for normal mate choices, then participants with damage to these target regions should make indiscriminate mate choices. More specifically, male target participants will associate physical attractiveness and relative age with less value compared to male comparison participants. Similarly female target participants will associate less value with socioeconomic status and paternal investment.

Given that a significant proportion of the target participants and comparisons are beyond their prime reproductive years, (*i.e.,* many women may have gone through menopause), the question may arise as to the validity of asking these participants about their mate choices. Despite the fact that these participants may not be making mate choices currently in their lives, the basic principles on which the brain operates likely continue well beyond one's reproductive years. Moreover, Buunk, Dijkstra, Fetchenhauer, and Kenrick (2002) found no age-related differences in mate selection criteria among a sample ranging from 19 – 61 years of age. Besides this experimental evidence and the lack of a solid, *a priori* reason (beyond personal relevance) for expecting age-related differences in mate choice, the age-matched sampling of comparison groups will provide a baseline response to which the target participants can be compared in the event that age-related differences do exist in the current paradigm.

Experimental Design

The Mate Choice Experiment

To examine whether or not the VMPC and amygdala are necessary to make normal mate choices, participants completed a task that was designed to be similar in many respects to on-line dating websites, however I manipulated four variables of interest. These variables included physical attractiveness, relative age, socioeconomic status, and parental ability. First, participants were asked a series of demographic

questions, I made measurements of their body (*i.e.*, height, weight, shoulder, chest, waist, hip sizes, and digit lengths), and they were asked to indicate their preferences for potential mates. These questions were done in order to create a mock 'match profile' of them and to gather appropriate data to generate a series of matches. Participants then selected one of two simultaneously presented matches, which varied in terms of the four variables of interest. Choices between matches were made for three relationship types: 1. which match would make the best partner in a purely sexual relationship; 2. which match would make the best long-term partner (for example in a marriage or other exclusive relationship); and 3. which match would be the best partner to have children with. While they made their match choices, psychophysiological data (including heart rate, respiration rate and magnitude, and skin conductance response) was be collected, although not analyzed as of yet. After they completed this mate choice task they completed two brief questionnaires.

The Hormone Questionnaire

Fluctuating hormonal levels, hormone therapies, or hormonal supplements may affect mate preferences given their role in reproduction. Furthermore, women using birth control and women who are post-menopause may have different mate preferences (and implicit mate-related goals) due to their altered reproductive status and hormone levels. Men's preferences too may be influenced by hormone therapies. Unfortunately these potential confounds are impossible to eliminate, given that a portion of our target participants and matched comparison participants were likely to be significantly affected by either hormonal contraceptive techniques, hormonal changes due to menopause, or even using hormone replacement therapies. To control for these possible differences in baseline hormone levels at the time of testing, a questionnaire to assess these aspects was administered. Questions included whether or not they are post-menopausal, if they are on any hormone therapy, date from last menstruation, duration and regularity of their cycle

(to allow calculation of their current menstrual stage), and whether or not they were taking hormonal birth control at the time of testing. For men, the questionnaire was simpler and asked whether or not they were taking any hormonal drugs at the time of testing (if they were in doubt of whether or not a given drug was a hormone they were asked to report it anyway).

The Social History Questionnaire

Unlike many of the studies that are done with brain-damaged participants, research on mate choice has an obvious, and ecologically valid measure of pre-morbid mate choice, provided the participants had made a real-life mate choice in the past (*e.g.*, marriage). Participants were thus asked about previous marriages, divorces, remarriages, children, paternity of their children, and they provided ratings and information about their spouse as they were at the time of their marriage.

Predictions

If the VMPC or amygdala is important for making choices related to reproduction, then participants with damage to these areas should show decreased preference for biologically relevant cues to potential mate quality. More specifically, target men should show decreased preference for attractive, younger women whom would arguably be more fertile. On the other hand, target women should show decreased preference for men of high socioeconomic status and paternal investment. These findings would support the hypothesis that these brain regions retain their evolutionary role in reproduction-related cognition.

Results

All analyses were conducted separately for men and women for this protocol, as men and women are expected to differ in their mate-related preferences and choices as a product of their reproductive roles and goals, moreover the potential choices for body

types were distinctly constructed with this in mind when creating this task. Since men and women received different body image stimuli any comparison between them is not possible for body type and attractiveness data.

Waist-to-Hip Ratio

Group differences in preferences for waist-to-hip ratio (WHR) were tested using a MANCOVA with brain damage group as a fixed factor, age and education as covariates and WHR ratio preferences for Most Attractive, Most Unattractive, Best Purely Sexual Partner, Best Long-term Partner, and Best Parental Partner as dependent variables.

In women, the overall model reveals no group differences ($F=1.236$, $p=0.256$), no significant effect of age ($F=1.653$, $p=0.168$), but a significant effect of level of education ($F=4.560$, $p=0.002$). Tests of between subjects effects hint at weak group effect on WHR preferences for parental partners only ($F=2.543$, $p=0.068$). Possibly driven by a preference among BDCs for larger WHRs compared to NCs (mean difference =0.041, $p=0.048$) (see Figures 8 – 9).

In men, the overall model revealed no differences based on group ($F=1.173$, $p=0.302$), age ($F=1.039$, $p=0.407$), or education ($F=0.545$, $p=0.741$) (see Figures 10 – 11).

Body Mass

Group differences in preference for body mass were tested using a MANCOVA with brain damage as a fixed factor, age and education as covariates and body mass (BM) preference for Most Attractive, Most Unattractive, Best Purely Sexual Partner, Best Long-term Partner, and Best Parental Partner as dependent variables.

In women, the overall model revealed no significant effect of group ($F=0.612$, $p=0.859$) or education ($F=1.246$, $p=0.306$), but a trend toward a significant effect of age ($F=2.292$, $p=0.064$) (see Figures 12 – 13).

In men, the overall model revealed no effect for group ($F=0.983$, $p=0.477$), age ($F=1.707$, $p=0.153$), or education ($F=0.624$, $p=0.682$). Between subjects tests hinted at a possible effect of group on Unattractiveness preferences for BM ($F=2.810$, $p=0.049$), possibly driven by a preference for larger BM among men with amygdala damage (vs. VMPC: mean difference = 0.569, $p=0.028$; vs. BDC: mean difference = 0.684, $p=0.007$; vs. NC: mean difference = 0.475, $p=0.055$) (see Figures 14 – 15).

Ideal Age, Education, and Income

Group differences in preferences for the ideal age, education, and income were tested using a MANCOVA with group as a fixed factor, age and education as fixed factors and ideal age relative to the participants age, ideal education level as indicated by highest degree obtained, and income measured on a scale anchored by $20,000 less than and more than the participant as dependent variables for purely sexual partners, long-term partners, and parental partners.

In women, significant effects of age ($F=2.752$, $p=0.015$) and education ($F=5.090$, $p<0.0005$) were observed, however there was not a significant effect of group ($F=1.115$, $p=0.338$). There was a hint of an effect of group on parental partner ideal age shown by between subjects tests ($F=3.559$, p-0.022), driven by BDCs preferring much older partners compared to NCs (mean difference = 17.281 years, $p=0.003$) (see Figures 16 – 18).

In men, there was again no significant effect of group ($F=0.888$, $p=0.627$), nor is there a significant effect of age ($F=1.407$, $p=0.218$); there was however a significant effect of education on ideal preferences ($F=7.563$, $p<0.0005$) (see Figures 19 – 21).

Importance Ratings

A MANCOVA was used to test for group differences in ratings of importance of certain variables on making different types of mate choices. Group was included in the model as a fixed factor, again age and education were used as covariates, and Importance

rankings were used as dependent variables. Separate MANCOVAs were run for ratings for sexual, long-term, and parental partners.

Purely Sexual Partner

The overall model revealed no effect of group (F=0.829, p=0.774), age (F=1.377, p=0.233), or education (F=1.529, p=0.167) for women and likewise no effect of group (F=0.787, p=0.842), age (F=0.841, p=0.657), or education (F=1.152, p=0.361) for men.

Long-term Partner

In women and men, there were no effects of group (Women: F=0.833, p=0.768; Men: F=0.970, p=0.548), age (Women: F=1.005, p=0.497; Men: F=1.530, p=0.149), or education (Women: F=1.329, p=0.259; Men: F=1.219, p=0.312).

Parental Partner

In women, there was no effect of group (F=1.371, p=0.103), however there was a trend toward an effect of age (F=2.011, p=0.056) and a significant effect of education (F=2.654, p=0.014). Between subjects tests suggested that there may be an effect of group on the importance of parental partner intelligence (F=3.170, p=0.034), driven by lower ratings of importance among women with amygdala damage compared to BDCs (mean difference = -0.661, p=0.013) and NCs (mean difference = -0.524, p=0.019) (see Figure 22). In men, there were no observed significant effects of group (F=0.843, p=0.761) or age (F=1.187, p=0.335), though there was a significant effect of education (F=2.260, p=0.024). Curiously, there may have be a trend for men with VMPC damage to report decreased importance of smell when deciding on parental partners (vs. AMG: mean difference = -1.832, p=0.082; vs. BDC: mean difference = -1.082, p=0.089; vs. NC: mean difference = -1.691, p=0.009) (see Figure 23). Though possibly due to chance, this consistent difference could possibly reflect the increased likelihood of anosmia due to

olfactory bulb damage in this group and a subsequent devaluing of olfactory stimulus due to lack of experience in daily life.

Morphological, Sociological, and Dispositional Ratings

To examine subjects ratings of important factors when making mate decisions, the variables where grouped according to what general aspect of the world they represent. To do this, three categories were generated, including: morphological, sociological, and dispositional types of variables. Morphological variables were defined as those that are concerned with the body of the individual in question and include: attractiveness, height, weight, shoulder size, chest/breast size, waist size, hip size, age and overall health. Sociological variables included all of those that were tested that involve other social agents other than the person in question, including: friendliness, parental ability, desire for children, income, their love the participant, the participants love for that person. Finally, dispositional variables involve all of those variables that are related to the personality or behaviour of the individual in question, including: intelligence, kindness, trustworthiness, masculinity/femininity, and personality. However, clustering the variables into these higher-order groups did not result in the observation of significant effects of group (Women: $F=0.910$, $p=0.589$; Men: $F=1.136$, $p=0.316$), age (Women: $F=1.640$, $p=0.147$; Men: $F=1.556$, $p=0.168$), or education (Women: $F=1.051$, $p=0.418$; Men: $F=1.137$, $p=0.360$) for men or women (see Figures 24 – 29). There was potentially a hint of a difference where female participants with amygdala damage rated sexual partner morphological variables as less important ($F=2.431$, $p=0.078$) compared to participants with VMPC damage (mean difference = -0.813, $p=0.140$), BDCs (mean difference = -1.096, $p=0.014$), and NCs (mean difference = -0.809, $p=0.035$) (see Figure 24). Likewise, women with amygdala damage displayed a consistent trend for morphological variables for long-term partners rating these variables as less important compared to BDCs (mean difference = -1.088, $p=0.032$) and NCs (mean difference = -

0.904, p=0.040). By contrast, brain damaged comparison men displayed a possible trend toward rating morphological variables for long-term partners as less important compared to men with amygdala damage (mean difference = -1.321, p=0.014) and NCs (mean difference = -0.789, p=0.025), and a weak trend for men with VMPC damage (mean difference = -0.695, p=0.094) (see Figure 27).

Match Choices

A MANCOVA was run to test for significant differences between groups on selection of matches based on Attractiveness, Age, Income, and Parental Ability for purely sexual partners, long-term partners, and parental partners.

In women the overall model produced no significant results for group (F=0.853, p=0.699), for age (F=1.732, p=0.107), or for education (F=0.648, p=0.785) (see Figures 30 – 33). Similarly in men, there were no effects of group (F=1.165, p=0.270), age (F=0.949, p=0.512), or education (F=1.401, p=0.210) (see Figures 34 – 37). Pairwise tests hinted at potential group differences for a few of the variables. In women with amygdala damage, income was potentially less important for making decisions for parental partners compared to women with VMPC damage (mean difference = -0.139, p=0.043), BDCs (mean difference = -0.122, p=0.028), and NCs (mean difference = -0.116, p=0.013) (see Figure 32). In men with VMPC damage, attractiveness may have been less important for making decisions on sexual partners compared to NCs (mean difference = -0.067, p=0.009) (see Figure 34) and parental skill may have been less important for making decisions on long-term partners compared to NCs (mean difference = -0.225, p=0.002) (see Figure 37).

When comparing groups on the change in importance across different relationship types, women displayed no significant differences for group (F=0.775, p=0.759) or education (F=0.894, p=0.532), but a significant effect of age (F=2.347, p=0.039). In men, no differences were observed for group (F=0.947, p=0.540), age (F=0.470,

p=0.870), or education (F=1.031, p=0.429) for changes in importance of attractiveness, age, income, or parental ability between relationship types.

Discussion

There were some intriguing results from the mate choice protocol. Consistent with the predictions made that VMPC and amygdala damage might lead to abnormal, indiscriminate mate choices, women with amygdala damage were less likely to choose potential parental partners based on income compared to other groups. This is consistent with the idea that socioeconomic status is an important and relevant indicator of male fitness and with the idea that the amygdala is involved in mate related decisions. This effect on parental partner choices is internally consistent with the observation that women with amygdala damage rate parental partner income as less important than other groups.

It is also interesting that women with amygdala damage consider morphological variables as less important for determining purely sexual partners as well as long-term partners compared to other groups. Similarly BDC men show a similar lack of importance for morphological variables when vetting long-term partners. This difference may hint at the possibility that men and women utilize different neural structures to make mate-related decisions. Another example of this is the observation that men with VMPC damage are less likely to use attractiveness to make decisions for purely sexual partners and long-term partners compared to other groups. However, men may too utilize the amygdala for some aspects of mate choice, for example men with amygdala damage tend to prefer larger body masses than other groups.

An interesting trend is noticeable in the data, where both men and women regardless of brain damage status tend to rate sociological variables as more important for long-term and parental partners. The result for parental partners may be in part due to the inclusion of ‘desire for children’ in this composite measure, though this cannot be the entire reason. It may be that this increased emphasis on sociological variables may be

evidence for sexual selection for sociality in humans, though further studies would be required to determine the validity of this claim.

Overall, it appears that there is mixed, though, weak support for the predictions that were made. Since the observed effects were relatively weak, the data may suggest that either the theoretical background is imprecise or the specific design of the task did not adequately allow probing of the contributions of the target brain regions. In hindsight, it may be that the task employed largely required perceptual abilities rather than the inferential processing predicted by the overall hypothesis. In this task, participants were directly given the information in order to make mate decisions. Thus participants do not need to infer any of the variables for themselves and could simply apply what they saw to the choices they made. A more direct interpretation of the Inferential Brain Hypothesis as described above may predict that deficits may arise in extracting or inferring these variables from behaviour or other exposure to others and not necessarily in applying them once they have been acquired.

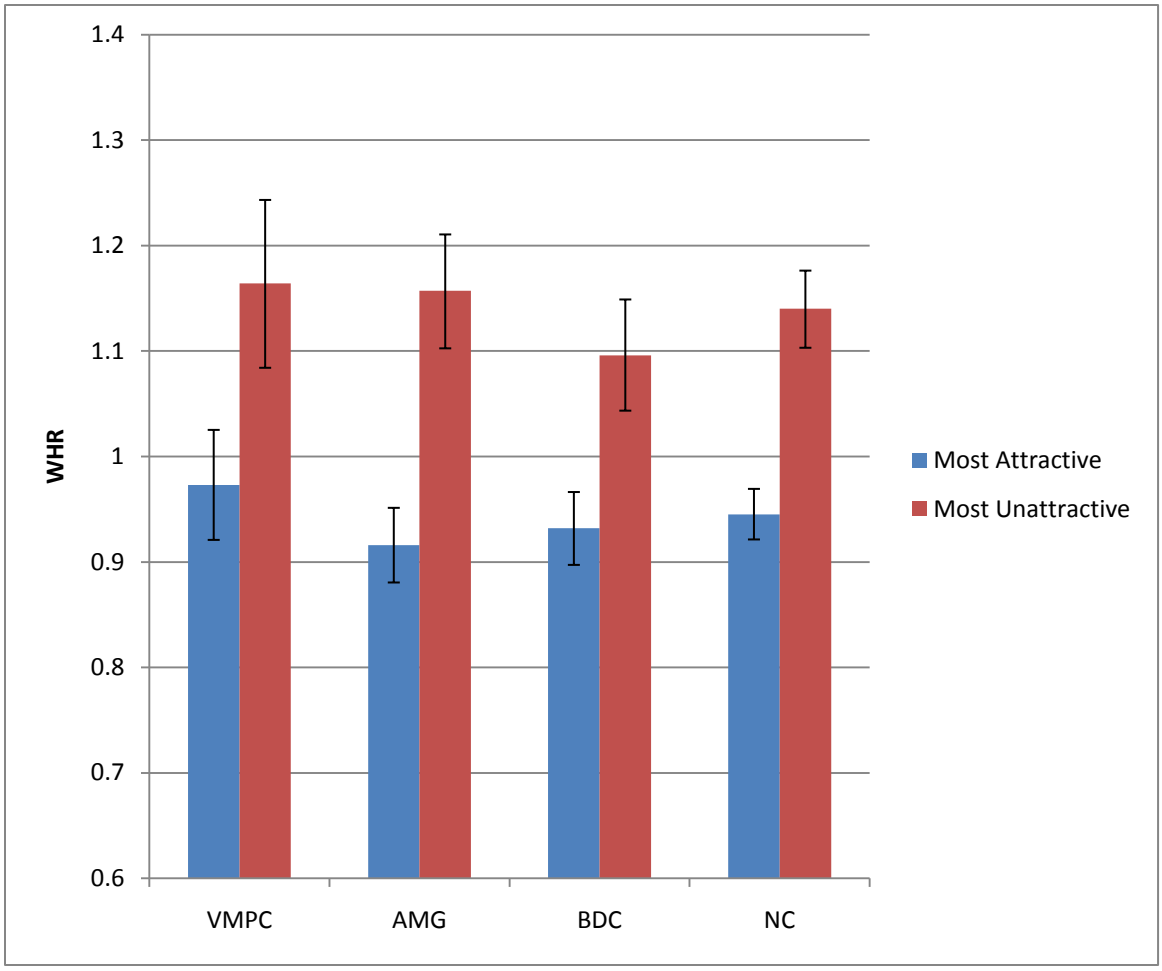

Figure 8 – WHR Preferences for Women for Most Attractive and Most Unattractive Body Types. Bars represent estimated marginal means for preferred WHRs. Error bars represent 95% confidence intervals.

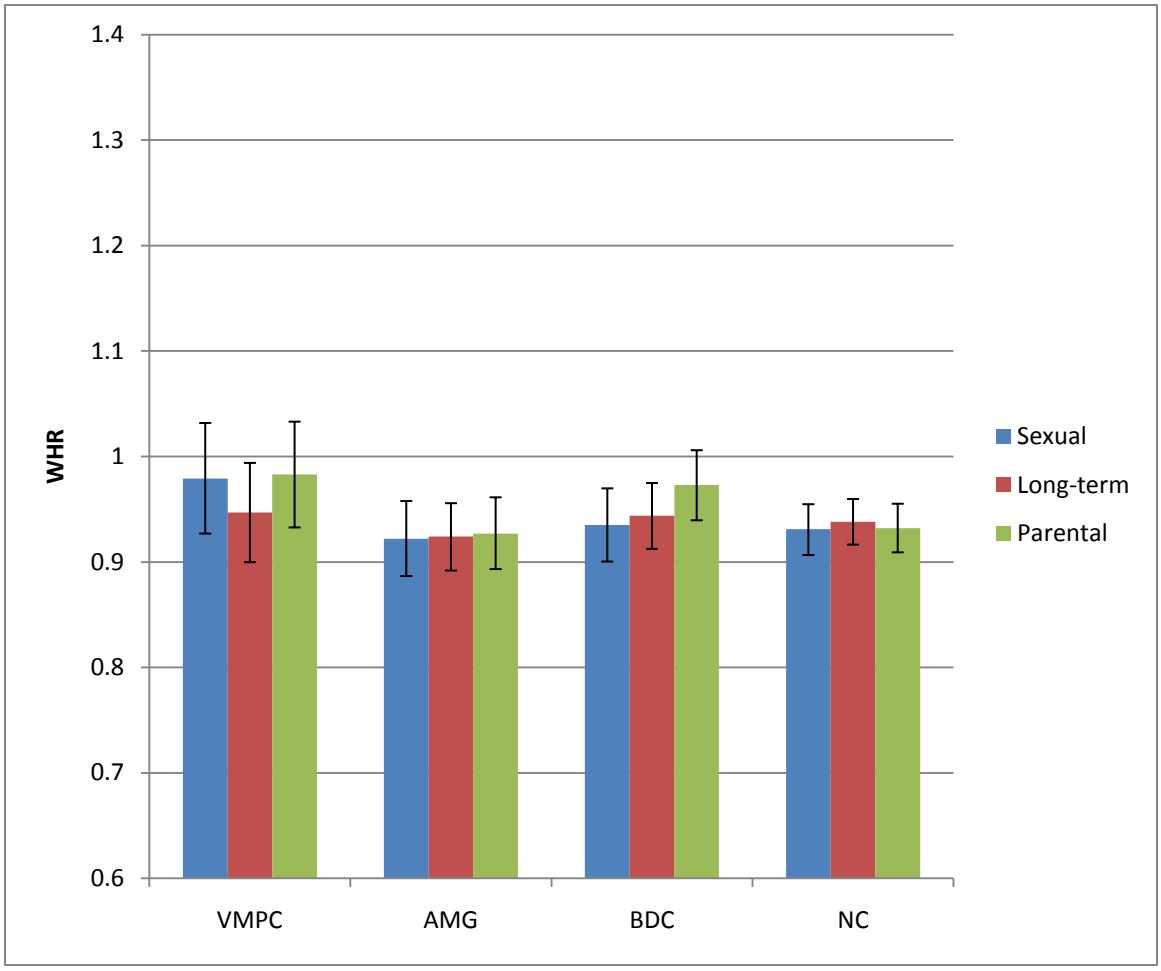

Figure 9 – WHR Preferences for Women for Purely Sexual Partners, Long-term Partners, and Parental Partners. Bars represent estimated marginal means for WHRs. Error bars represent 95% confidence intervals.

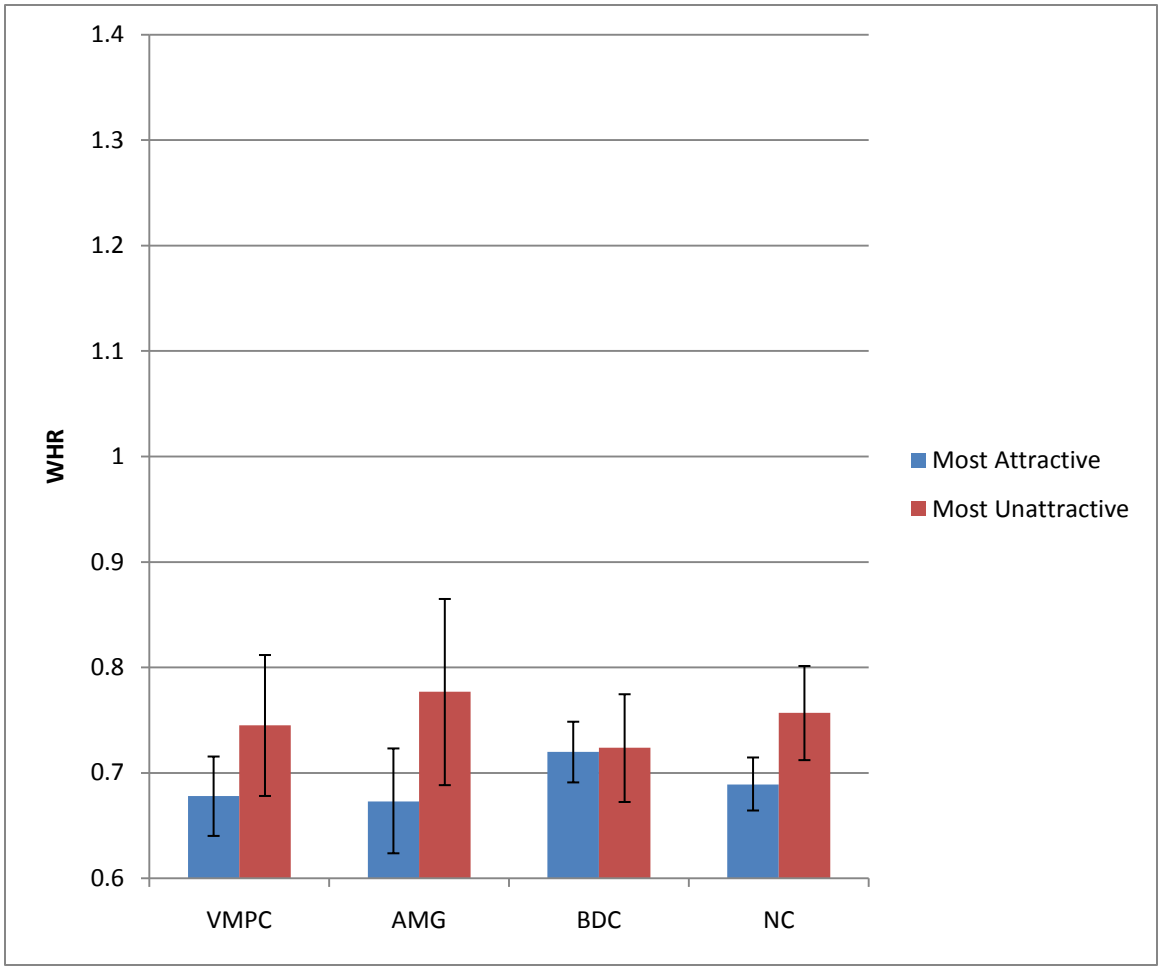

Figure 10 – WHR Preferences for Men for Most Attractive and Most Unattractive Body Types. Bars represent estimated marginal means for WHR preferences. Error bars represent 95% confidence intervals. (This graph is scaled to maintain comparison between sexes, see Figure 8).

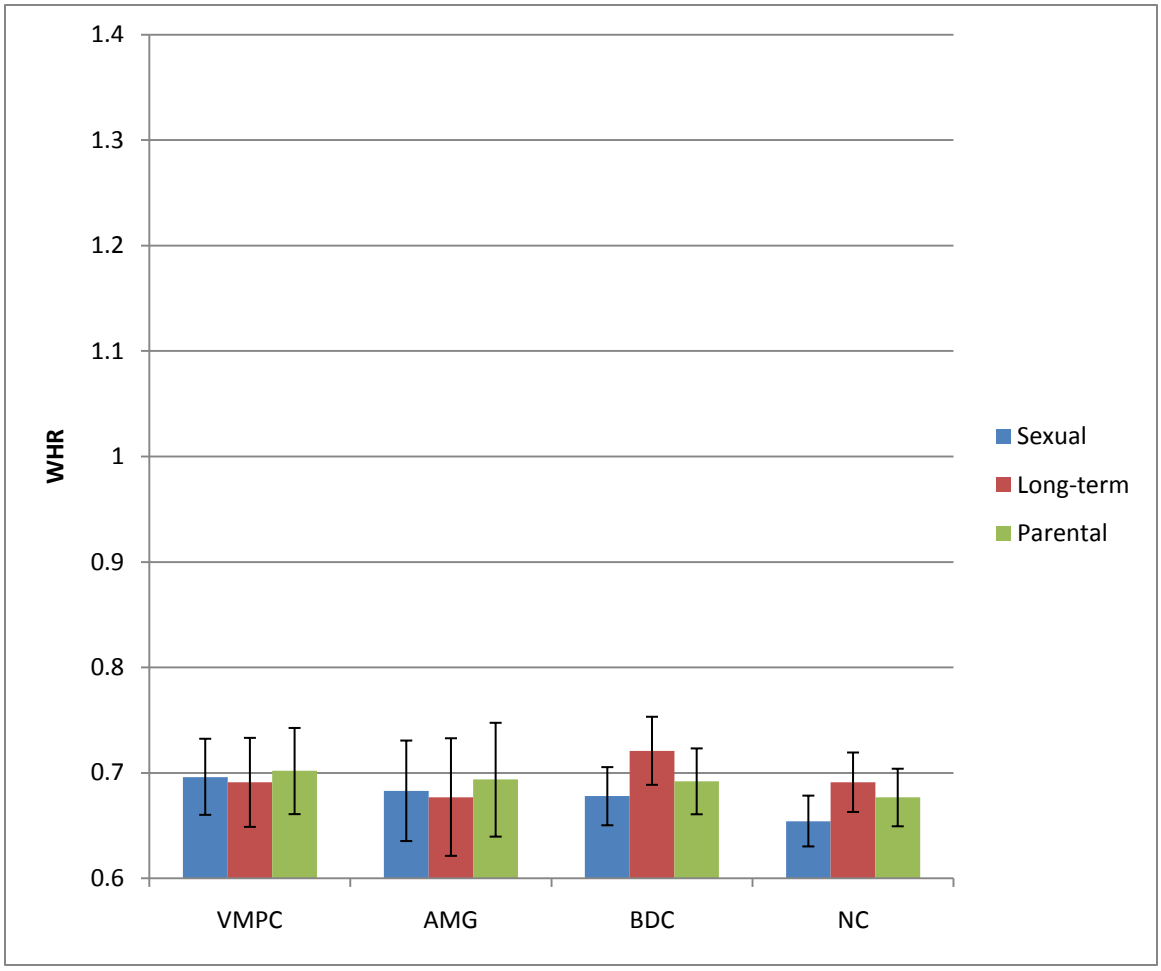

Figure 11 – WHR Preferences for Men for Purely Sexual Partners, Long-term Partners, and Parental Partners. Bars represent estimated marginal means for WHR preferences. Error bars represent 95% confidence intervals.

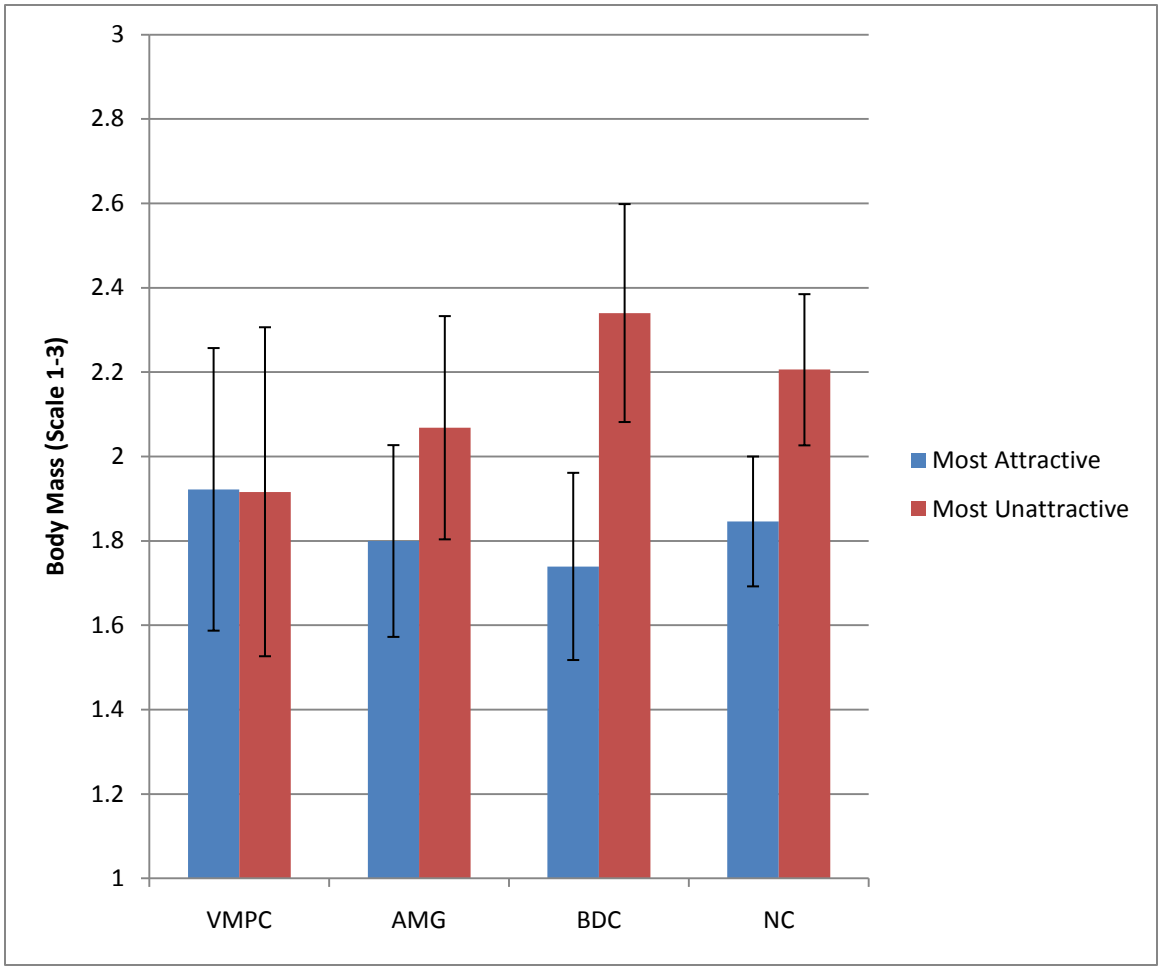

Figure 12 – Body Mass Preferences for Women for Most Attractive and Most Unattractive body types. Bars represent body mass preferences, higher values represent higher body mass. Error bars represent 95% confidence intervals.

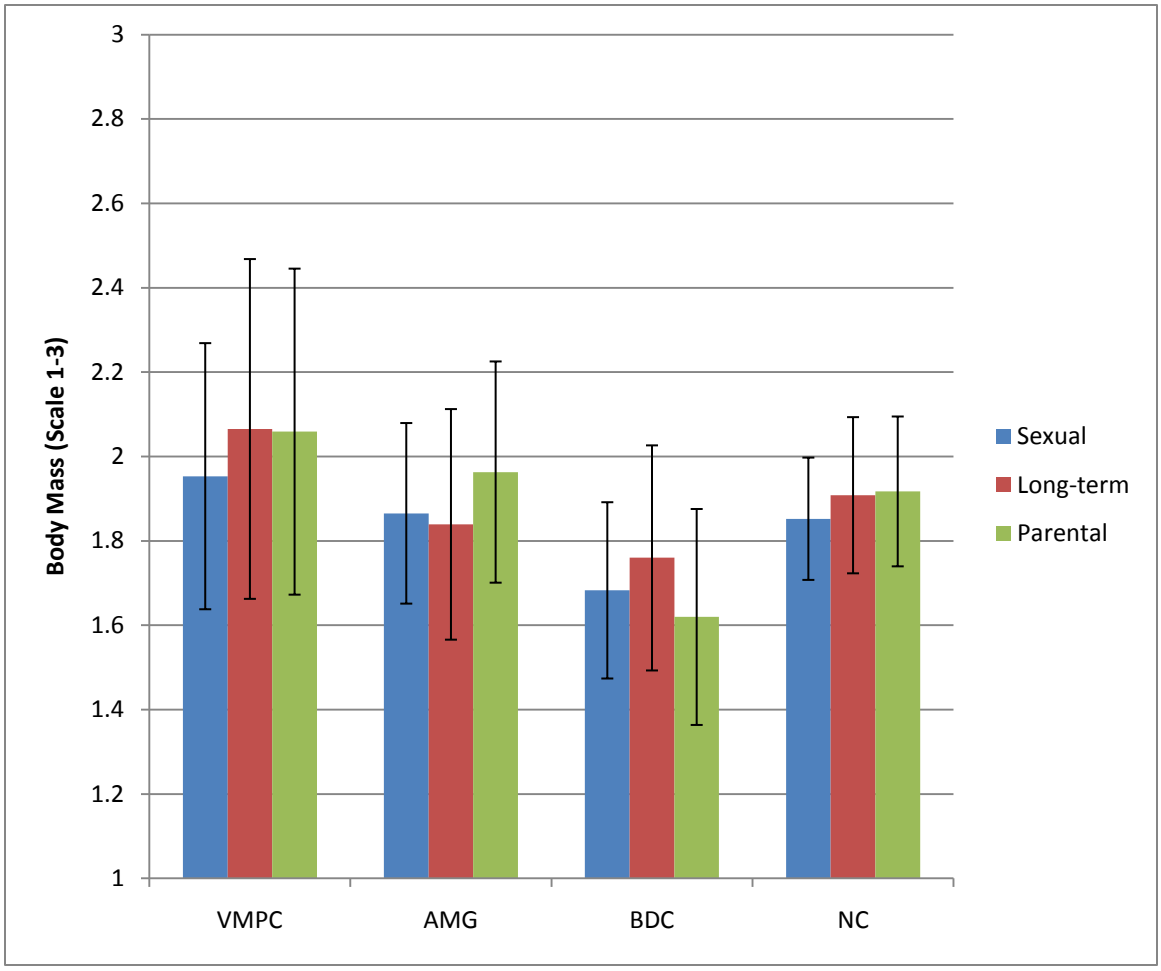

Figure 13 – Body Mass Preferences for Women for Purely Sexual Partners, Long-term Partners, and Parental Partners. Bars represent body mass preferences, higher values represent higher body mass. Error bars represent 95% confidence intervals.

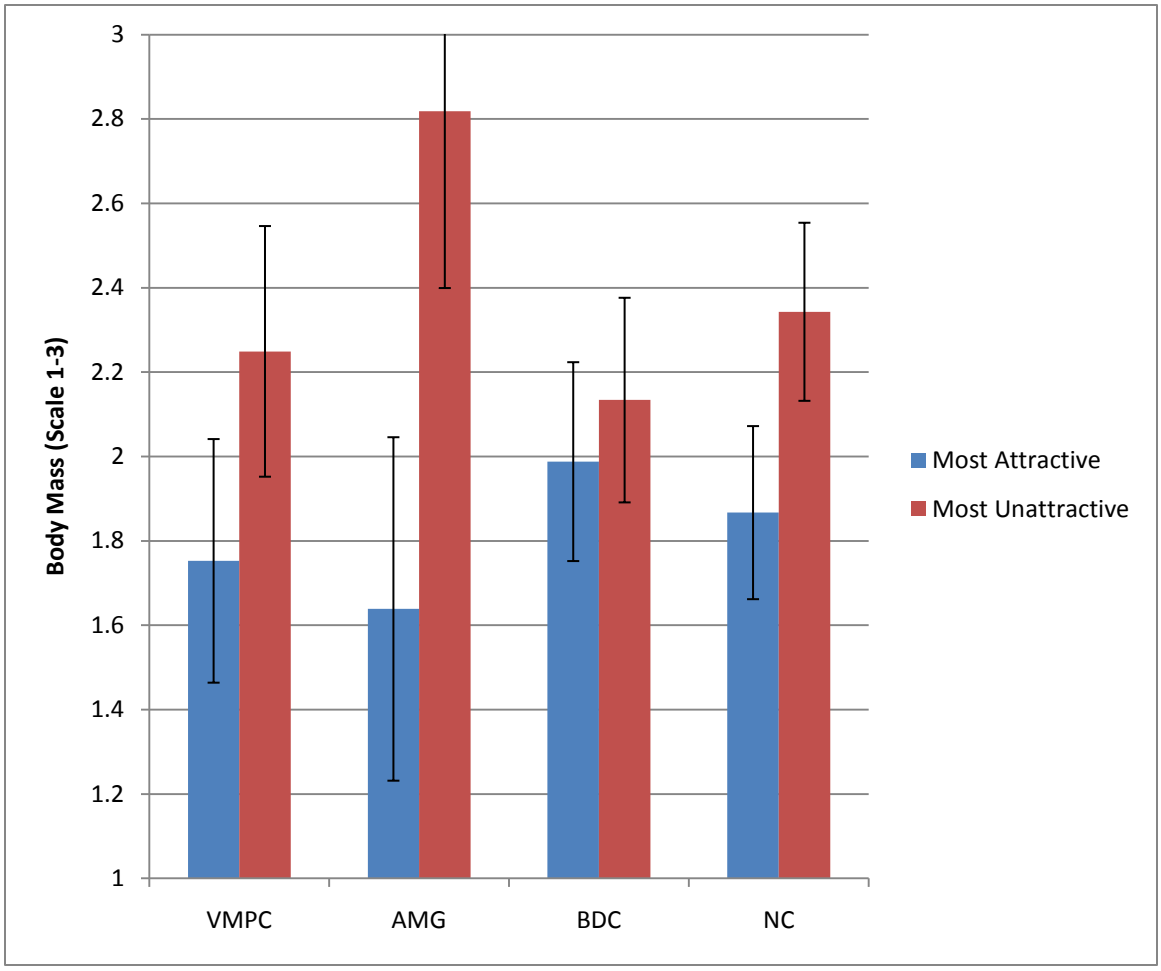

Figure 14 – Body Mass Preferences for Men for Most Attractive and Most Unattractive Body Types. Bars represent body mass preferences, higher values represent higher body mass. Error bars represent 95% confidence intervals.

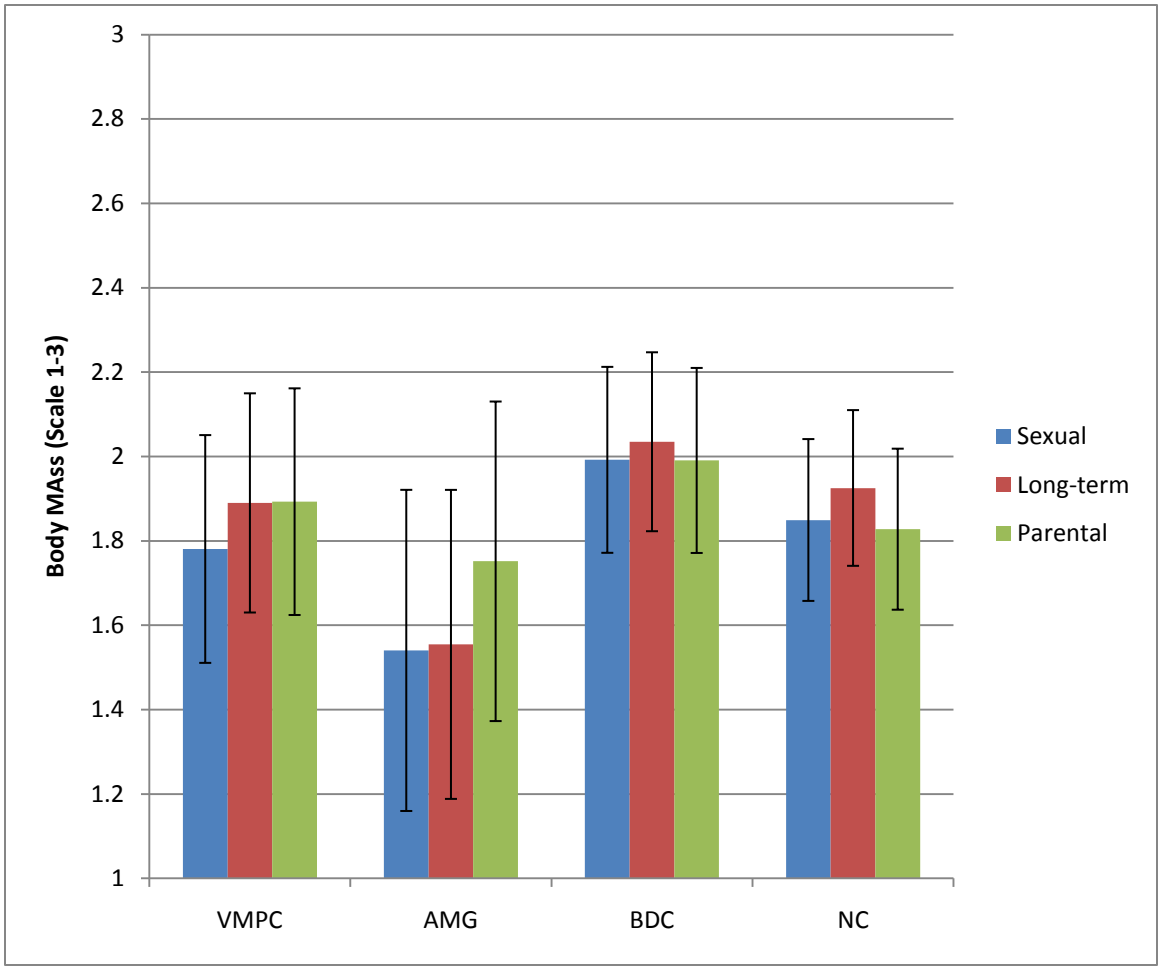

Figure 15 – Body Mass Preferences for Men for Purely Sexual Partners, Long-term Partners, and Parental Partners. Bars represent body mass preferences, higher values represent higher body mass. Error bars represent 95% confidence intervals.

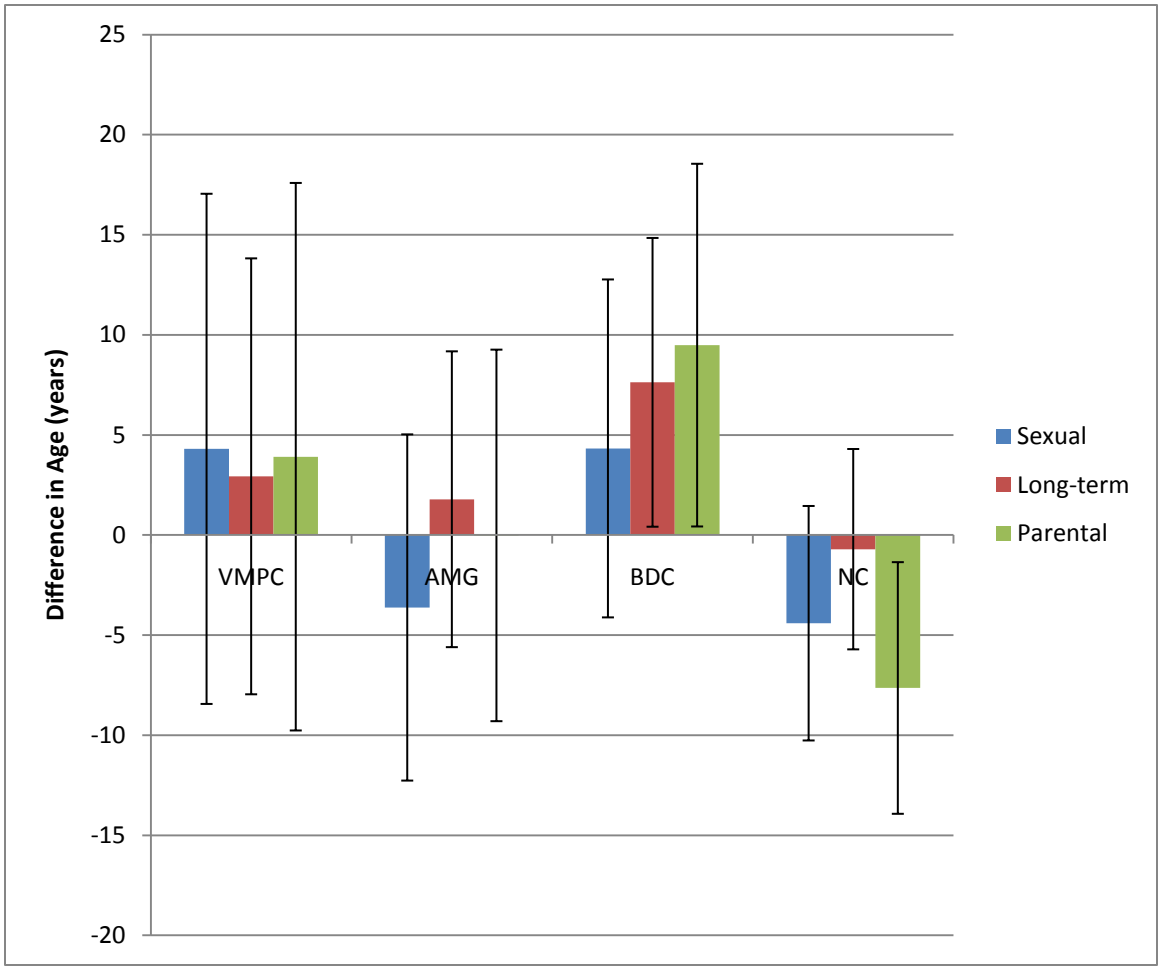

Figure 16 – Ideal Age preferences for Women for Purely Sexual, Long-term, and Parental partners. Positive values represent preferences for older partners, negative values represent preferences for younger partners relative to the age of the participant. Error bars represent 95% confidence intervals.

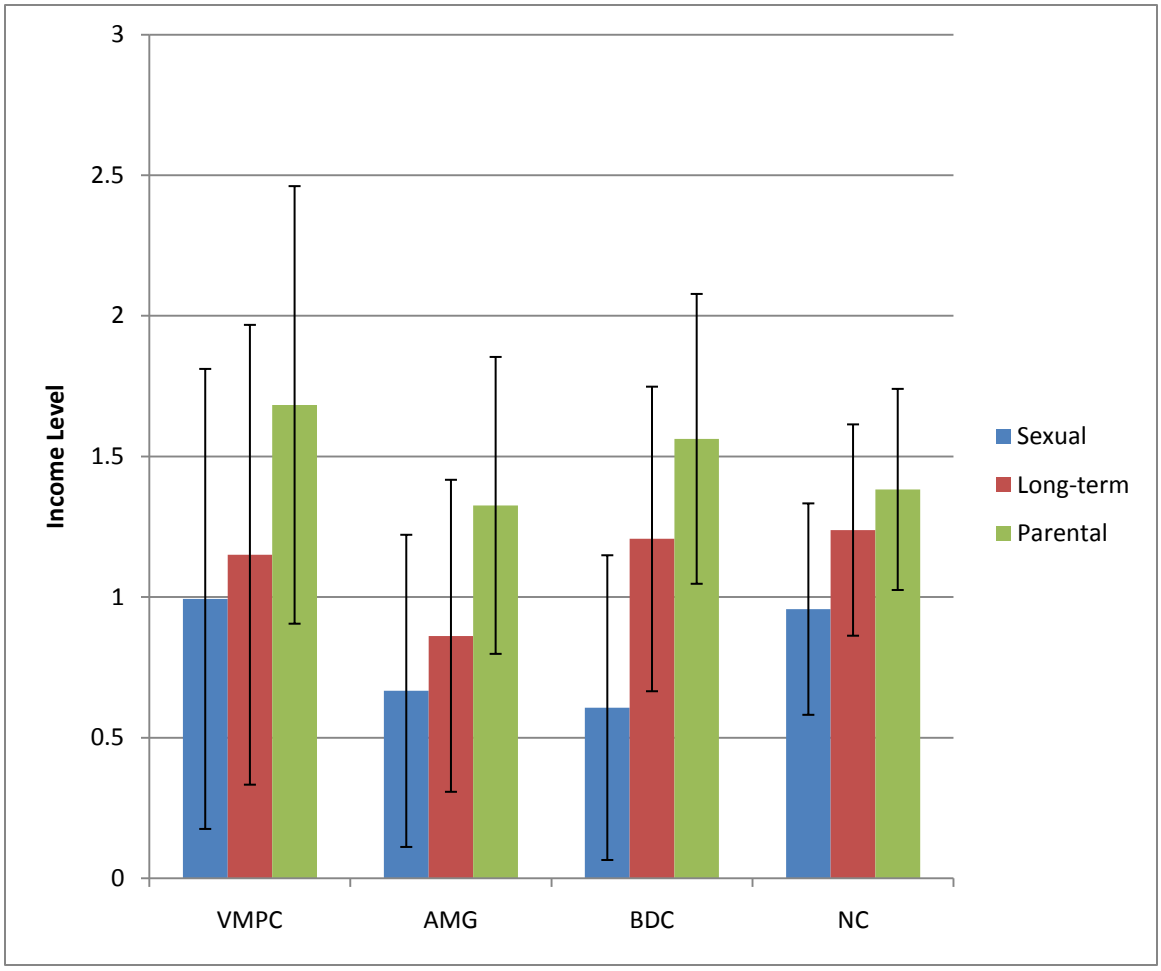

Figure 17 – Ideal Income Preferences for Women for Different Relationship Types. Higher values represent relatively higher income. Zero represents an income equivalent to the participant. Error bars represent 95% confidence intervals.

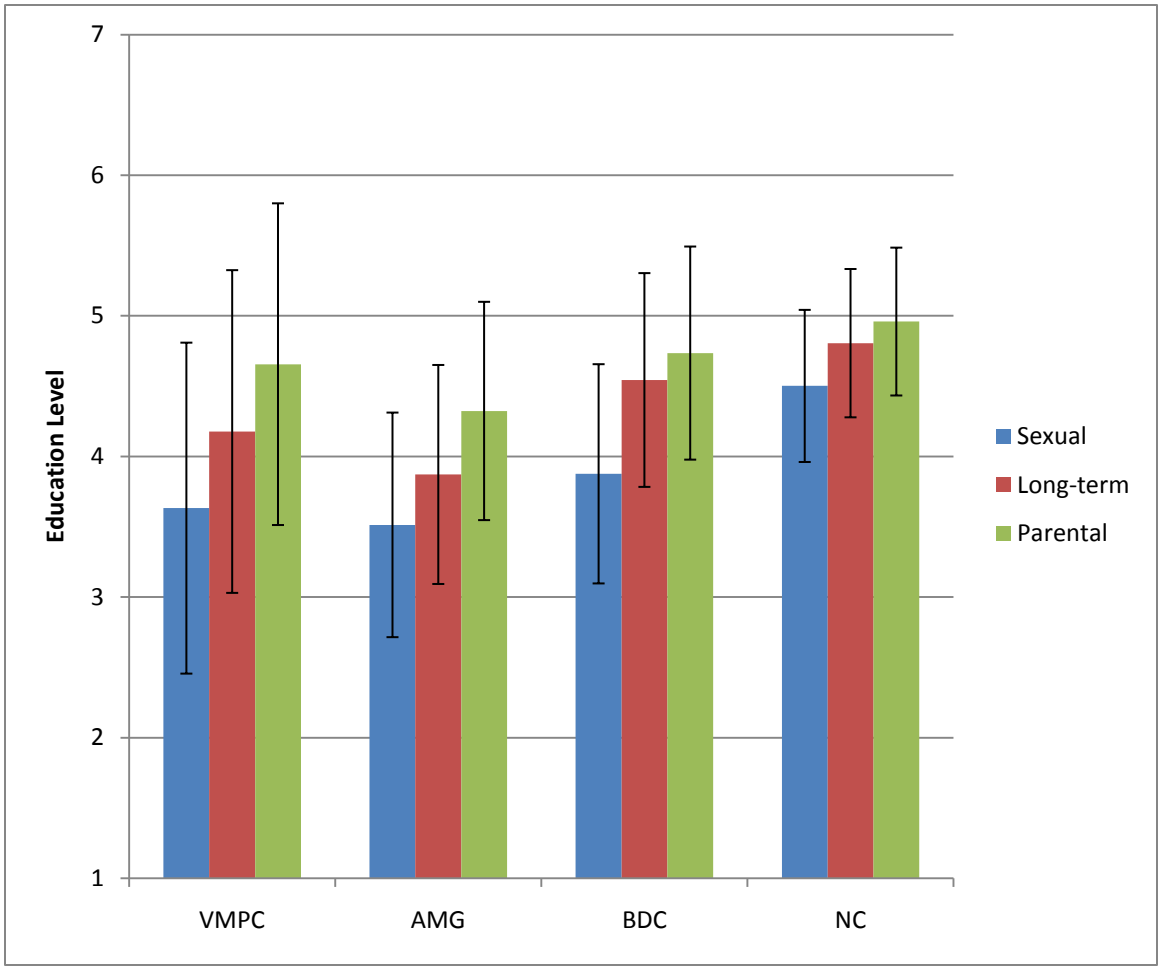

Figure 18 – Ideal Education Preferences for Women for Different Relationship Types. Higher values represent higher levels of education. Error bars represent 95% confidence intervals.

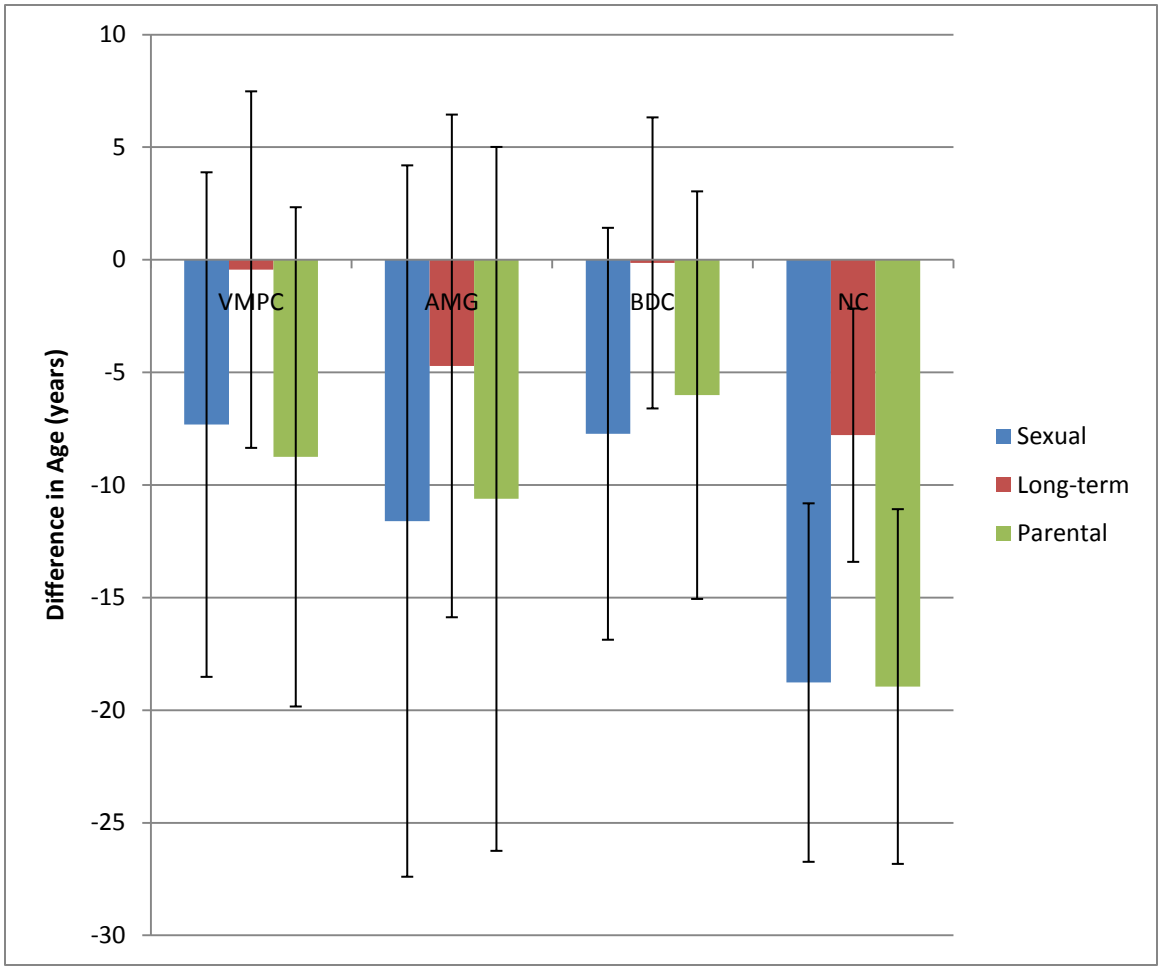

Figure 19 – Ideal Age Preferences for Men for Different Relationship Types. Negative values represent ages younger than the participant, positive values represent older ages. Error bars represent 95% confidence intervals.

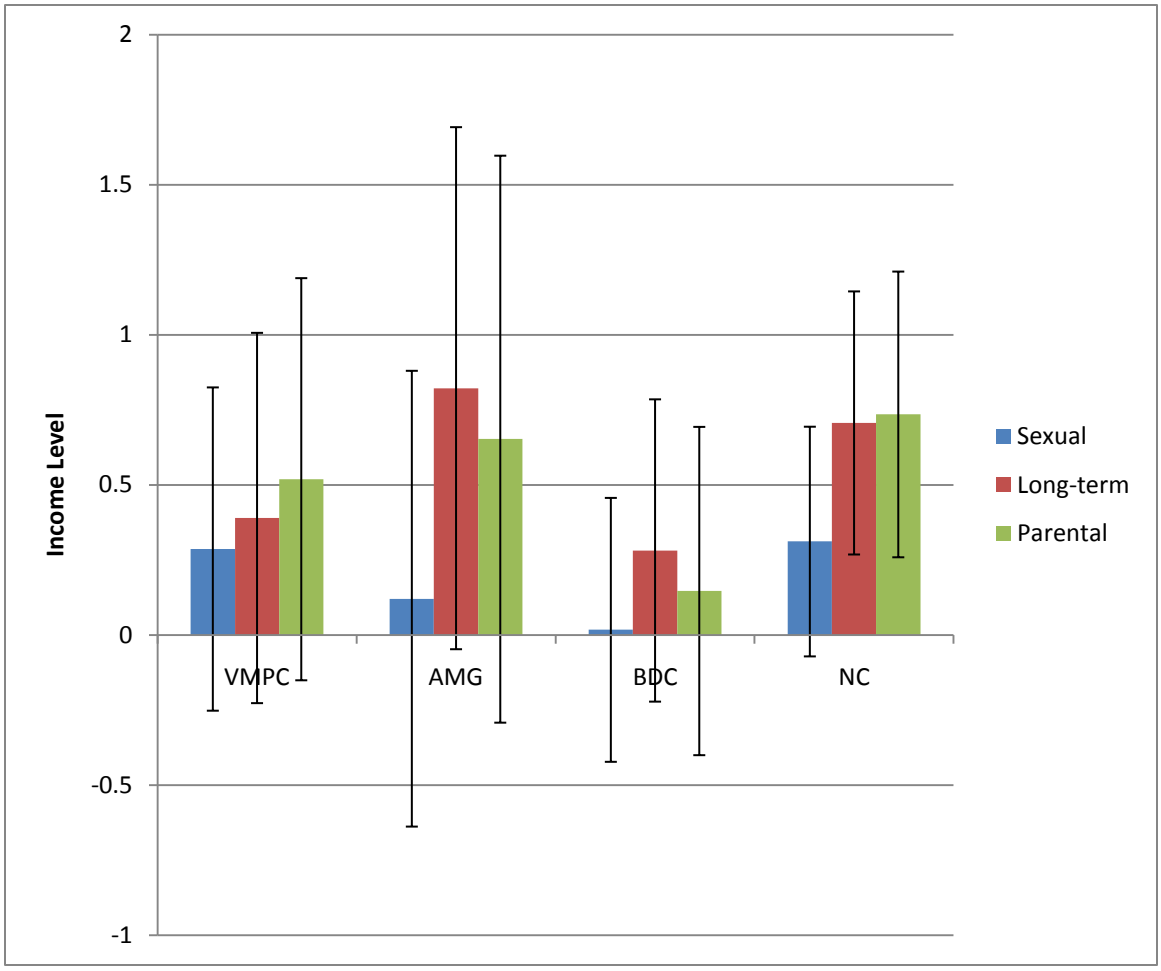

Figure 20 – Ideal Income Preferences for Men for Different relationship Types. Positive values represent preferences for greater income than the participant; negative values indicate preferences for lower income. Error bars represent 95% confidence intervals.

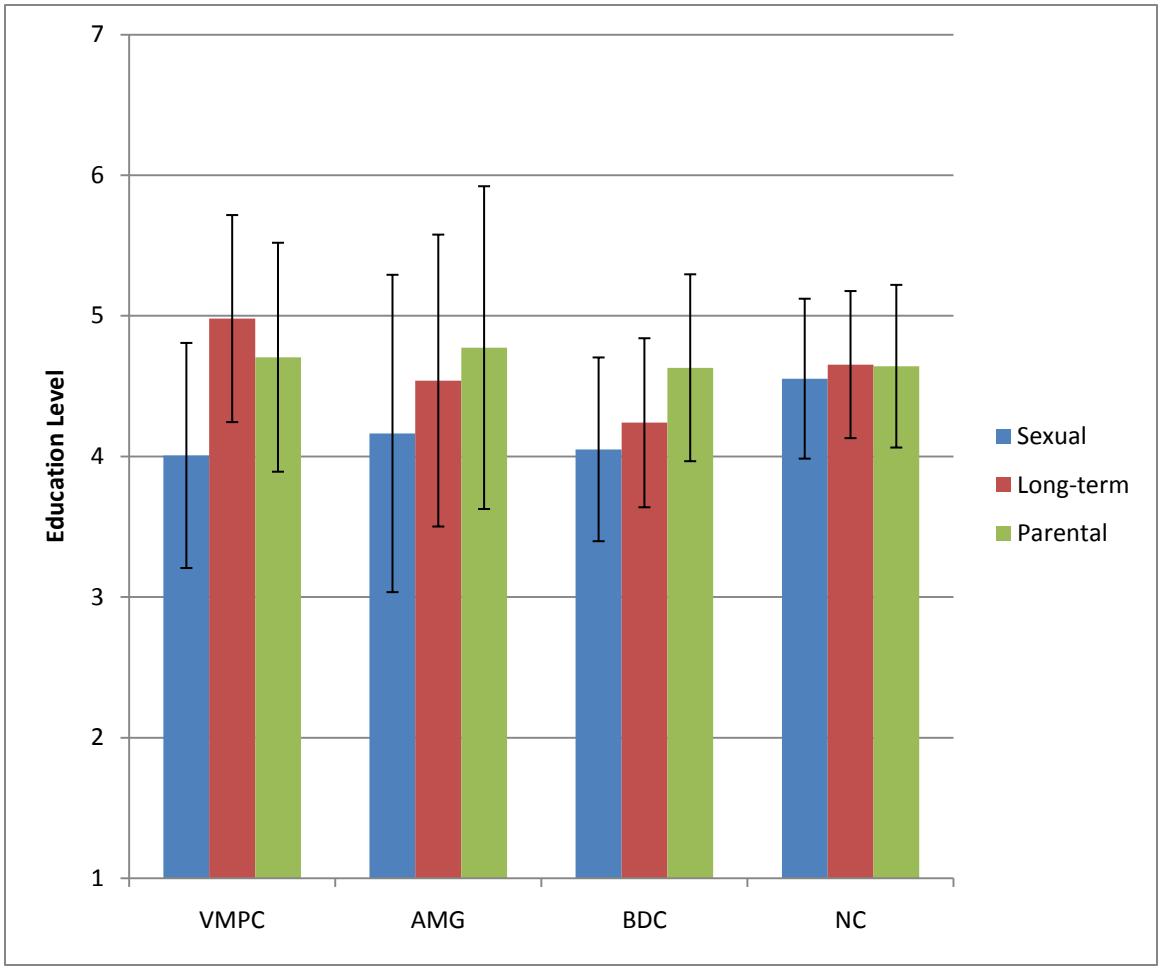

Figure 21 – Ideal Education Preferences for Men for Different Relationship Types. Higher values represent higher levels of education. Error bars represent 95% confidence intervals.

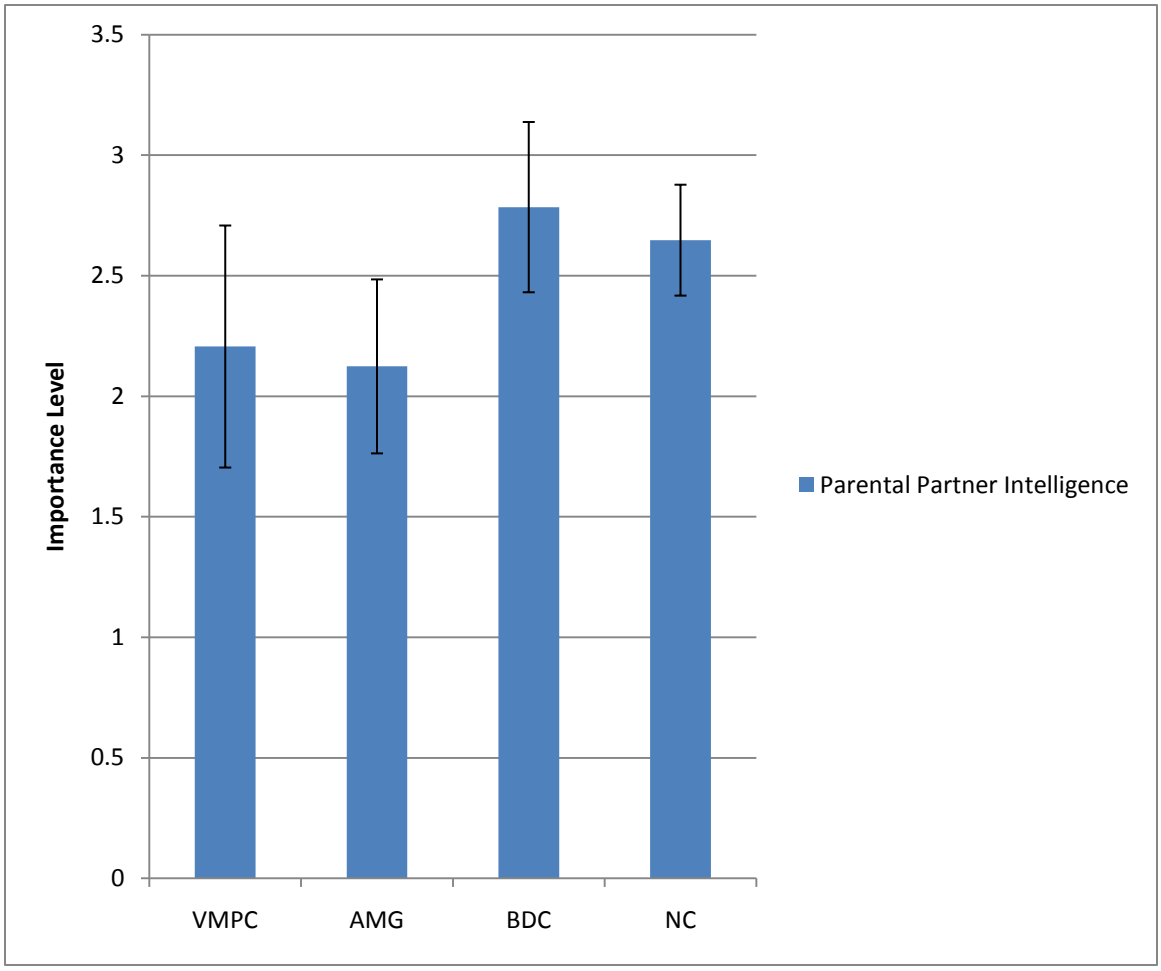

Figure 22 – Importance Rankings for Parental Partner Intelligence for Women. Higher values represent ratings of greater importance. Subjects with amygdala and possibly VMPC damage may consider intelligence to be slightly less important than BDCs and NCs. Error bars represent 95% confidence intervals.

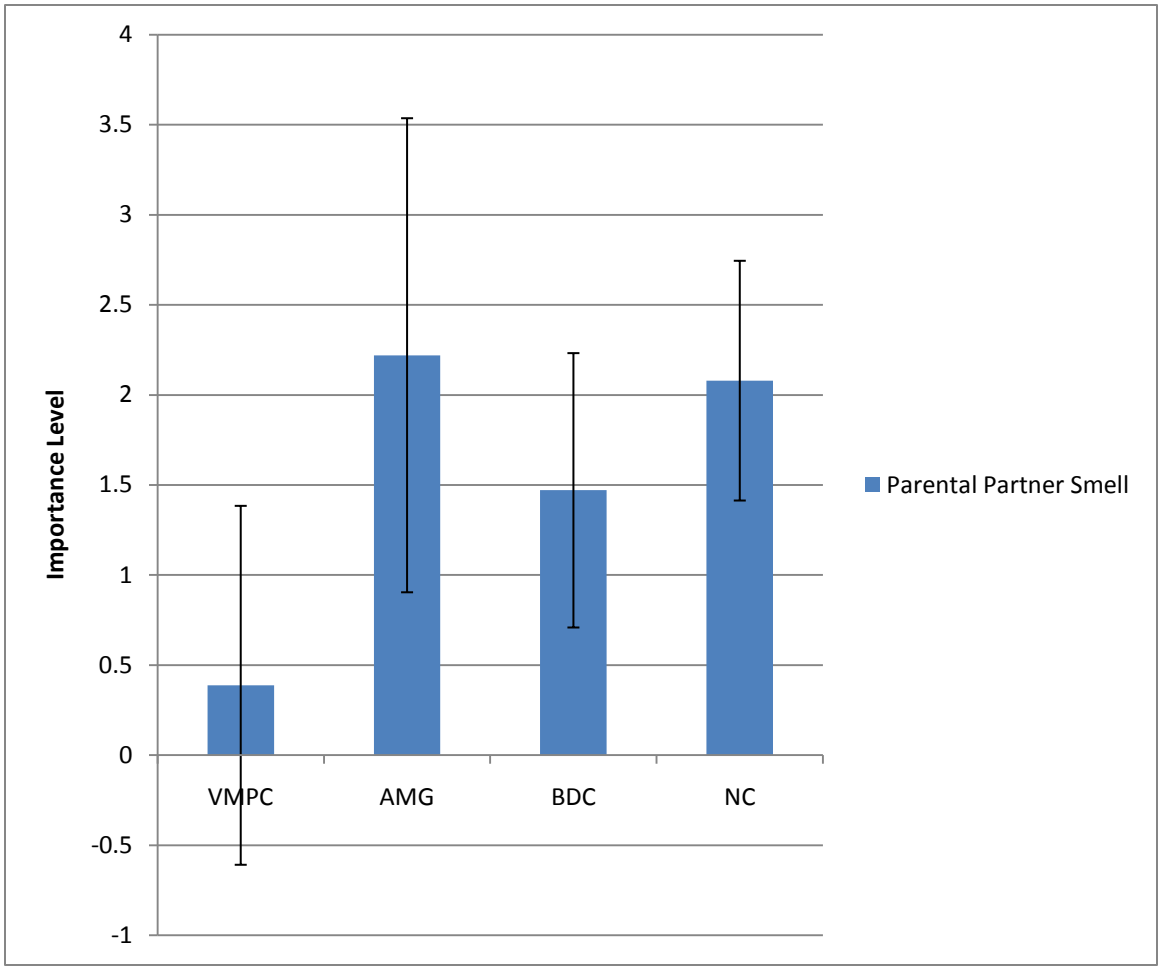

Figure 23 – Importance rankings for parental partner smell for men. Higher values indicate increased importance. Men with VMPC damage appear to place less importance on their partner's smell.

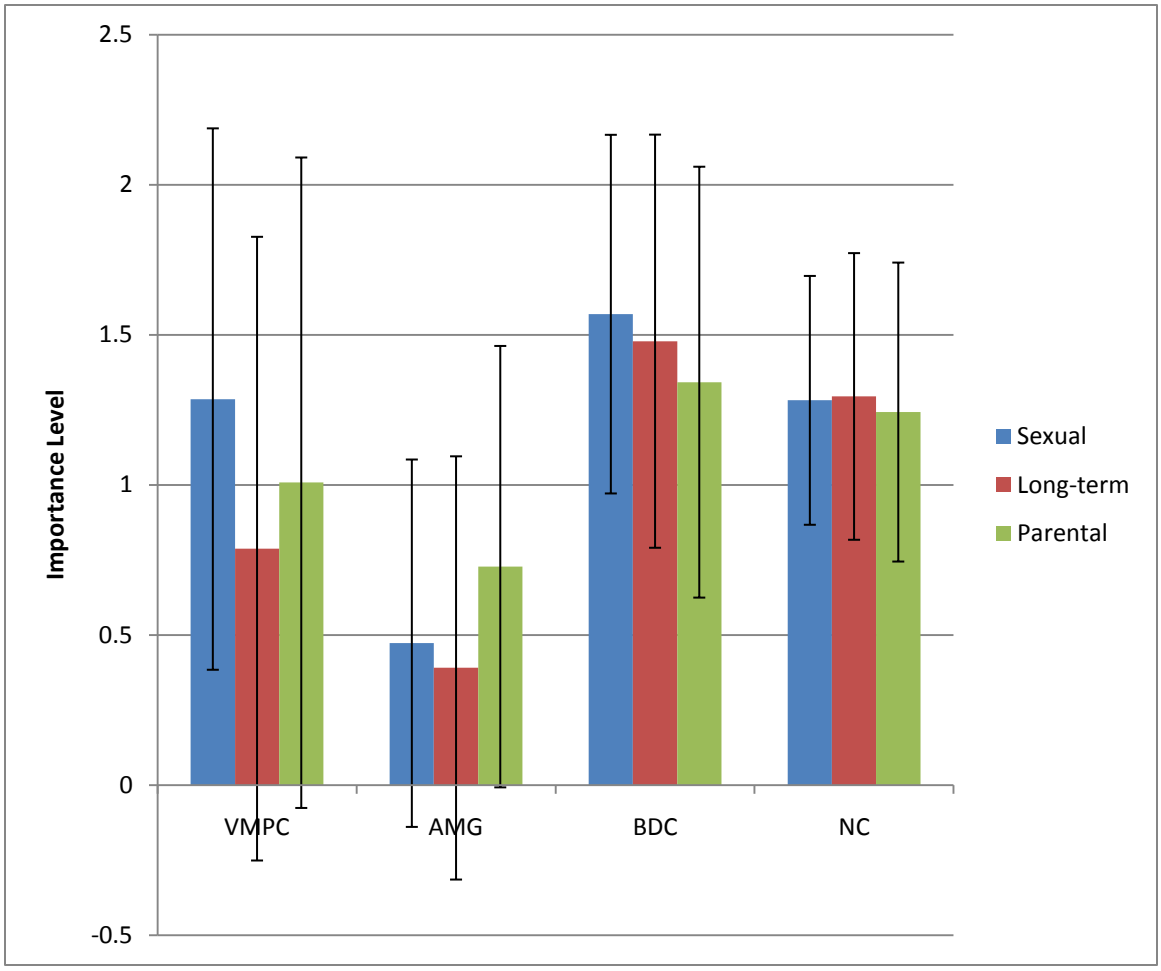

Figure 24 – Importance Rankings for Morphological Variables for Women. Higher values represent higher importance rankings. Women with amygdala damage appear to consider morphological variables as less important. Error bars represent 95% confidence intervals.

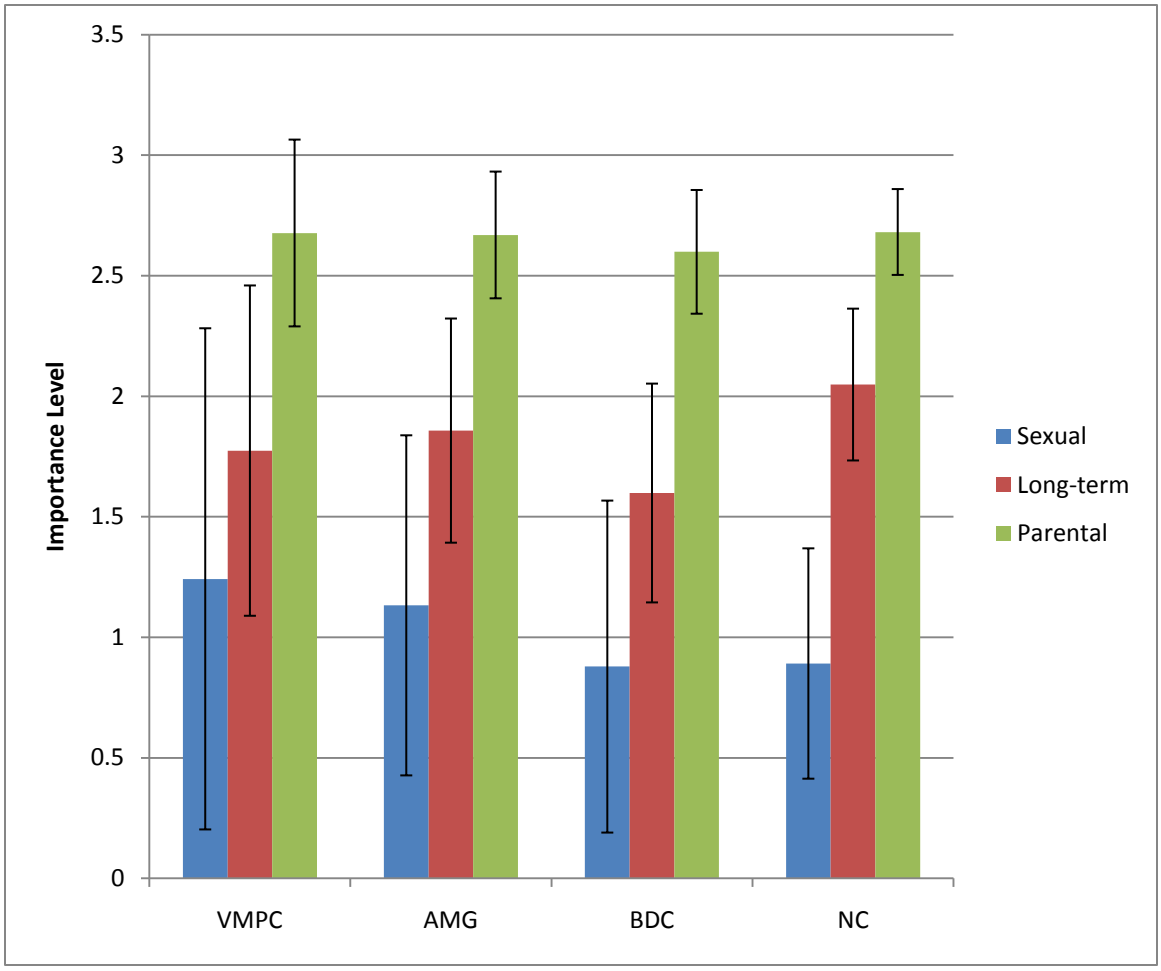

Figure 25 – Importance Rankings for Sociological Variables for Women. For all groups, sociological variables are of increasing importance for long-term and parental relationships. Error bars represent 95% confidence intervals.

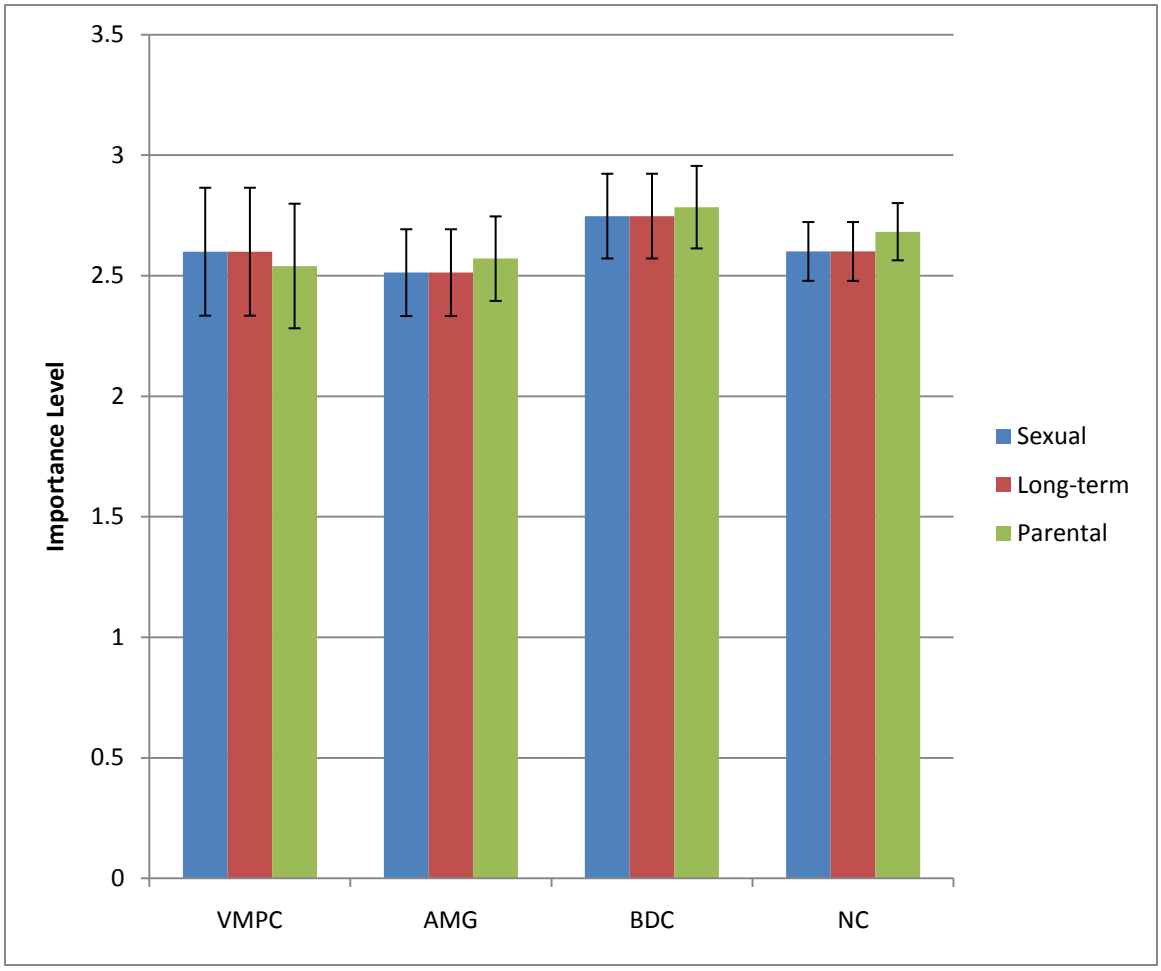

Figure 26 – Importance Rankings for Dispositional Variables for Women. Error bars represent 95% confidence intervals.

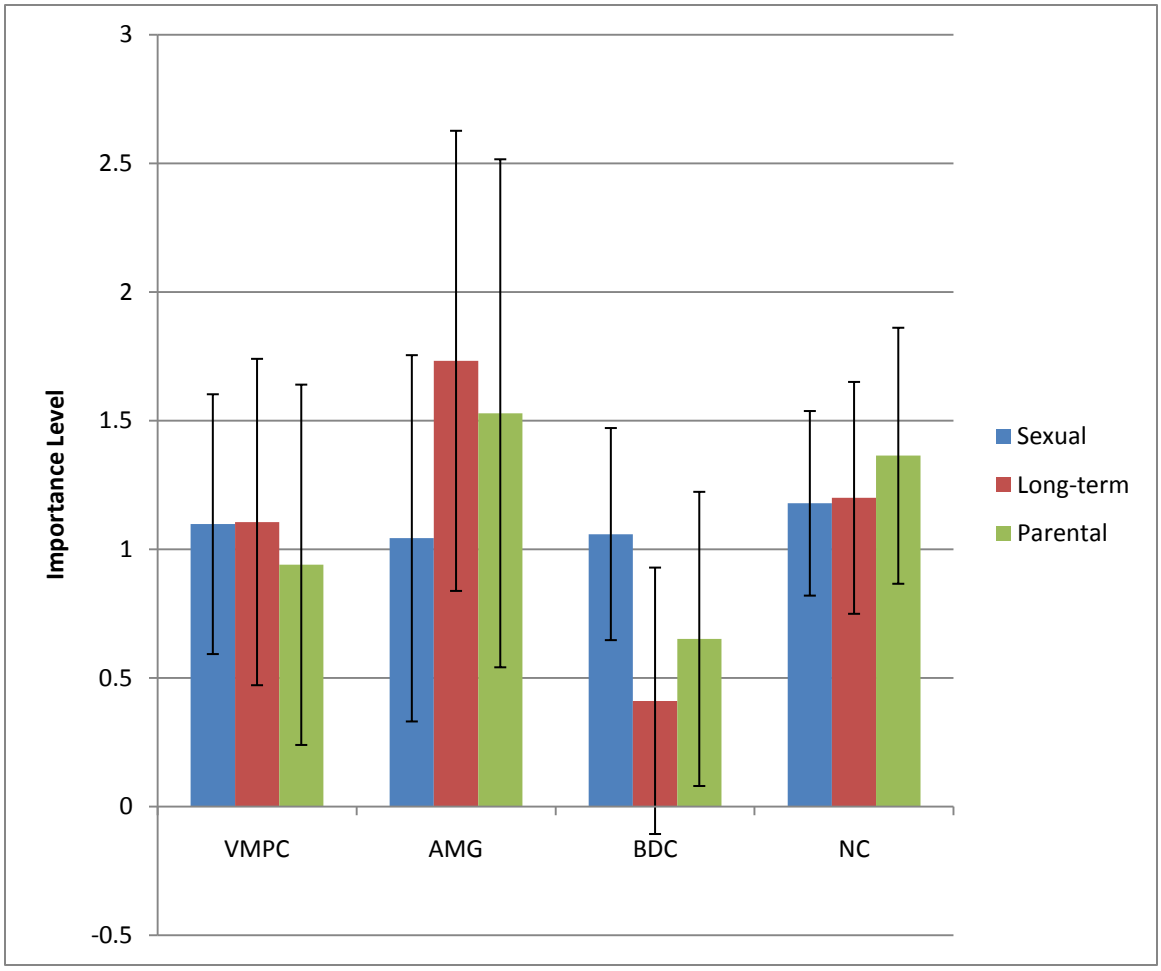

Figure 27 – Importance Rankings for Morphological Variables for Men. BDC men rank morphological variables as less important for long-term and parental relationships. Error bars represent 95% confidence intervals.

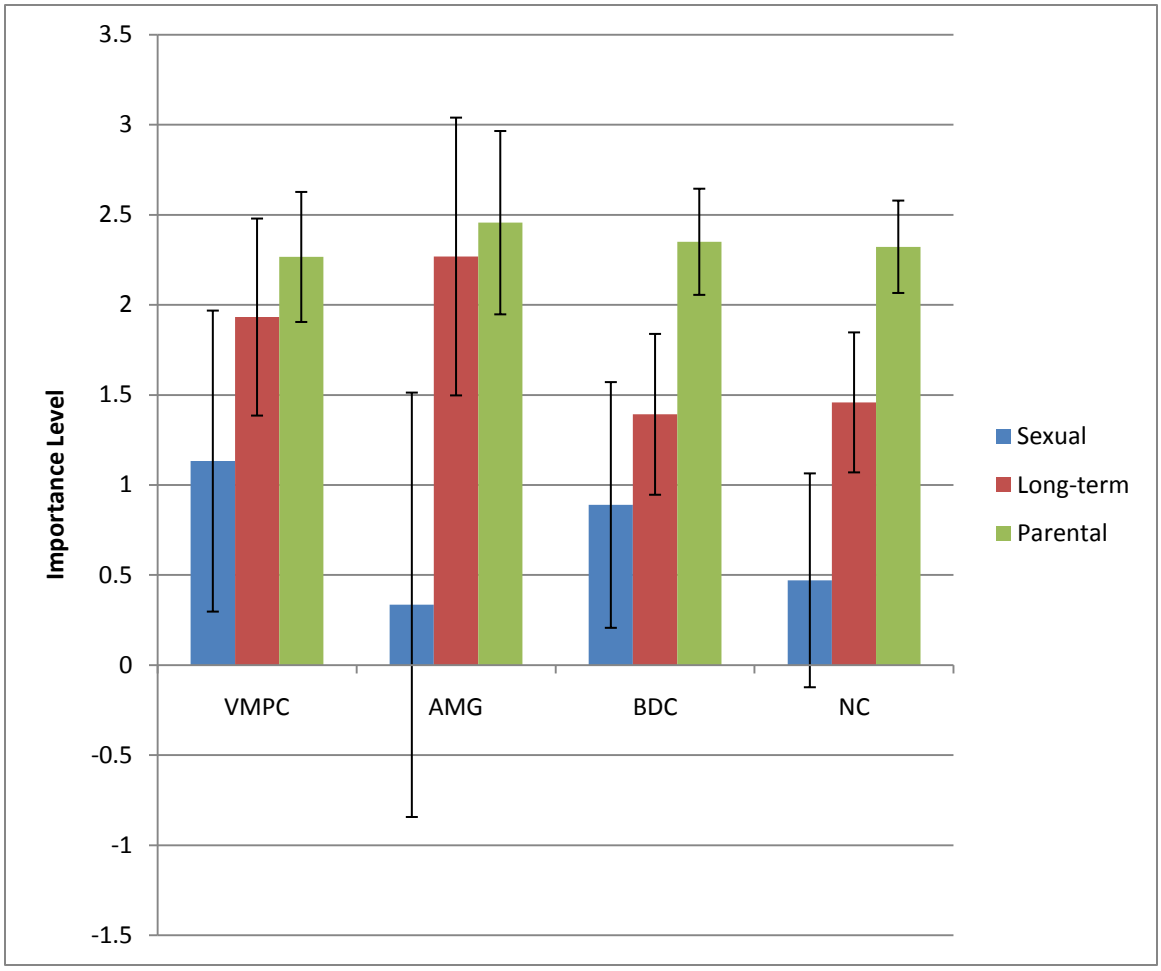

Figure 28 – Importance Rankings for Sociological Variables for Men. As is observed in women these variables are more important for long-term and parental relationships across all groups. Error bars represent 95% confidence intervals.

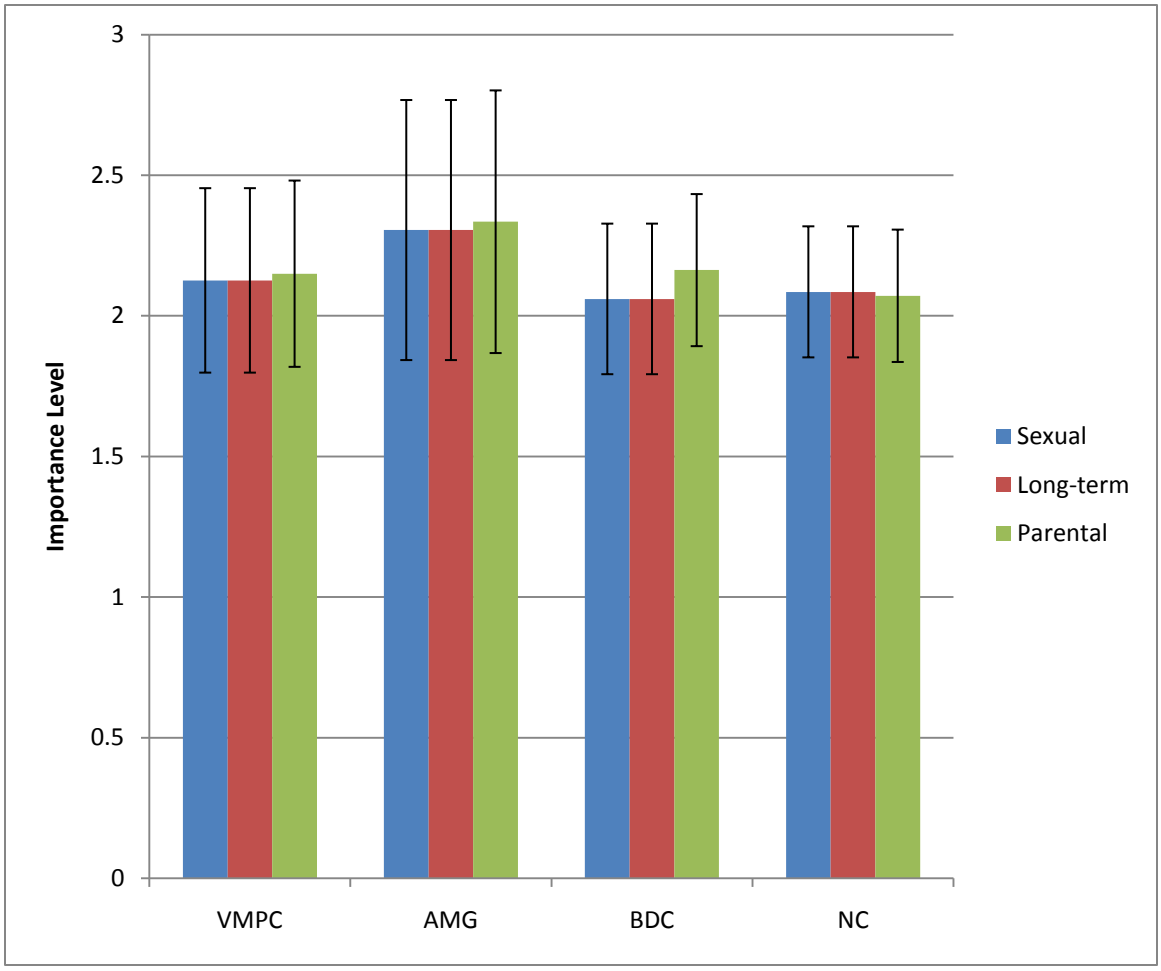

Figure 29 – Importance Rankings for Dispositional Variables for Men.
Error bars represent 95% confidence intervals.

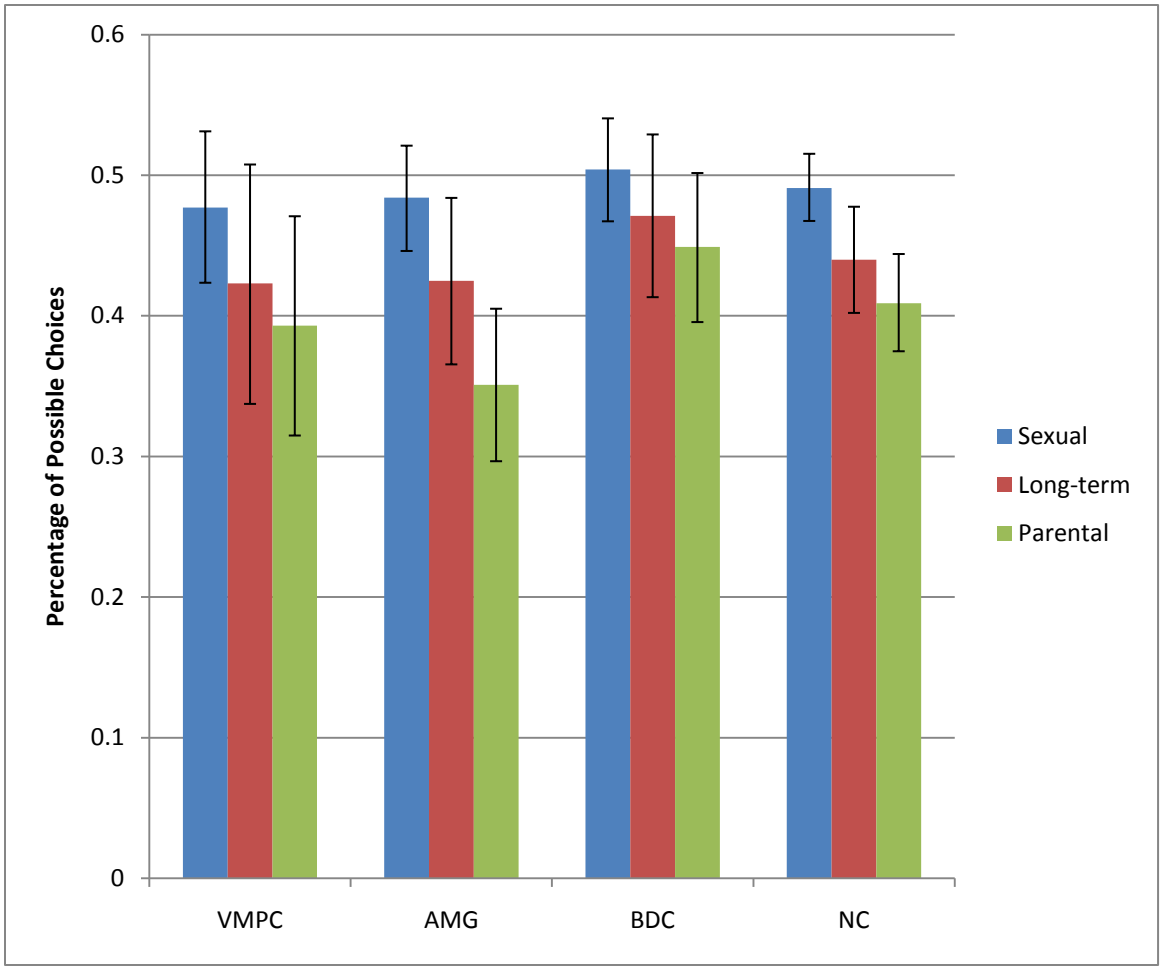

Figure 30 – Choices Based on Attractiveness for Women across Relationship Types. Higher values represent increased preferences for choices based on attractiveness over other variables. Error bars represent 95% confidence intervals.

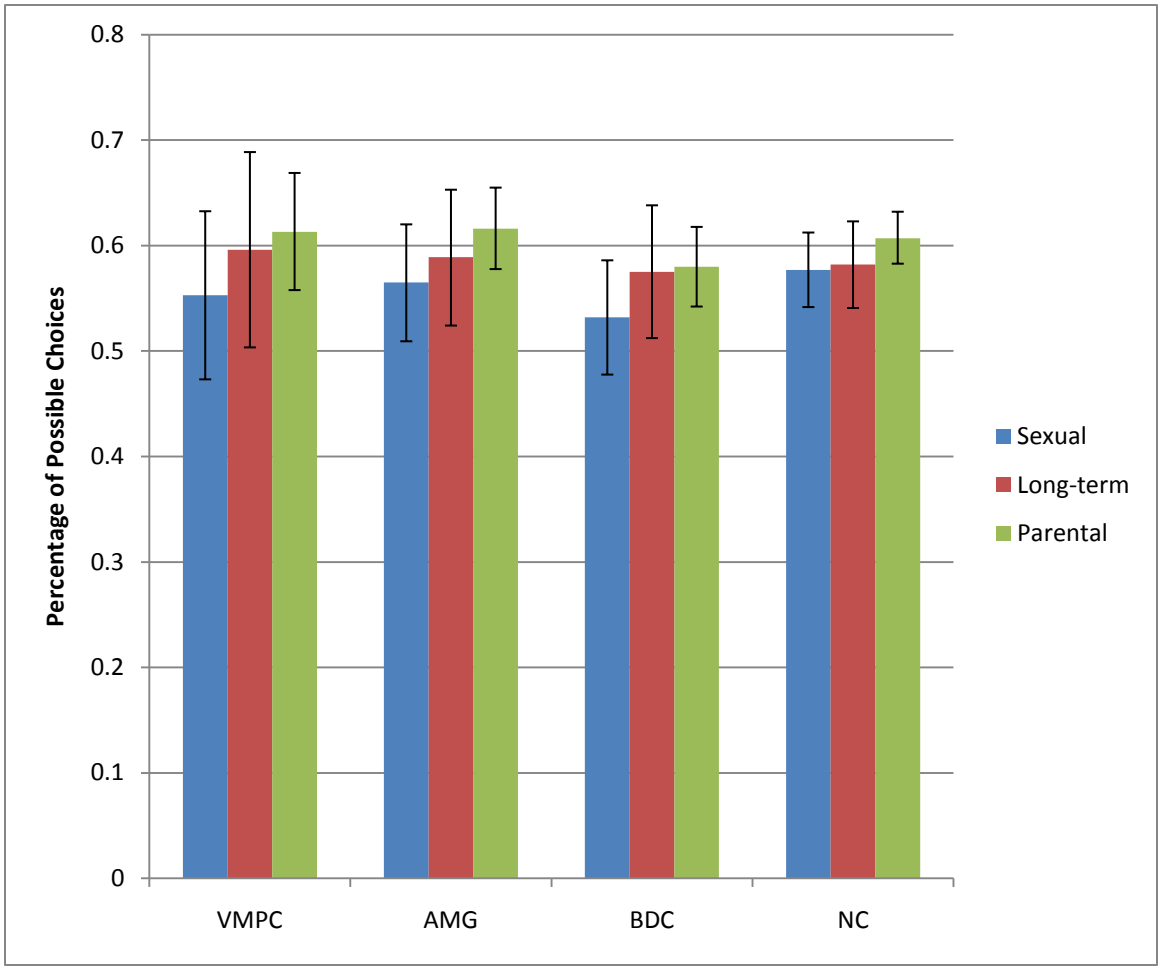

Figure 31 – Choices Based on Age for Women across Relationship Types. Higher values indicate increased preference. Error bars represent 95% confidence intervals.

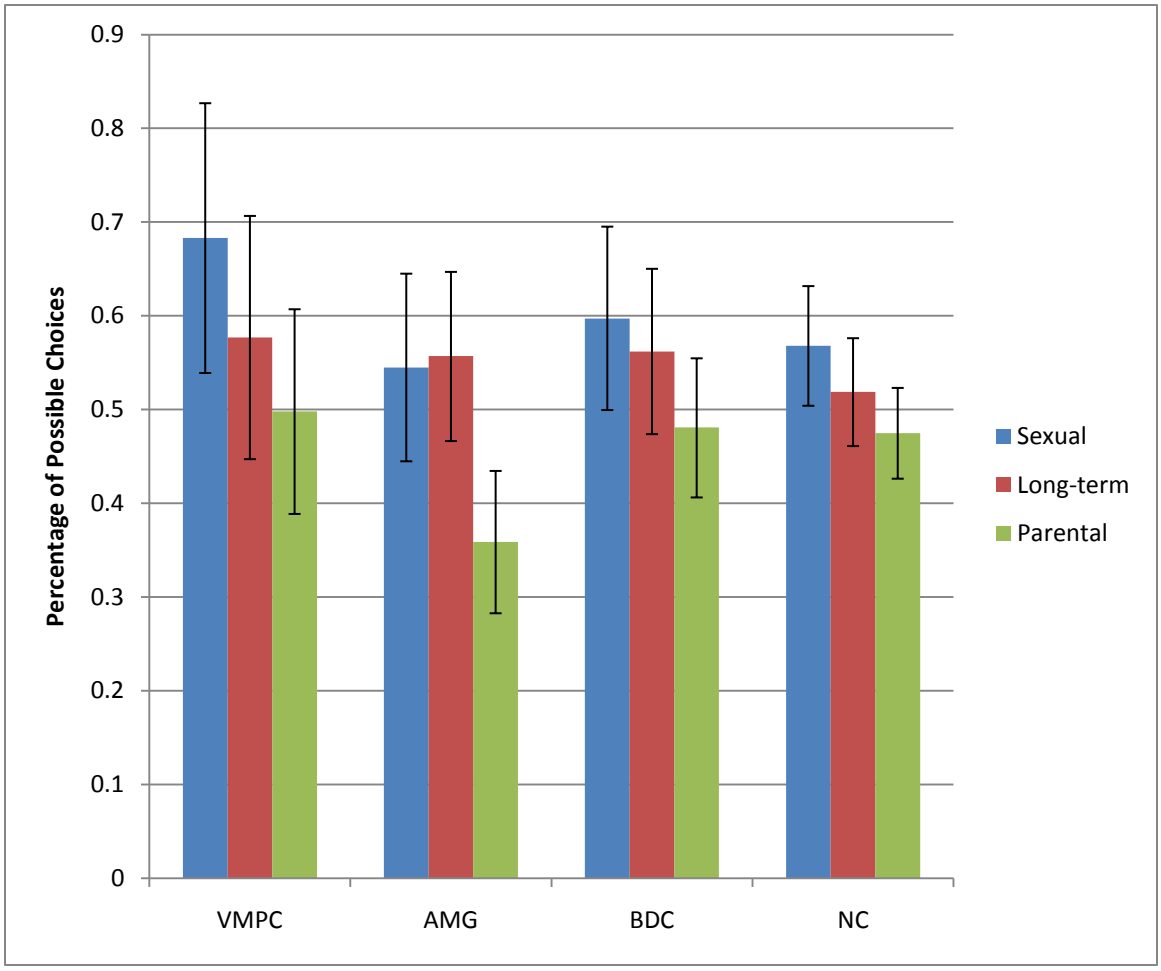

Figure 32 – Choices Based on Income for Women across Relationship Types. Higher values indicate increased preference for income. Women with amygdala damage appear to prefer income less than other groups when choosing between parental partners. Error bars represent 95% confidence intervals.

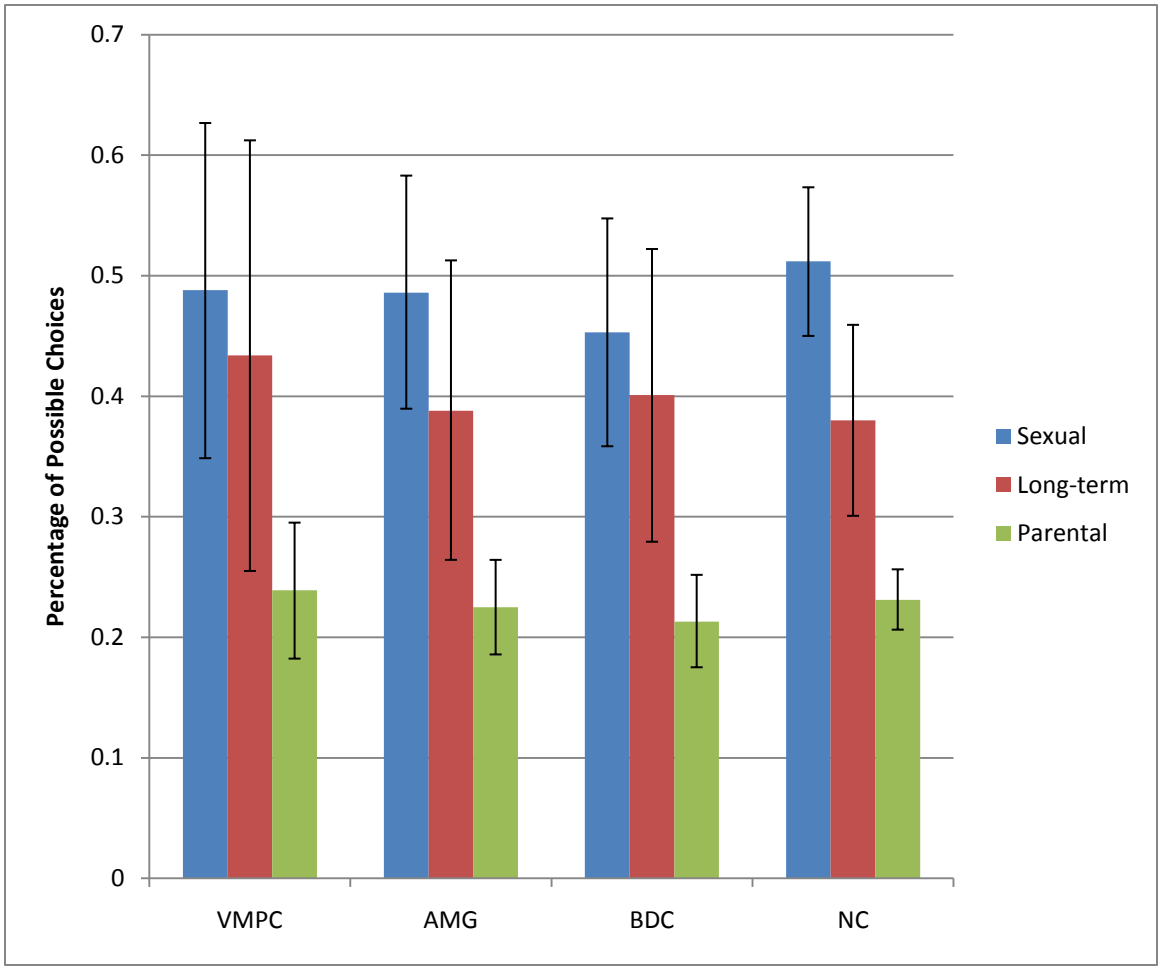

Figure 33 – Choices Based on Parental Ability for Women for Different Relationship Types. Higher values indicate increased preference. It is counterintuitive that all groups show decreased preference for parental ability when vetting parental partner choices. Error bars represent 95% confidence intervals.

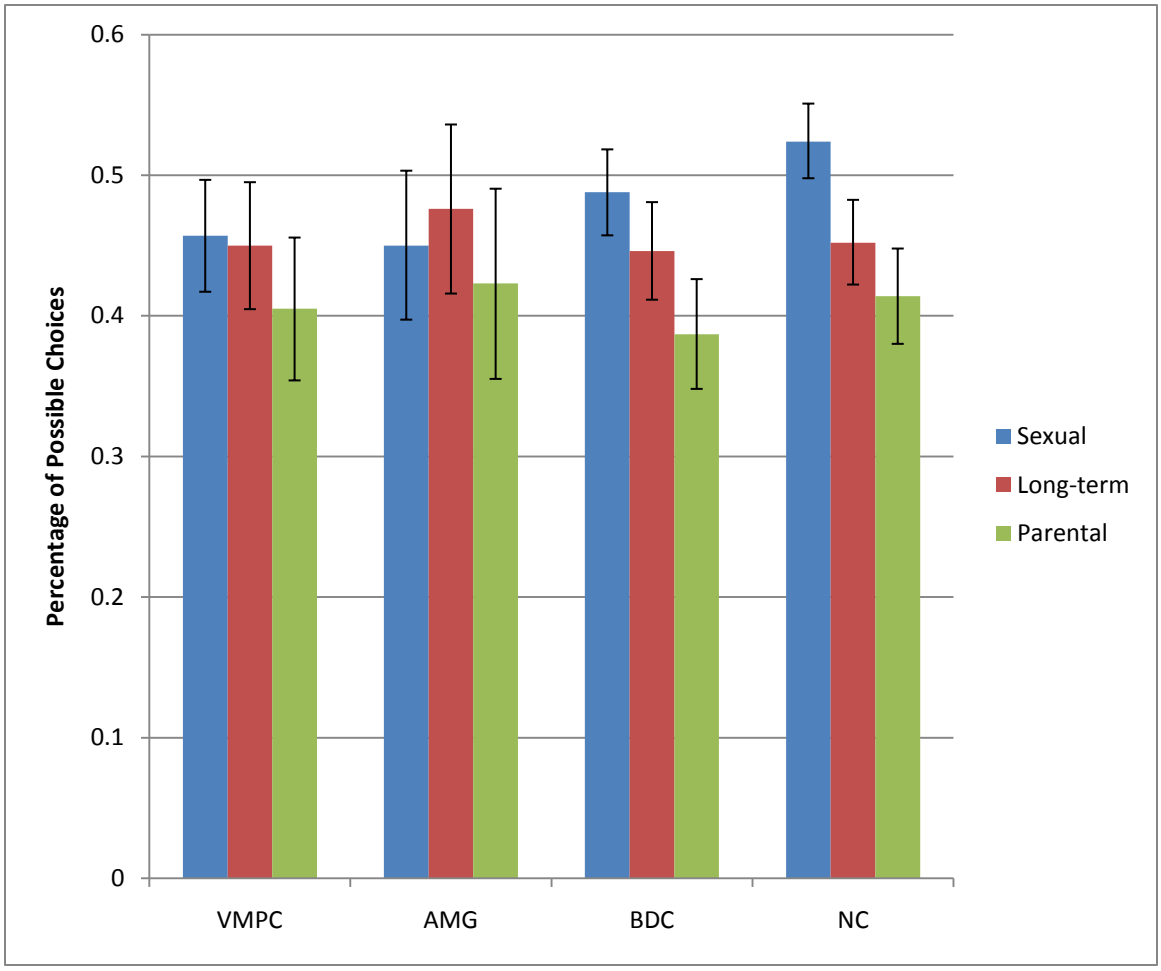

Figure 34 – Choices Based on Attractiveness for Men for Different Relationship Types. Higher values indicate increased preferences. Error bars represent 95% confidence intervals.

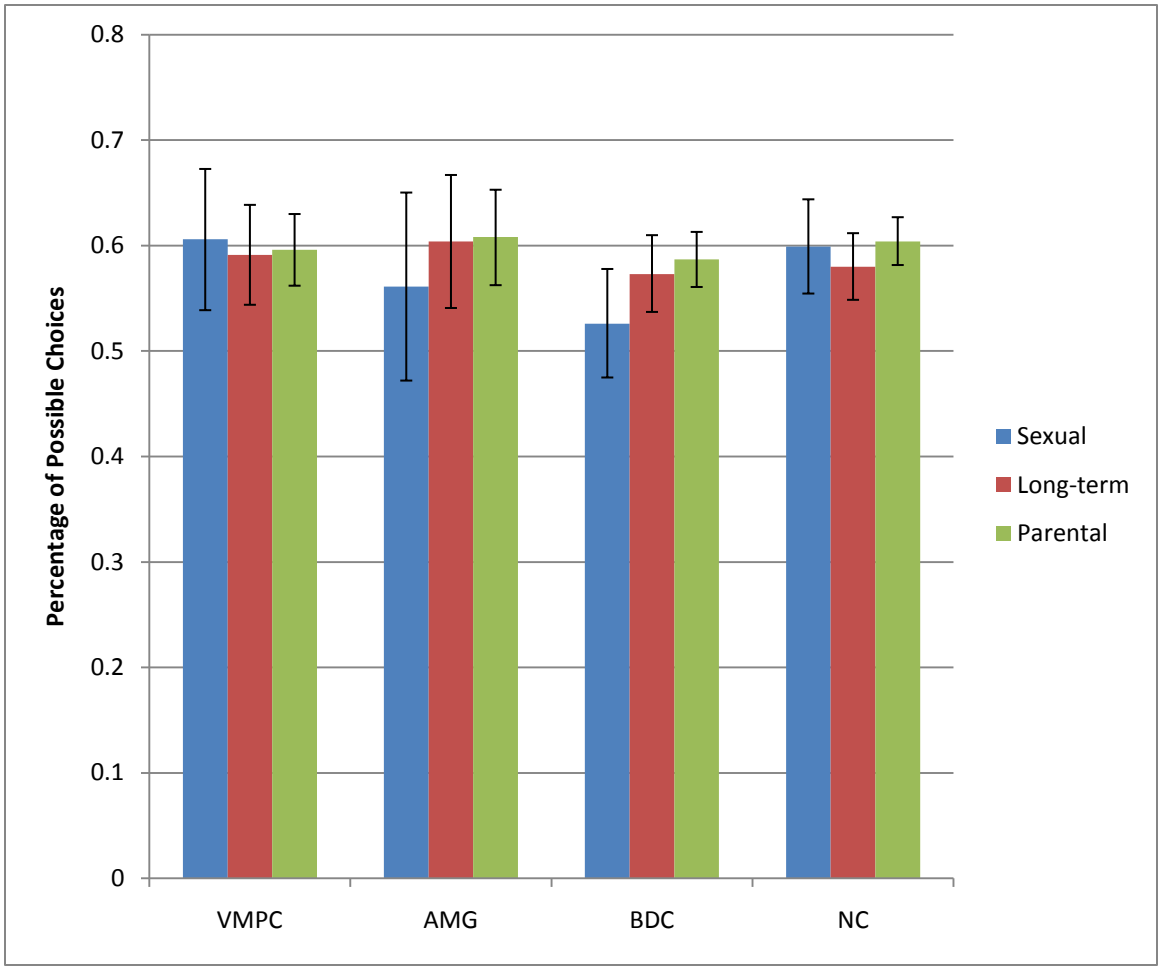

Figure 35 – Choices Based on Age for Men for Different Relationship Types. Higher values indicate increased preference. Error bars represent 95% confidence intervals.

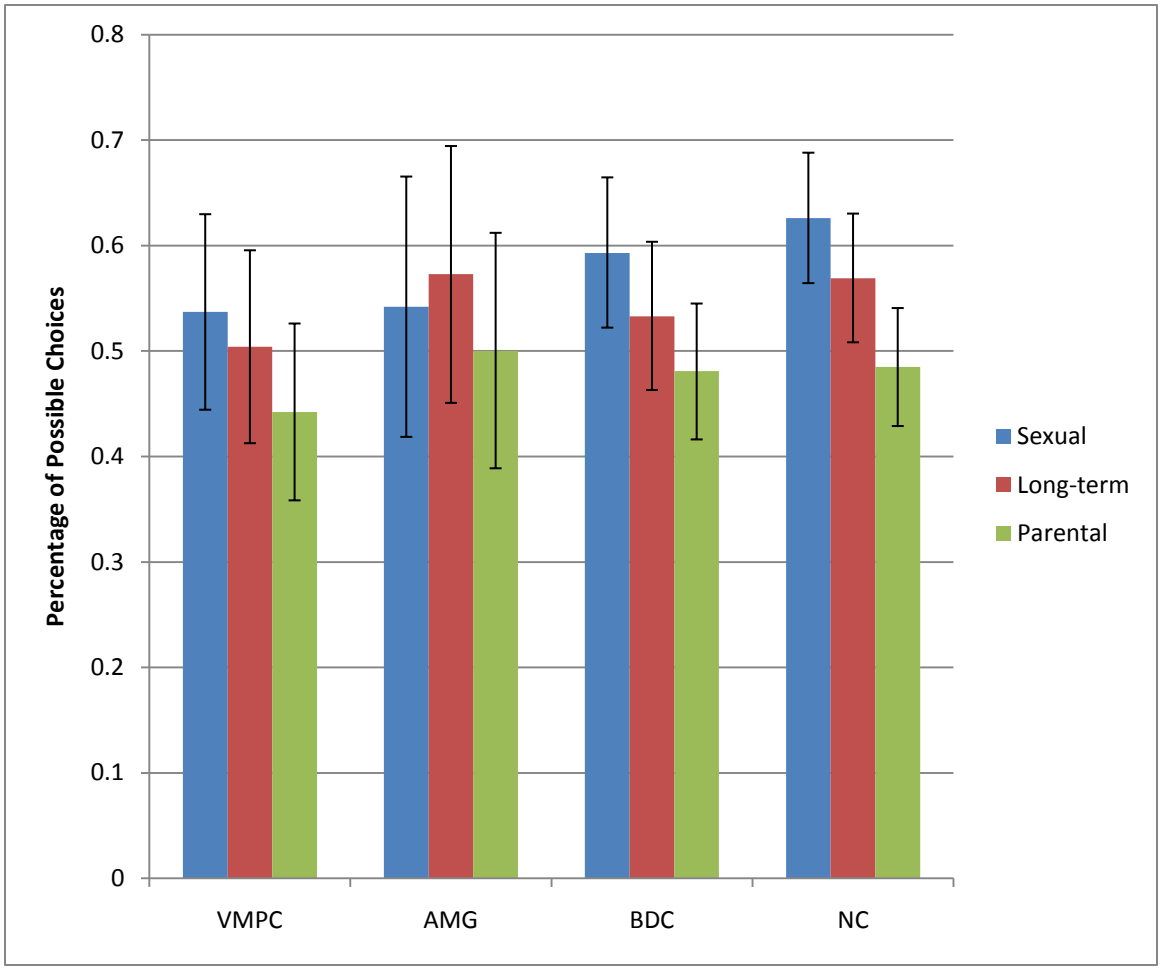

Figure 36 – Choices Based on Income for Men for Different Relationship Types. Higher values indicate increased preference. Error bars represent 95% confidence intervals.

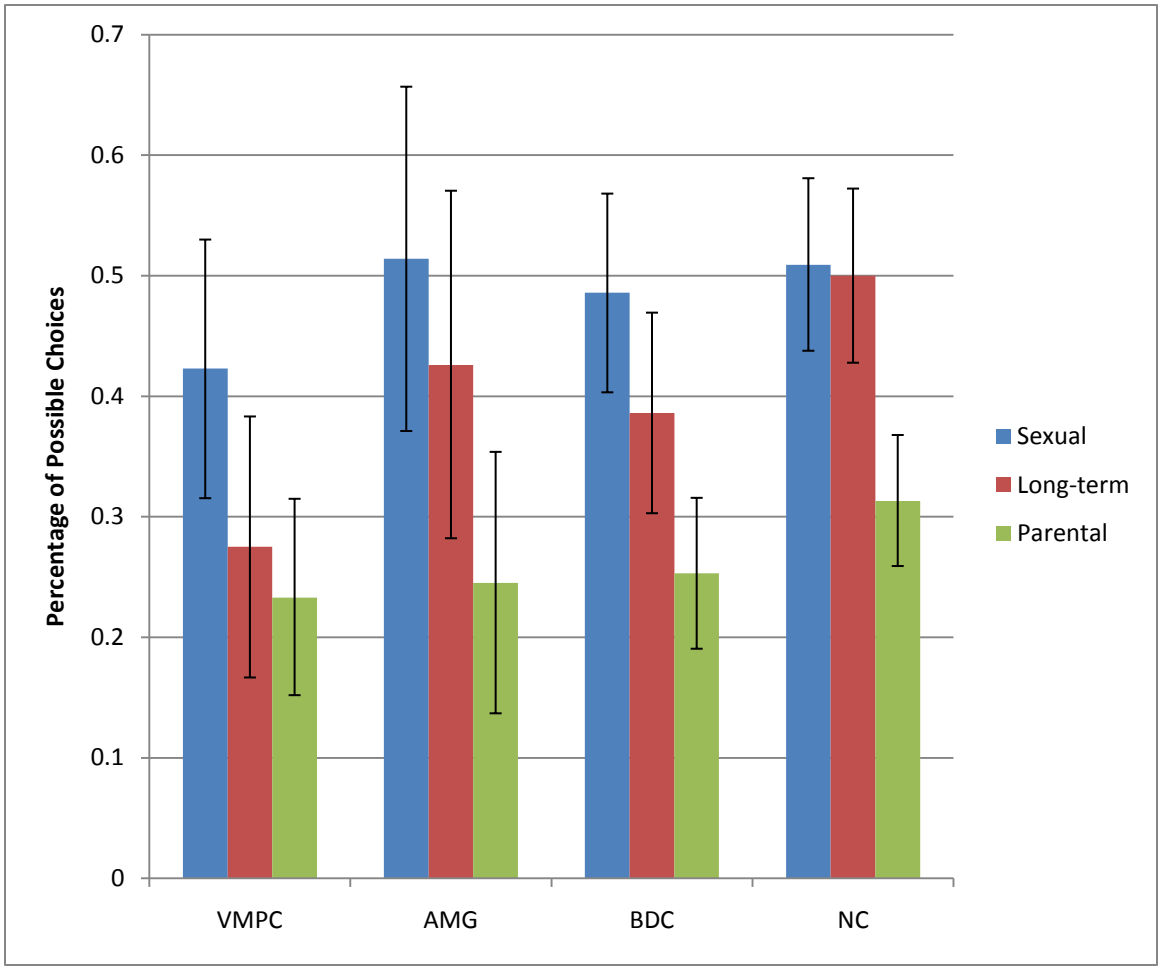

Figure 37 – Choices Based on Parental Ability for Men for Different Relationship Types. Higher values indicate increased preference. Just as is observed for women it is counter-intuitive that men display a decreased preference for parental ability when vetting parental partners. Error bars represent 95% confidence intervals.

CHAPTER 8

SOCIAL ATTRIBUTION

Logic

An ability to make social inferences is a key aspect of adaptive social behaviour. It is often important to know whether an individual's behaviour is due to their disposition, and thus the individual would be likely to behave in that way again, or if an individual's behaviour is being dictated by environmental pressures, and thus the individual's behaviour would be unlikely to occur again. Through making appropriate social inferences, or social attributions, it is possible to reduce the uncertainty in predicting the future behaviours of others. The current hypothesis predicts that the ventromedial prefrontal cortex and amygdala are essential for making social attributions. Perhaps an obvious way of falsifying the current hypothesis would be if experimental results indicate that damage to the VMPC or amygdala has no effect on attributional processes.

The correspondence bias forms one of the cornerstones of social psychology (for a review see Gilbert & Malone, 1995). The correspondence bias is the tendency for people to infer that a person's behaviour reflects their disposition even from situationally constrained behaviour[41]. In other words, normal healthy people tend to assume that a person's behaviour is caused by that person rather than being dictated by the situation that the person is in. A related and often synonymous phenomenon, the fundamental attribution error refers to the underestimation of situational influences on behaviour (Gawronski, 2004). The correspondence bias has been referred to as one of the most replicable and robust findings in all of psychology yet it has also been referred to as

41 As a cognitive bias, it is not necessary that a person behaves or thinks in a certain way all of the time, rather that there is a tendency in a certain direction and when 'all things are equal' they behave in a predictable manner.

untenable and completely bogus (Funder, 2001). In a recent article and accompanying commentary, some researchers have suggested that the correspondence bias (more specifically the fundamental attribution error) is itself conceptually flawed as all human behaviours are multiply determined and the dichotomy between dispositional and situational causes is a false one (Sabini, Siepmann, & Stein, 2001). I do not disagree with this analysis, however the current research and the vast majority of the literature on the correspondence bias is not concerned with the ultimate causes of a person's behaviours (as they are indeed multiply determined). Rather the current work is concerned with the inferences about behavioural causes that the layperson draws. The actual accuracy of laypersons inferences in relation to the ultimate causes of another's behaviour is difficult if not impossible to determine (L. Ross, 2001), moreover this accuracy is somewhat immaterial to the present work. To use an example given by Sabini, *et al.*, "Did Tom eat this piece of candy because he liked sweets or because the candy was sweet?" (Sabini, et al., 2001). Both internal and external causes are likely true, however the important missing component from this is what a layperson thinks is the cause. One might think Tom ate the candy because he was hungry (an internal cause) and this might help them predict that Tom would have eaten anything in the same situation. I predict that VMPC and/or amygdala damage will basically result in a deficit in attaching values to others that are useful in predicting others' behaviour as well as one's behaviour toward others. Thus it is not necessary that the correspondence bias as a concept is generally valid or that these inferences are ultimately accurate. Instead what is needed to test this idea is a paradigm in which normally and consistently a dispositional bias is observed such that a deviation away from making dispositional attributions might be observed in the target participants.

Potentially the correspondence bias could result from underestimation or inadequate use of situational influences, or over estimation or over utilization of dispositional influences. Regardless of the root cause of the correspondence bias, it does

appear to be a robust phenomenon observed cross-culturally (e.g.,Krull et al., 1999; Miyamoto & Kitayama, 2002), however it does appear that observation of the correspondence bias in non-Western cultures may depend on the specifics of the paradigm used to examine it. For example, if the behaviour in question is highly diagnostic of a certain attribute, the bias may be more prominent than when diagnosticity is low (Gawronski, 2004). Similarly young children do not tend to make dispositional attributions (e.g., P. White, 1988), though it has been reliably found in adolescents (e.g., in 14 year-olds Block & Funder, 1986). Some have argued that this means the correspondence bias is "almost certainly learned" (Langdridge & Butt, 2004, p. 359) though an equally viable alternative is that it is unlearned but offline until activated by the surge of hormones that activates many physical and cognitive changes associated with puberty.

The present hypothesis, in line with the Error Management Theory of Haselton and Buss (2000), would suggest that being biased toward making relatively small errors, like the correspondence bias, helps avoid making more costly errors that might otherwise occur. Any deviation from the normal occurrence of the correspondence bias, as is expected for patients with VMPC or amygdala damage, may result in more costly errors. Indeed, some data suggest that individuals who are more prone to the correspondence bias tend to score higher in social engagement, social competence and emotional adjustment (Block & Funder, 1986). Specifically, an inability to make appropriate dispositional attributions in these target patients may lead them to make more costly errors of social conduct. For example, people may avoid cheaters regardless of the cause of their infractions to err on the side of caution. Specifically, I predict that the target patients will not exhibit the correspondence bias in a classic paradigm, the 'Quiz Game,' nor will they effectively utilize dispositional information about others when making neuroeconomic decisions.

Experimental Design:

To examine whether or not patients with damage to these brain regions exhibit the correspondence bias. Participants completed a variation of the classic 'Quiz Game' experiment (L. Ross, Amabile, & Steinmetz, 1977). Following completion of this paradigm, participants completed a neuroeconomic paradigm in which participants are given either dispositional information or situational information about potential investment partners.

Quiz Game

Participants took the role of 'observer,' and watched a video of a Quiz Game and then rated the general knowledge of the confederates playing the game. At the beginning of the video, two confederates were randomly assigned to either the role of 'questioner' or 'contestant.' The questioner was instructed to create 10 challenging questions based on their own esoteric knowledge and the contestant was asked to generate 10 easy questions that are answerable by 90% of high school freshmen to get them in the mood of the game. This manipulation puts the questioner in an advantageous position to express their knowledge while putting the contestant in the disadvantageous position of having to answer questions they are very unlikely to know the answer to. Since this role-conferred advantage is random (*i.e.*, the roles were assigned randomly), knowledge of this information should allow participants to rate the confederates as having relatively similar levels of general knowledge. However, normal healthy individuals tend to rate the questioner as being more knowledgeable than the contestant, either underestimating the role conferred advantage or overestimating the questioner's disposition, *i.e.*, they exhibit the correspondence bias.

Investors Game

At the beginning of each round, participants completed a task to earn facsimile money ($100 for each round). The money that was earned was used in the later portions

of each trial. The tasks that each participant completed to earn facsimile money were intended to be control tasks for the rest of the experiment. This gave participants incentive to complete the control tasks as well as potentially provided incentive to invest money wisely as it was earned and not just given. After earning money in the control task, participants (the investors) read descriptions of two people with whom to potentially invest. Descriptions included a picture of an individual and varied in terms of containing either dispositional or situational information. Dispositional information included a reference to something internal to the individual, whereas situational information referred to circumstances that were external to the individual and beyond their control. For example, dispositional information, "John Smith: Investors made 10% last year due to his hard-working nature," versus situational information, "Bill Johnson: Investors made 10% last year due to economic growth in China." After reading the descriptions, investors decided how much of their money to invest in each potential investee. Participants were able to invest some or all of their money for the round ($100) at their discretion, although a minimum of 10% of the money needed to be invested on each round. A new trial began with another control task, where the participant could earn more money, and began the process again. At the end of the game, before participants are informed of how much money the earned on their investments, they were asked to predict how successful each investee was with their invested money. The participants were then informed of the results of each investment, one at a time, immediately followed by an evaluation of each investee in terms of how much the participant would potentially reinvest with that person.

Covariation Detection Task

Participants were presented with a series of 20 images. Each image was accompanied by two values. Participants were instructed to notice which of the two values is highest and also to pay close attention to the images. Participants were then presented with 8 novel images and asked to predict the covarying values. There were two

versions of this task: an easy version in which the values (coffee vs. soda consumption) correspond 80% of the time with a feature of the image (blue flags) (Block 1), and a hard version in which the values (the number of teachers vs. the number of doctors) correspond ~66% of the time with a feature of the image (presence of the union jack) (Block 2). The purpose of this task was to examine whether or not individuals can detect covariation among variables without explicitly being told to do so. If participants cannot do this, then it may be reasonable to infer that any deficit shown in social attributional processes may be due to an inability to detect covariation. Specifically, social inference assumes an ability to detect covariation among observable behaviours and relate them to dispositional characteristics, if one cannot do the former, the latter is not applicable.

Inhibition of Return

Participants viewed a display which consisted of a central fixation point and two box outlines arranged on the vertical or horizontal meridian. On a given trial, a peripheral cue was presented followed by a target and participants made a key press when they saw the target. On this task, normal participants display increased response latency when returning to a point of previous fixation, *i.e.*, they are inhibited to return to previously looked at regions. However, if a participant is unable to inhibit attention to specific stimuli, *e.g.,* because they are more stimulus-driven, the inhibition of return effect should not be seen. In the case of social inference, particularly in the Quiz Game experiment, an inability to inhibit (or discount) situational information may result in a lack of the CB as predicted. However, the current hypothesis suggests that a deficit in the CB is due to an inability to infer dispositional characteristics as opposed to an inability to inhibit situational information. Thus in the case that target participants did not display an inhibition of return effect, it may be a more parsimonious explanation of any deficit in the CB that they simply have a general problem of inhibiting information.

Predicted Results

If the VMPC or amygdala is necessary for inferring the qualities of others then damage to these regions should interfere with the normal CB.

Specifically, when rating the Contestant and Questioner in the Quiz Game, patients with damage to the target regions should not systematically rate the questioner as more knowledgeable than the contestant. Furthermore, target participants were predicted to behave the same as comparisons on the control tasks, both the covariation detection task and the inhibition of return task. That is, target participants were predicted to have no significant difficulty in detecting covariation among variables (a prerequisite for inferring dispositions from behaviours) and would be able to inhibit situational information, *i.e.,* show a normal inhibition of return effect.

As a potential alternative, if the correspondence bias is due to social desirability motives to save face or avoid embarrassment (as suggested by Sabini, et al., 2001) a different pattern of results would be expected. Potentially, any decrease in rating of the questioner's general knowledge would be due to a decreased desire to maintain social desirability. However, if target participants indeed displayed a decreased drive to maintain social desirability one would expect the ratings of the contestant to be lowered well below average in ability as well. Thus, if social desirability is driving the correspondence bias one would predict that target participants would rate the questioner as average in intelligence (and not give them a dispositional boost) and simultaneously rate the contestant below average (unlike normal participants for whom it would be more socially desirable to rate them as average). The current hypothesis predicts that social desirability will remain unaffected but the role-conferred advantage will not result in a dispositional boost. Specifically, target participant ratings for the contestant will remain at average but questioner ratings will be average as well, thus not exhibiting the correspondence bias.

In the Investors Game, there are two predicted modes of behaviour. The first is a 'rational' model of behaviour in which individuals will invest more money with the people for which they have relevant, positive information (dispositional) compared to those for which they have only extraneous, non-relevant information (situational). In an alternative, or 'biased,' model of behaviour, investments would not differ between dispositional and situational conditions, as the situational information would 'erroneously' be treated as informative and relevant due to the correspondence bias where situational information would be given the same weight as dispositional information. The current hypothesis predicts that VMPC or amygdala damage should affect the extent to which one makes dispositional attributions; thus these participants should follow the 'rational' model, systematically investing more when given positive dispositional over situational information. In contrast comparison groups will display the correspondence bias and thus follow the 'biased' model where they invest similar amounts with both dispositional and situational information.

Results

Quiz Game

To investigate group differences in performance on the Quiz Game, I used two separate approaches. First, a difference score was calculated to represent the difference between knowledgability ratings for the Questioner minus the Contestant, such that a value greater than 1 represents the presence of correspondence bias and values of zero or lower represent its absence. An ANCOVA was run to assess group differences in the correspondence bias with group as a fixed factor, and age and education as covariates.

ANCOVA revealed no effect of group ($F=0.602$, $p=0.615$) or age ($F=0.972$, $p=0.326$) but a significant effect of education ($F=5.235$, $p=0.024$). When sex is included in the model as a fixed factor, there were no observed effects of group ($F=0.539$, $p=0.656$), sex ($F=0.852$, $p=0.0358$), or a group by sex interaction ($F=1.671$, $p=0.177$).

When including side of brain damage as a fixed factor in the analysis there was no effect of group (F=1.232, p=0.298), side (F=0.192, p=0.826), or a group by side interaction (F=0.866, p=0.489); in addition there was no effect of education in this model (F=2.099, p=0.152). Preliminary analysis had suggested that there may be an interaction between brain damage location and etiology where tumor removals tended to occupy anterior regions including the frontal pole where brain damage due to aneurysm rupture and clipping tended to be rostral to the frontal pole in subgenual medial prefrontal cortex. However, when including etiology in the ANCOVA as a fixed factor, there were no observed effects of group (F=0.047, p=0.954), etiology (F=1.286, p=0.286), or a group by etiology interaction (F=0.743, p=0.566) (see Figure 38).

A relatively simpler analysis was conducted by counting the number of individuals in each group that displayed the correspondence bias (the Questioner – Contestant difference was greater than 0) and those that did not (difference equal or less than 0). A Chi-squared test revealed that there are no group differences between groups on the presence or absence of the correspondence bias in the Quiz Game (X^2=1.04, df=3, p=0.7916) (see Figure 39).

Investors Game

Results of the investor game were calculated by finding the difference between the amount of money invested when given dispositional information and the amount of money invested when given situational information. An ANCOVA was used with group as a fixed factor, and age and education as covariates, to test for group differences. This revealed a trend toward a significant effect of group (F=2.347, p=0.076), and no effect of age (F=1.210, p=0.274) or education (F=0.901, p=0.344). Planned comparisons revealed an increased difference between participants with VMPC damage compared to BDCs (mean difference = 0.168, p=0.012) and NCs (mean difference = 0.124, p=0.055) (see Figure 40). When sex is included as a fixed factor in the ANCOVA, there is a significant

effect of sex (F=5.315, p=0.023), where the difference is greater for women than men (mean difference = 0.101, p=0.023), but no group by sex interaction (F=1.131, p=0.340). There was no observed effect of brain damage side (F=0.944, p=0.394) or a group by side interaction (F=1.702, p=0.160). Likewise, there was no effect of brain damage etiology (F=0.421, p=0.738) or etiology by group interaction (F=0.554, p=0.697).

There were no observed group differences when predicting how investments did (F=0.084, p=0.969) (see Figure 41) or when deciding how much to potentially reinvest with the same individuals (F=1.662, p=0.179) (see Figure 42), suggesting that the group differences were somewhat transient. As a check to test whether or not the groups differ in their perceptions of potential investment partners, memory for the faces of the investors was tested as well as ratings for the faces on several personality and emotional characteristics were assessed. A MANCOVA with group as a fixed factor and age and education as covariates revealed no significant differences between groups (F=1.158, p=0.322), in terms of correct identifications (F=0.902, p=0.443), correct rejections (F=0.610, p=0.610), false rejections (F=0.879, p=0.454), and misses (F=0.645, p=0.588). None of the groups displayed performance much better than chance in memory for the faces (percent correct: VMPC 52.5%, AMG 56.4%, BDC 58.2%, NC 54.5%), perhaps due to the design of the stimuli to be relatively similar in appearance and neutral in expression. Similarly a MANCOVA revealed no significant differences between groups in ratings of the faces of the investor's in the task (F=0.776, p=0.830). The groups rated all of the faces similarly in terms of likeability (mean=4.2, F=0.276, p=0.842), attractiveness (mean=4.3, F=0.520, p=0.669), kindness (mean=4.3, F=0.450, p=0.718), trustworthiness (mean=4.2, F=0.447, p=0.720), masculinity/femininity (mean=5.4, F=0.211, p=0.889), intelligence (mean=4.6, F=0.662, p=0.577), how natural they appear (given they were computer generated) (mean=4.7, F=1.193, p=0.316) (scale 1-7, 4 is neutral), as well as in terms of happiness (mean=1.5, F=0.785, p=0.505), sadness (mean=1.3, F=0.370, p=0.775), anger (mean=1.4, F=0.985, p=0.402), surprise

(mean=1.3, F=0.613, p=0.608), disgust (mean=1.3, F=0.217, p=0.885), and fearfulness (mean=1.3, F=0.850, p=0.469) (scale for emotions 1 – 4, 1 is neutral). Further analysis of ratings of the faces used in the Investors Game compared the difference between the ratings for faces associated with dispositional information with those that are associated with situational information. A MANCOVA suggested that there are no group differences between dispositional and situational associated faces (F=1.079, p=0.352), with a possible exception of fearfulness ratings where amygdala subjects rated situational associated faces as more fearful than dispositional faces compared to other groups (F=2.756, p=0.046).

Covariation Detection

As a control task, participants completed a hidden covariation detection task, and as expected there were no group differences in detecting hidden covariations (F=1.339, p=0.241). However, pairwise comparisons suggest that there may have been a subtle increase in performance among participants with amygdala damage when detecting more regular covariations (that is when variables covary more often, making these detections relatively easier) compared to VMPC damage (mean difference = 0.151, p=0.022) and NCs (mean difference = 0.113, p=0.047).

Inhibition of Return

As another control task, participants were tested on an Inhibition of Return paradigm. In this task there were several different types of items that participants respond to, including instances of: cues and targets in the same location (IOR suggests these trials should be slower), cues and targets in distinct locations, cues and targets within the same object (IOR suggests these trials should be slower), cues and targets within distinct objects, cued locations with object-based targets, cued objects and location-based targets, and uncued location-based and object-based targets. MANCOVA with group as a fixed factor and age and education as covariates reveal a significant effect

of group (F=1.728, p=0.020) and age (F=5.799, p<0.0005) but not education (F=1.346, p=0.229). There is no significant group effect on IOR (when cues and targets are in the same location or object) (Location: F=1.475, p=0.225; Object: F=1.053, p=0.372). Significant group differences were observed for uncued location-based targets (F=3.802, p=0.012), where NCs were significantly slower than all brain-damaged groups (vs. VMPC: mean difference = 0.292, p=0.005; vs. AMG: mean difference = 0.211, p=0.036; vs. BDC: mean difference = 0.208, p=0.010); a trend for cued locations and object-based targets (F=2.572, p=0.058), where participants with amygdala damage were significantly slower than VMPCs (mean difference = 0.212, p=0.032) and NCs (mean difference = 0.212, p=0.013); and a trend for uncued object-based targets (F=2.225, p=0.089), where NCs were slower than VMPCs (mean difference = 0.209, p=0.055) and BDCs (mean difference = 0.191, p=0.025).

Discussion

It is curious that the results of the two tasks to assess the presence of the correspondence bias yield different results. Since no differences were observed between groups on the Quiz Game, it may be that this particular experiment was under-powered to detect differences in the variable behaviour of brain damaged subjects. There have also been hints at potential differences in specifics related to the precise lesion location, where frontal polar regions may be less important but since these regions are well sampled within the VMPC group this may be overshadowing the potential differences due to damage in more caudal regions of medial prefrontal cortex. To adequately test this potential difference based on etiology, which in turn is related to lesion location, more precise mappings of the lesions are required, though as mentioned above this is the rate-limiting step to this type of work.

As predicted, participants with VMPC damage are less likely to display the correspondence bias when making investment decisions. It is interesting that this lack of

correspondence bias allows the VMPC participants to make ‘more rational’ decisions, by investing with individuals with whom some of their skill is known compared to individuals about whom nothing is known. As mentioned above this may be explained by Error Management Theory, where these more ‘rational’ decisions may actually lead to costly errors. Further investigation might lead to a better understanding of whether or not this increased ‘rationality’ produces socioeconomic costs.

In the analysis of the Investors Game, it is observed that differences between dispositional and situational investments do not translate into similar differences when predicting how these investments would do or when asked how much they would like to reinvest with these same partners after receiving feedback on their investment. It may be that the effect is transient and simply did not last long enough to influence these judgements, which occur generally about a half hour later. It may be that the information associated with each investor was not remembered in enough detail to be utilized in the same manner as it was for the first investments. For reinvestments it may be that descriptions become irrelevant after receiving direct feedback on investment success, and since all investments performed the same in this task design any effect of the previous descriptions may have been washed out. It would be interesting to see how these initial biases translate into effects on the formation and maintenance of long-term relationships or if they simply have no lasting effect whatsoever.

It is difficult to reconcile the observations between the Quiz Game and the Investors Game. On one hand there is no observed correspondence bias in knowledgability ratings of others in the Quiz game, however there is an observed lack of correspondence bias in making investment decisions in the Investors Game. Previous research has suggested that following VMPC damage deficits in social behaviour are manifest however deficits in social knowledge are not observed. It may be that the reason for observing a normal correspondence bias in the quiz Game is that it reflects intact social knowledge or at least an intact ability to articulate social information and

norms. On the other hand the Investor game requires individuals to act upon social information and thus given the abnormal social behaviour observed in VMPCs their social deficit was manifest as a lack of correspondence bias in behaviour rather than ratings.

As mentioned in the first section of this chapter, studies examining the correspondence bias in cross-cultural contexts often discover that there are task-specific factors that influence the presence or absence of the correspondence bias (Gawronski, 2004). Likewise, given the observation of the normal correspondence bias in participants on the Quiz Game but not the Investor's Game may relate to specific aspects of these tasks to which they are differentially sensitive. As mentioned above it may be due to the fact that the two paradigms differ in probing social knowledge compared to probing a type of social behaviour. In addition, there are other factors that could have an effect such as, the participant's level of engagement, where in the Quiz Game participants are observers and the Investors Game they are actors. It might be interesting to perform further experiments in these groups to assess actor-observer biases. Another interesting extension of this work would be to examine whether attributions of opposite sex individuals are similar or different from those of same-sex individuals. Given the present theoretical framework it may be reasonable to assume that assessing social value to individuals of your sex would be different from those of the opposite sex due to reproductive relationships and the differing goals therein. Likewise, future extensions of this work might benefit from considering the social and motivational goals that an individual brings to a given social situation for effects on attributions.

Another possible explanation of the conflicting findings from the Quiz Game and the Investors Game may help to reconcile these disparate findings with the predictions made by the Inferential Brain Hypothesis. It may be that the comparison participants when making investment decisions based on situational information made an inferential leap beyond the information given. On the other hand participants with VMPC damage

who are hypothesized to have a specific deficit in social inference do not make this additional inferential leap. It is possible that normal comparison participants inferred that the situational information was known by investor and that may have been why they earned money. For example, if the information given was something like, "John Smith's Investors made 15% last year due to economic growth in China." It is possible that normal comparison participants inferred that this meant that John Smith knew there would be economic growth in China and thus invested there, where this inference involves extending beyond the information given to link it to the particular investor. This is in contrast to the dispositional information for investors, where the information is explicitly given, *i.e.*, "John Smith's Investors made 15% due to his hard-working nature." In the case of the Quiz Game, it is not clear whether or not the same type of inferences need to be made. Participant judgements could be based solely on the observed performance of the Questioner and Contestant, leading to expression of the correspondence bias, or participants could have inferred that the confederate's performance was an indicator of the person's knowledgability, and still made the same correspondence bias. It would be interesting to follow up the present experiments to examine more clearly whether or not the correspondence bias is present specifically under conditions where social inference is required compared to when information need not be inferred.

Of the control tasks employed in this protocol the results are not necessarily clear for participant's ability to detect hidden covariations. An ability to detect whether or not one variable can be used to predict another is assumed to be a cognitive prerequisite to linking social behaviours and dispositions. However, the task employed here did not reveal that any of the groups could reliable detect the hidden covariation better than chance. Although, VMPC and amygdala groups did not show any selective deficits on this task, and amygdala subjects may actually perform better than all other groups on the easiest version of this task. It may be that the covariation was in fact too hidden, that

participants simply did not attend to the aspects of the stimuli that were needed to detect the covariation. Perhaps, more training trials were needed to actually learn the covariation or the covariation needed to be stronger to be detected.

On the other control task, the Inhibition of return task there are some interesting results. As expected no group shows selective deficits in normal inhibition of return. And none of the groups seemed selectively slower than other groups across stimulus types. One perplexing finding is the observation that all brain damaged groups are significantly faster at responding to uncued stimuli than normal healthy adults. Perhaps it is indicative of an increased attentional capture by external stimuli following brain damage, or perhaps there is some unknown and unmeasured sampling bias within the normal comparison group. Perhaps, since age and level of education were included as covariates in the analysis, this produced artificial inflation of NC responses given that they are more highly educated group, assuming that education may be in some way correlated to reaction times. Though, there is not a good explanation why education level would influence reaction speed on uncued targets selectively.

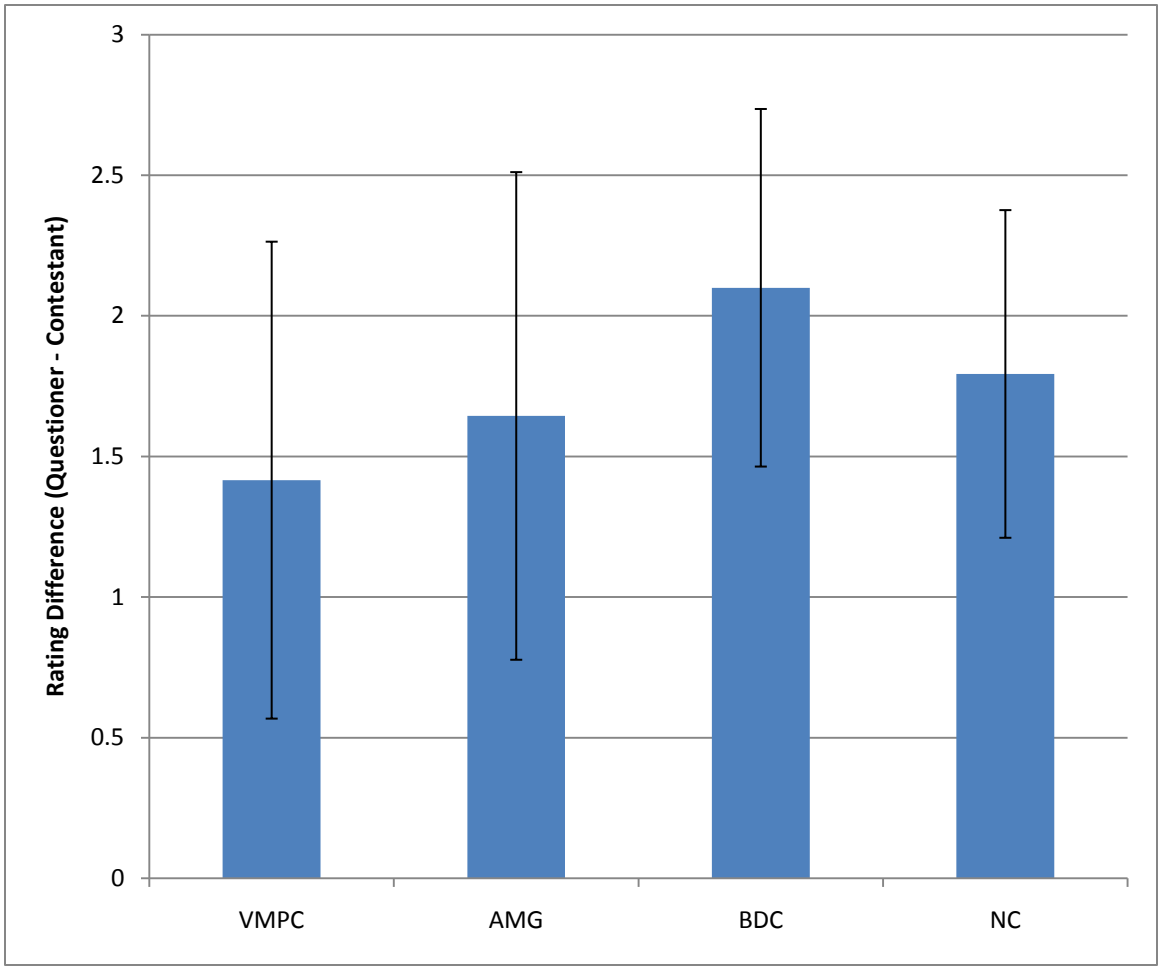

Figure 38 – Quiz Game Correspondence Bias. Bars represent the group average for the difference between the knowledgability ratings between the Questioner and the Contestant. Positive values indicate the presence of the correspondence bias. Error bars represent 95% confidence intervals.

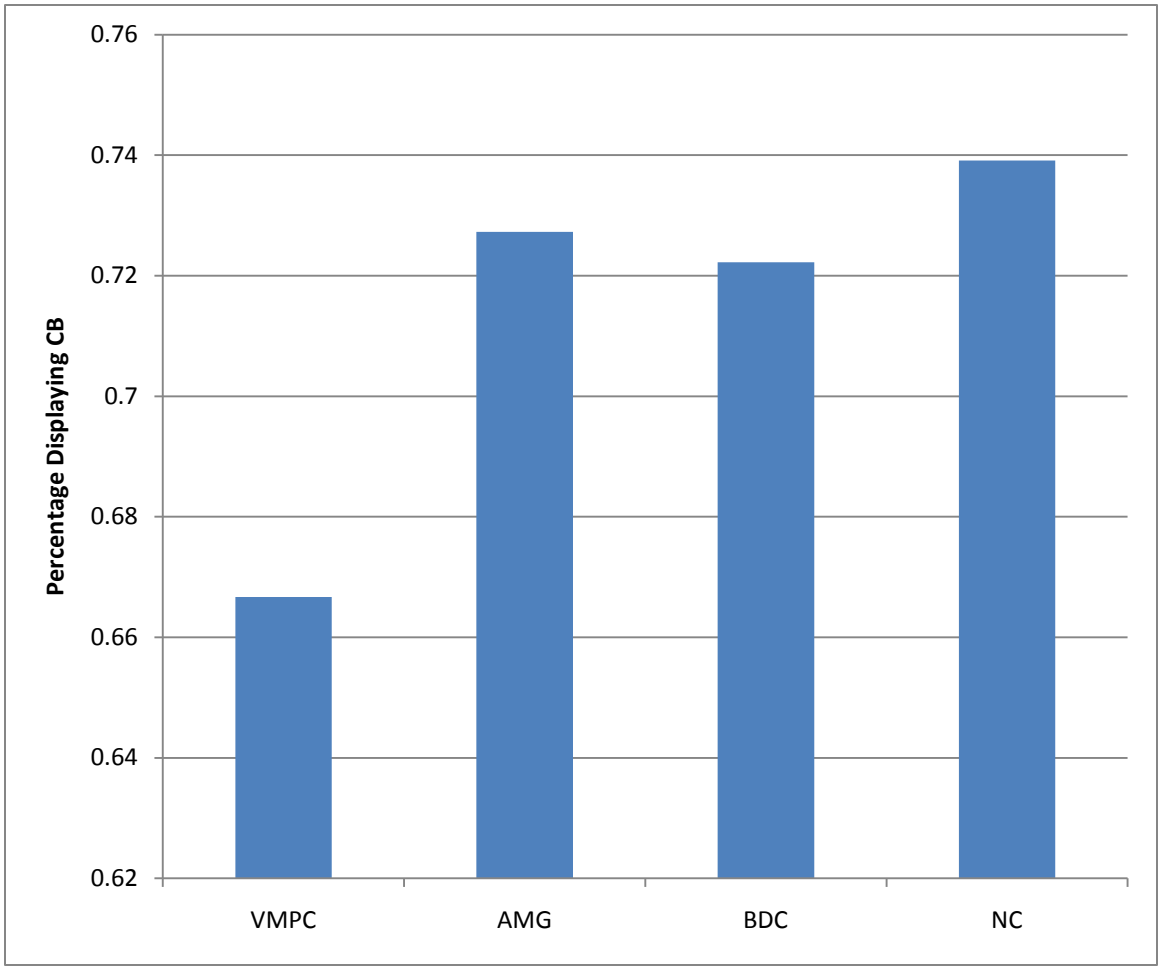

Figure 39 – Quiz Game Correspondence Bias Frequency. Bars represent the percentage of each group that displayed the correspondence bias. The VMPCs displayed the lowest frequency, however this is non-significant and the scale of the graph has been stretched to exaggerate the difference.

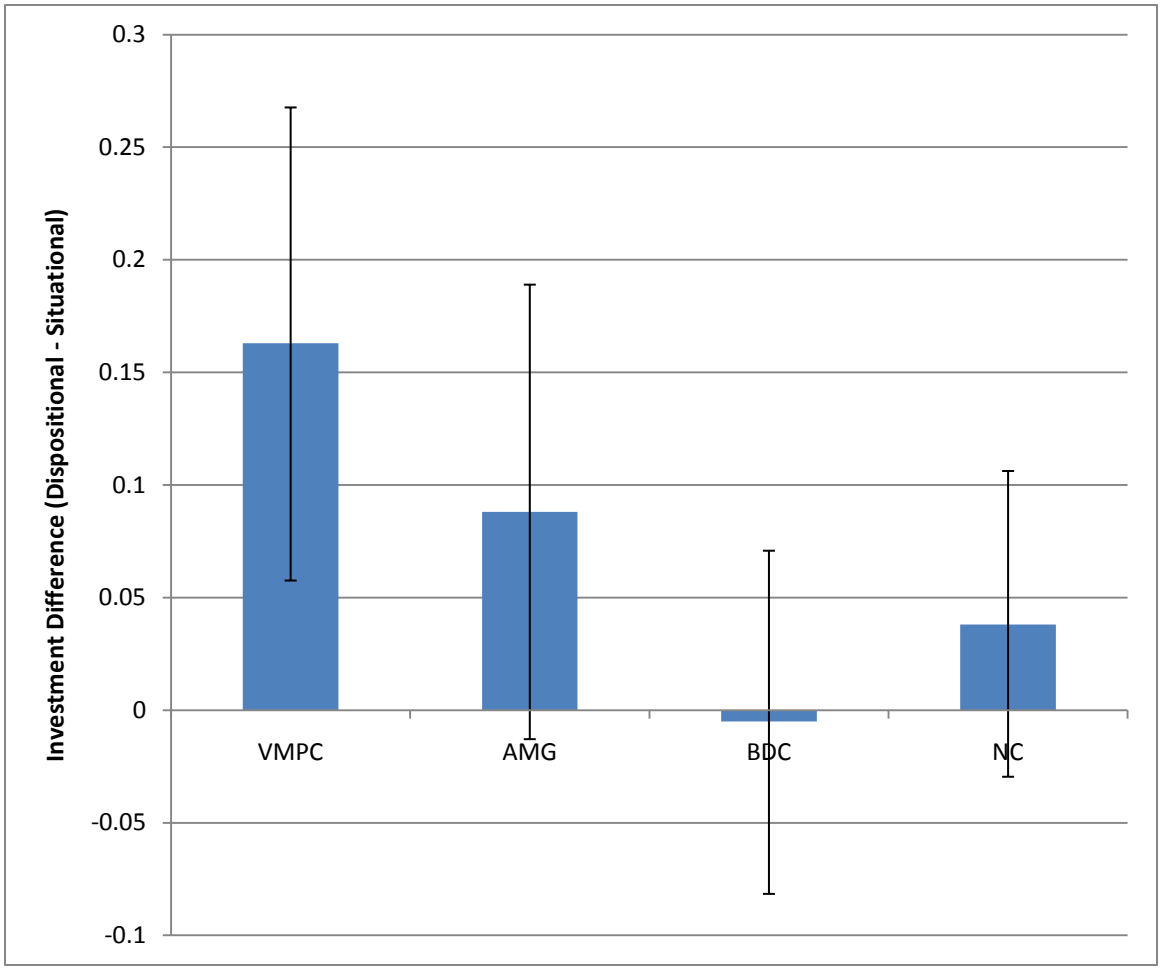

Figure 40 – Investors Game Correspondence Bias. Bars represent the difference between the amount invested when given dispositional information and the amount when given situational information. Higher values indicated increased investment when given dispositional information. The correspondence bias is apparent in BDCs and NCs where situational information is treated similarly to dispositional information.

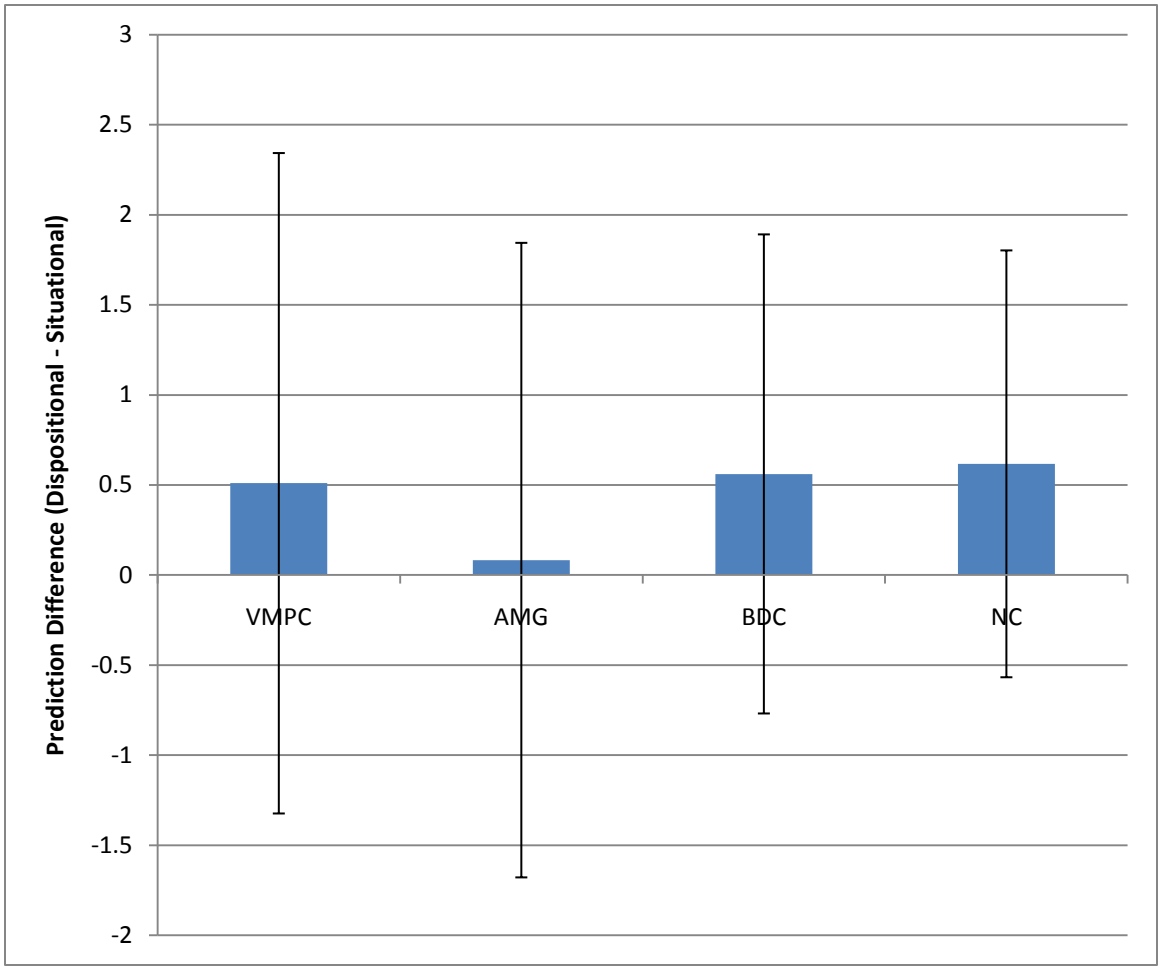

Figure 41 – Investors Game Predictions. Bars represent the difference between how well participants predicted their investments would do when given dispositional information compared to when given situational information.

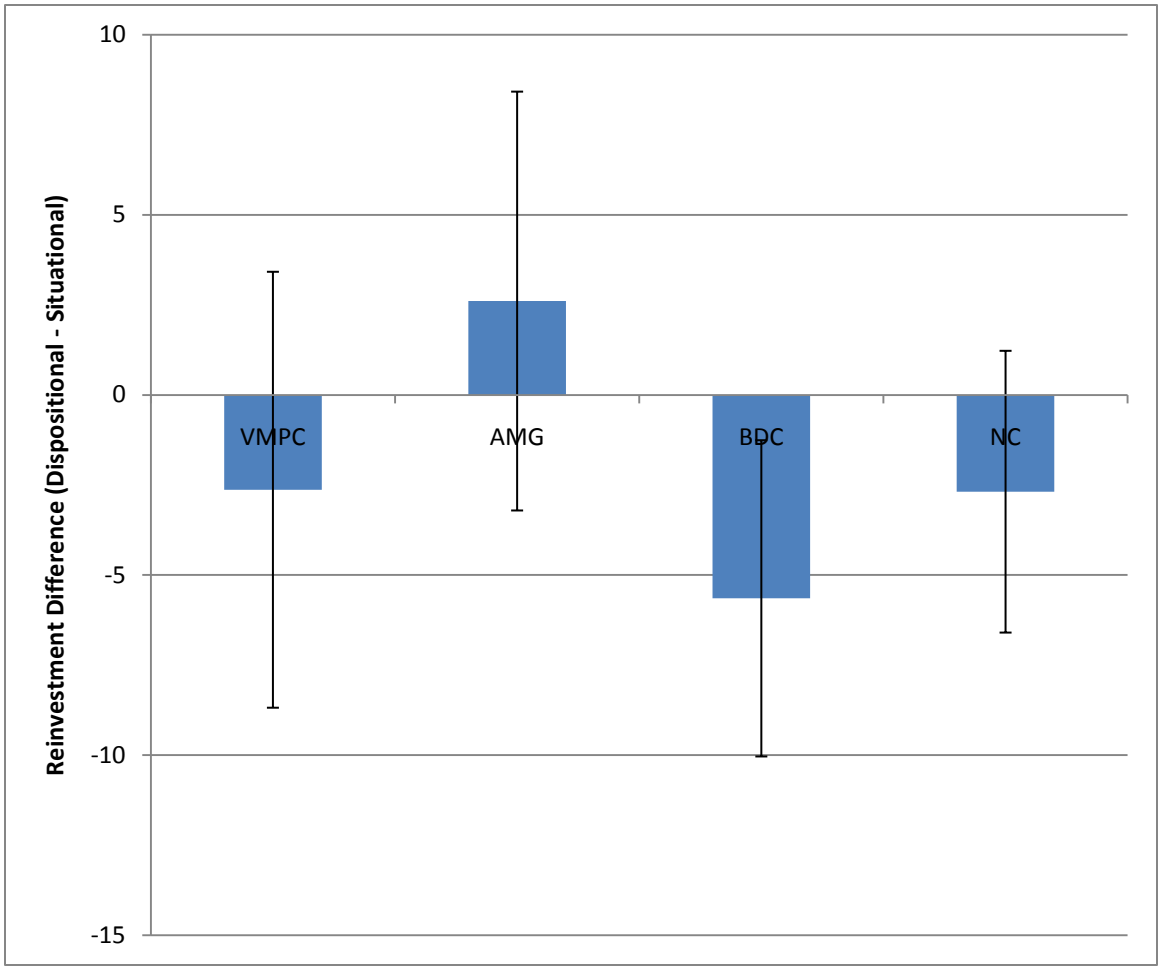

Figure 42 – Investors Game Reinvestments. Bars represent the difference between the amounts that the participants would reinvest when given dispositional compared to situational information.

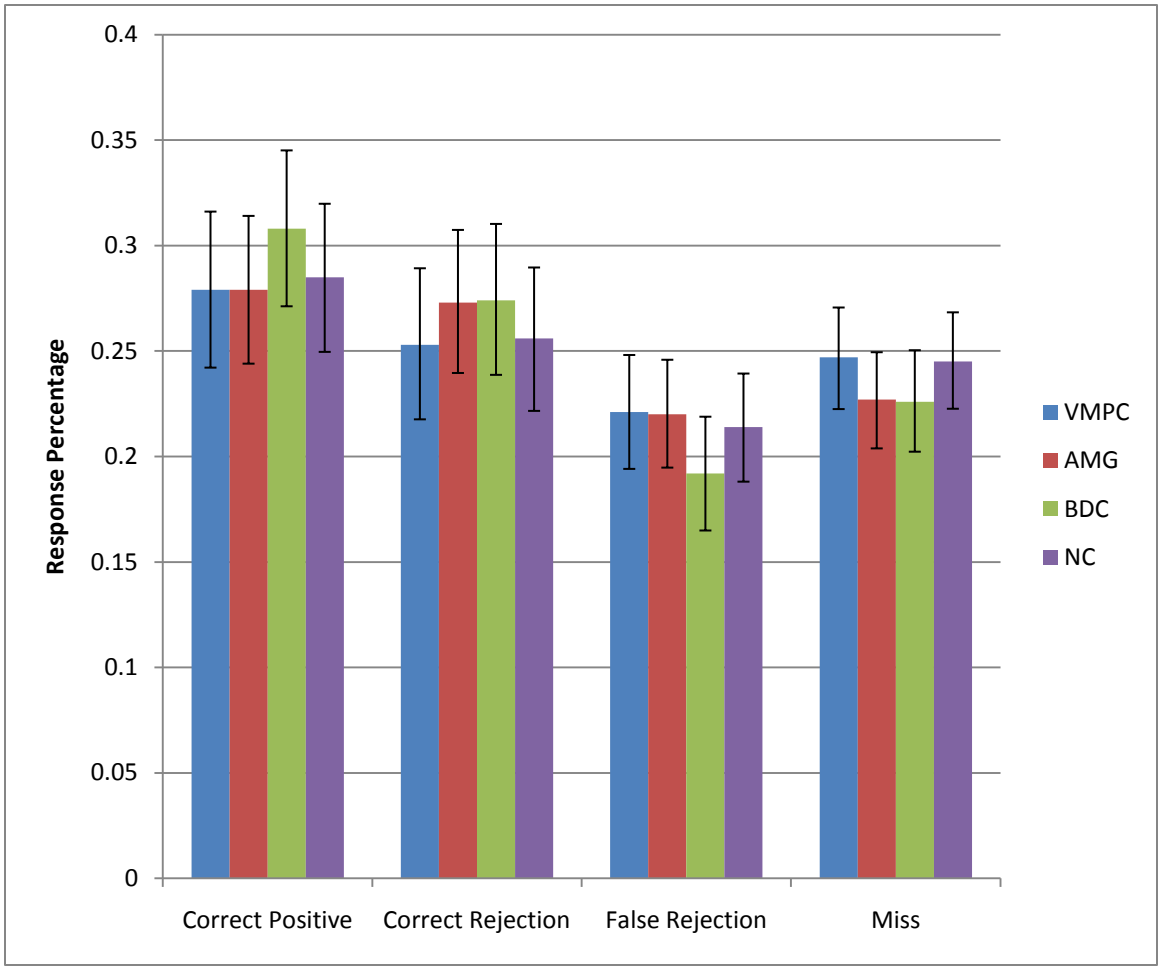

Figure 43 – Investors Game Face Memory. Bars represent responses to whether or not the faces probed were used during the investors game. Chance performance is 25%.

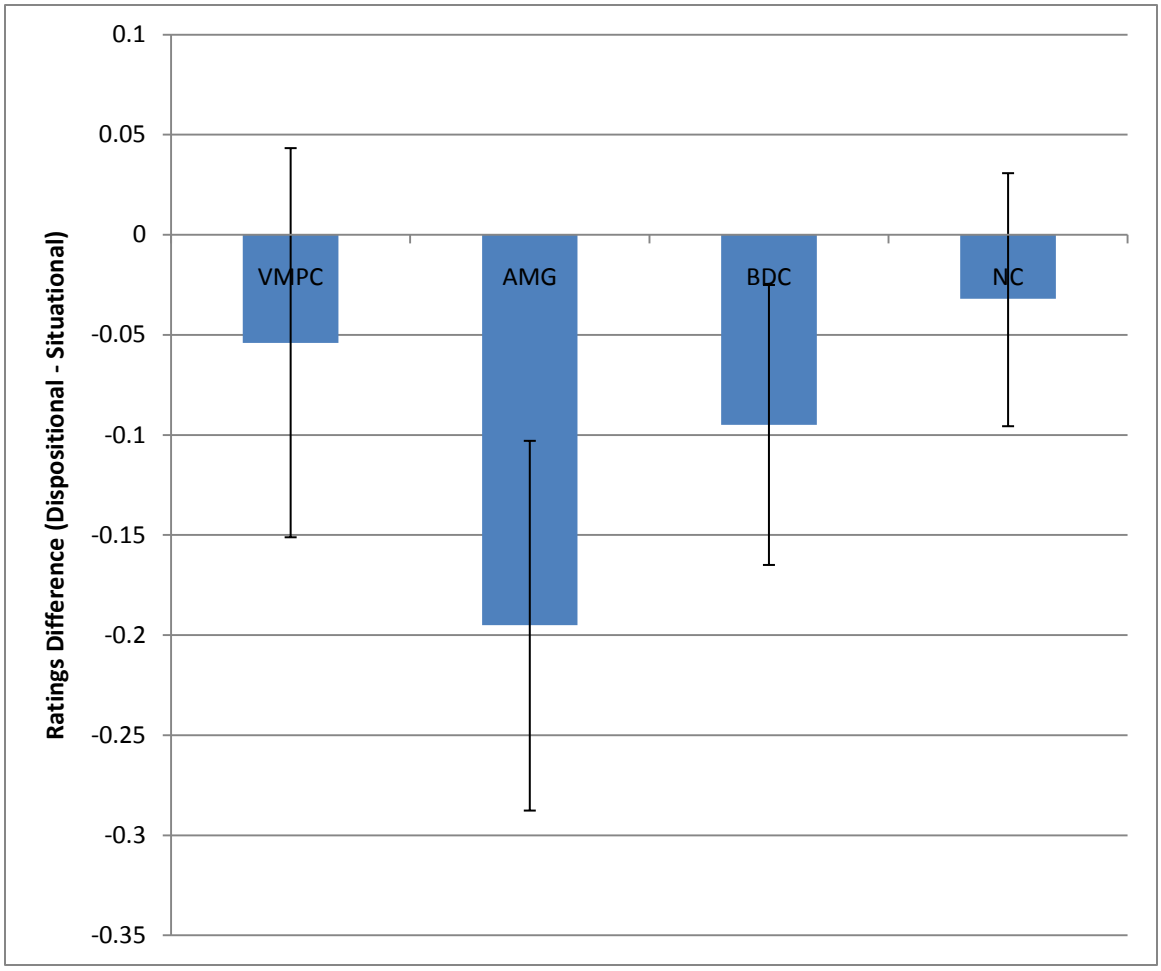

Figure 44 – Investors Game Fearfulness Ratings of Faces. Bars represent the difference between ratings of fearfulness of the faces associated with dispositional information and those associated with situational information. Amygdala subjects show a trend to rating the situational faces as more fearful than the other groups.

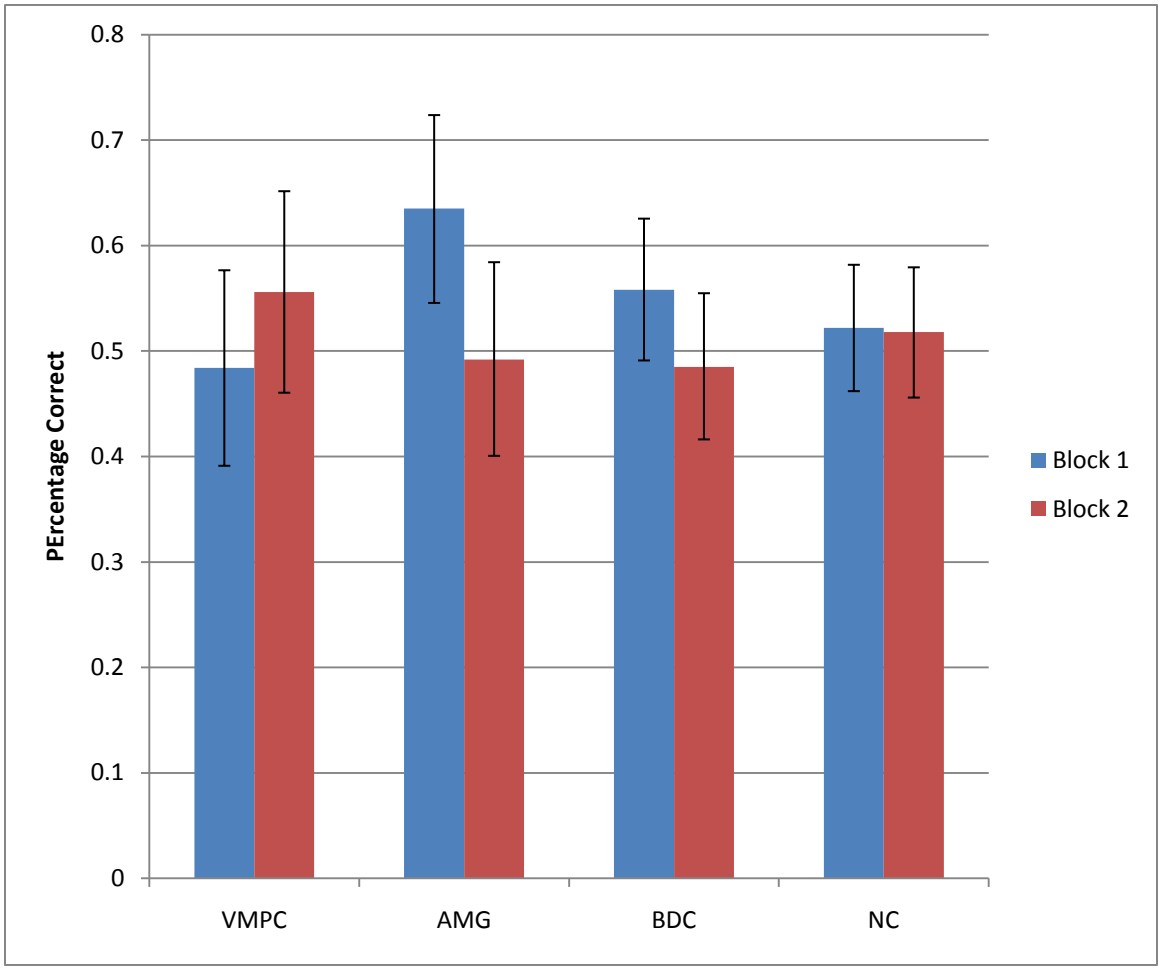

Figure 45 – Covariation Detection. Bars represent the group averages for percent correct responses. Chance performance is 50%. Subjects with amygdala damage are the only group that display significant detection of the hidden covariations on block 1. Block 1consisted of easier items, where the covariation was higher on training trials than in block 2.

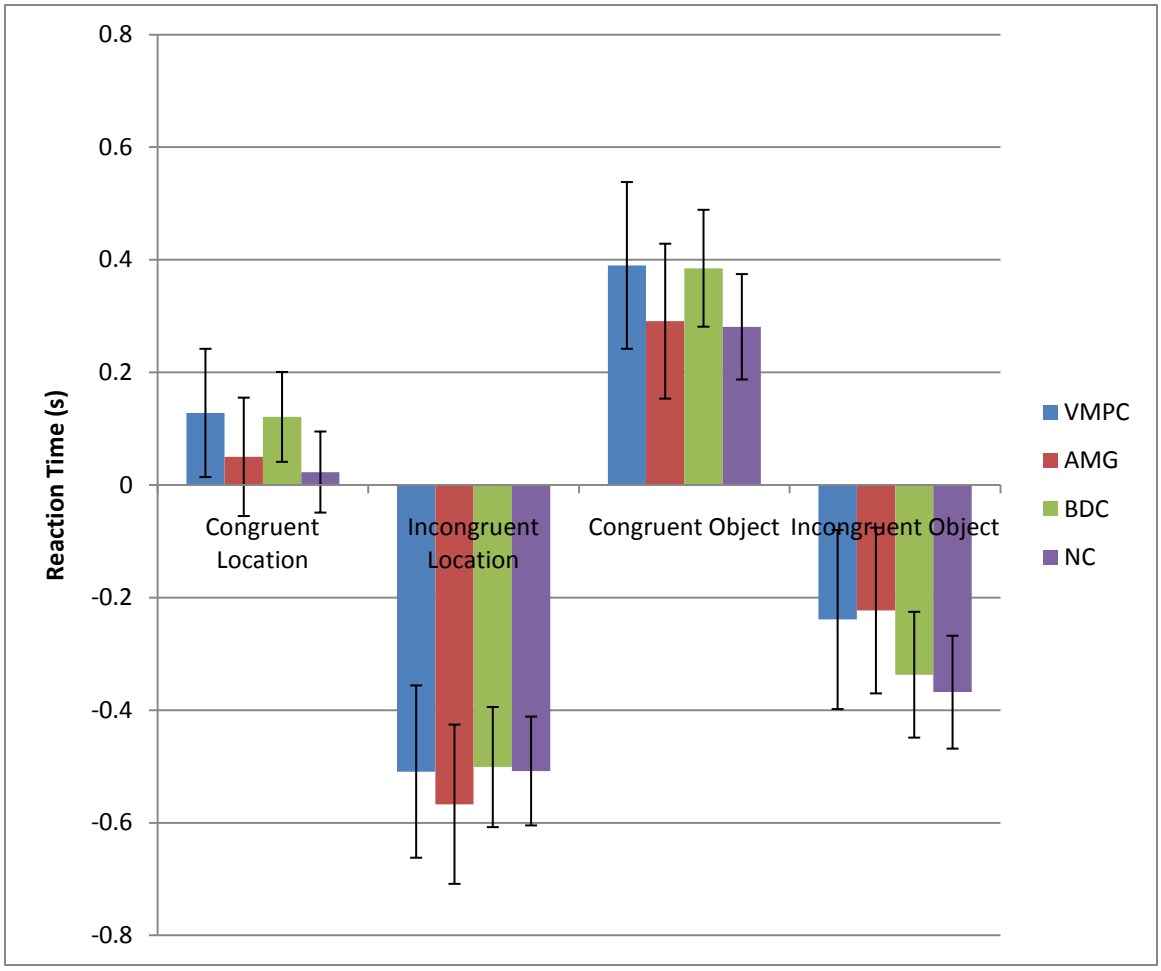

Figure 46 – Inhibition of Return. All subjects display a normal IOR effect. Items on which cues and targets are in the same location or within the same object take longer to respond to compared to items on which the cue is in an alternate position to the target which participants are relatively quicker at responding to.

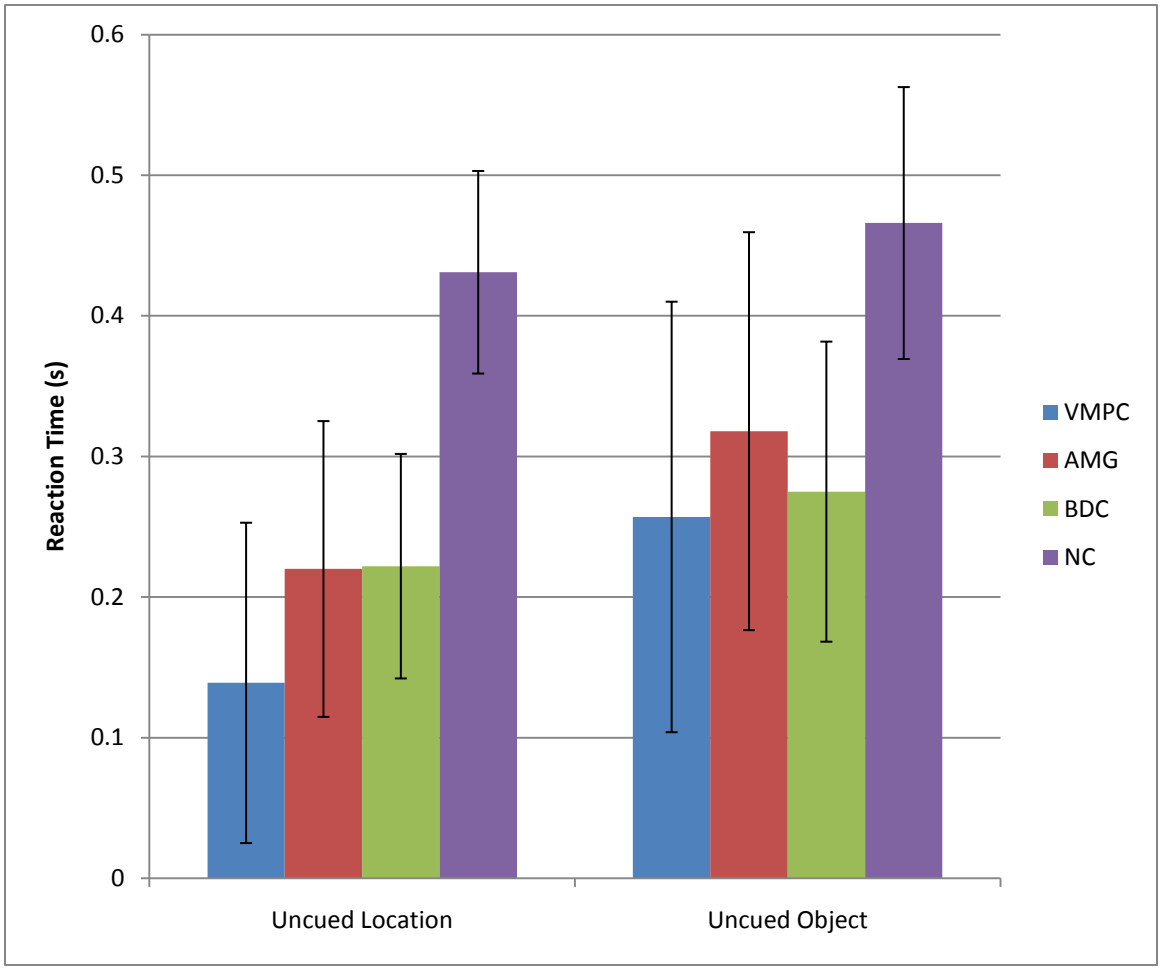

Figure 47 – IOR Task Uncued Targets. The bars represent estimated marginal means for reaction times on items on which targets were uncued. Normal, healthy adults are significantly slower than all brain damaged groups on uncued location-based targets.

CHAPTER 9

PERSPECTIVE-TAKING

Logic

The purpose of this portion of the study is to examine the effects of social group size on the ability to take the perspective of others. The current hypothesis suggests that the inferential complexity of making social judgements is an integral factor driving brain evolution. In social groups of increasing size the sheer volume of information undoubtedly increases. Despite the increased burden that this places on memory there is not a necessary concomitant increase in inferential complexity. The current hypothesis argues that increased cognitive processing demands require the neural substrates to support it and that increased inferential complexity is much more cognitively demanding than increased memory storage. The present experiment aims to test this possibility by examining the relationship between social group size, higher-order perspective-taking, and brain structure. As active agents in a social world, individuals have intentions and understand that other agents have their own thoughts and intentions. Higher-order perspective-taking refers to the fact that we not only have our own thoughts or understand that others' have their own thoughts, but we have thoughts about others' thoughts about our thoughts, and so on.

According to some reports, humans are extremely good at such complex social interactions up to a point of about 5th-order perspective-taking (involving 5 iterations of thoughts about thoughts (Lewis, 2009); however, performance drops off steeply with the addition of further social agents. The Social Brain Hypothesis (Dunbar & Shultz, 2007b) posits that large human brains (particularly prefrontal regions) developed out of necessity to deal with these higher-order relationships as group size increases. For example, grey matter volume within a small portion of VMPC was reported to relate to both clique-size (*i.e.,* number of individuals in one's immediate social group) and ability to understand

higher-order perspective (Lewis, 2009). These researchers suggested that the existence of this relationship is positive evidence supporting the Social Brain Hypothesis, *i.e.*, they argued that larger VMPC evolved to support higher-order perspective-taking, which was necessitated by increased clique size. The Social Brain Hypothesis would predict that participants with damage to the VMPC (and perhaps the amygdala, though it is not explicitly included) should show deficits in higher-order perspective-taking and a positive relationship with social group size.

The current hypothesis makes a different prediction. If human brain evolution has been driven by the inferential complexity of deriving social information rather than shear amount of information available due to more numerous sources of information, then there should be no relationship between perspective-taking ability and social group size. Inferential complexity is independent of the number of agents; each inference about a social agent is relatively equal in difficulty. In other words, inferential complexity does not increase with the number iterations of the inferential process. Alternatively, higher-order perspective-taking ability may be limited largely by memory capacity and unrelated to one's social group size.

Experimental Design

This experiment was designed to resemble and extend the protocol of Lewis (2009) and other published studies. There are several published studies examining the relationship between perspective-taking[42] and the VMPC (e.g., Shamay-Tsoory, Aharon-Peretz, & Perry, 2008; Stone, Baron-Cohen, & Knight, 1998; Stuss, Gallup Jr, & Alexander, 2001), however these studies have some limitations that need to be addressed. First, the available literature has largely found involvement of VMPC in perspective-taking tasks based on social faux pas or deception detection. Social faux pas and

42 For the purposes of the current work, perspective-taking will encompass the concept of Theory of Mind.

deception are not devoid of emotional content, *i.e.*, there is an intrinsic social evaluation. The present study aims to eliminate this confound by examining perspective-taking in a value-free context. Second, previous research has focused largely on lower-order perspective-taking, that is, first- and second-order perspective-taking. The present study aimed to extend previous findings by examining perspective-taking from lower-order to higher-order to provide a more complete and comprehensive view of complex social cognition.

Vignettes Task

In this task, participants read a series of vignettes and then answered some true or false questions about the content. The vignettes were designed to resemble, as closely as possible, common social situations (*e.g.*, dining in a restaurant, attending a party, *etc.*) each with multiple interacting agents. A subset of the vignettes were designed to be social and emotional in content (including instances of faux pas, cheating, lying, stealing, helping, caring, *etc.*). Another set was designed to resemble the emotional vignettes in terms of relational structure; however, they were designed to be devoid of any moral or other value judgement. The final set of vignettes was designed to be non-social, though similar in relational content (*e.g.*, objects and their spatial, temporal, and functional relationships). After reading each of these vignettes, participants answered a series of questions about the thoughts of the agents in the vignette, as well as thoughts about others' thoughts of others, *etc.* (*e.g.*, "I think that Jack knows that Jill likes Joe's taste in shoes"). By manipulating the number of recursions of thoughts about thoughts we can manipulate the level of perspective-taking (or relational complexity) required to answer the question.

Social Network Index

This questionnaire was designed to give a measure of a person’s social network, including an estimate of social group size (Cohen, Doyle, Skoner, Rabin, & Gwaltney,

1997). The questions probed the number of people that the person interacted with in a variety of situations ranging from family interactions to work-related interactions.

Scores from the Vignettes Task were given as a percentage of items of a certain difficulty that the participant answered correctly. Chance performance is 50% (since there are two options, true or false). Participants were given a rating determined by the highest level of perspective-taking for which they answered above chance, *e.g.*, if someone scores 100% on levels 1 through 5 but then at chance for levels 6 and above, they will be given a score of 5. This perspective-taking score was correlated to their social group size as determined by the Social Network Index. There were several ways that these data could be analyzed: potentially Fisher's r-to-z transformation could have been used to detect differences between the correlations within groups, or potentially an ANOVA could be used to examine a three-way interaction effect between social group size, perspective-taking score, and brain-damage. Typical studies published on the topic of perspective-taking within brain-damaged populations have relatively small sample sizes. For example, Stuss, Gallup, & Alexander (2001) found an effect in a sample of 4 right frontal, 8 left frontal, and 7 bilateral frontal patients. Stone and colleagues (1998) report significant effects in a sample of 5 orbitofrontal and 5 dorsolateral frontal cases.

Predicted Results

As mentioned above the Social Brain Hypothesis and the current hypothesis make different predictions about the relationship of perspective-taking score and social network index. If there is a significant relationship between perspective-taking score and social group size then the Social Brain Hypothesis is supported, however if there is no significant relationship then the current hypothesis is supported. Also, instead of observing stable performance up to 5^{th} order perspective-taking after which performance drops to chance, as in the Social Brain Hypothesis, the current hypothesis predicts that performance will drop of gradually as a function of memory capacity.

Typical studies published on this topic within brain-damaged populations have relatively small sample sizes. For example, Stuss, et al. (2001) found a significant effect in 4 right frontal, 8 left frontal, and 7 bilateral frontal patients. Stone, et al. (1998) report significant effects in a sample of 5 orbitofrontal and 5 dorsolateral prefrontal cases. I am confident that our much larger sample size will be sufficient to test the main hypotheses.

Results

Several statistical tests were used to assess potential group differences in perspective-taking ability as measured by the vignettes task as well as any association between perspective-taking ability and social network size as predicted by the Social Brain Hypothesis.

Vignettes Task

First, A MANCOVA with group as a fixed factor and age and education as covariates was used to probe for group differences in perspective-taking ability across all levels of difficulty. There were no significant differences between groups in the overall model ($F=1.013$, $p=0.445$) or age ($F=1.515$, $p=0.181$) or education ($F=0.899$, $p=0.499$). There was a hint of a group difference for 6th order perspective-taking ($F=2.939$, $p=0.037$), where amygdala subjects may have scored significantly worse than NCs (mean difference = -0.156, $p=0.013$). To assess potential effects of sex, sex was added as a fixed factor in the MANCOVA, however, there were no significant effects of group ($F=0.996$, $p=0.464$), sex ($F=0.857$, $p=0.530$), or a group by sex interaction ($F=0.813$, $p=0.684$). In this model, the potential group difference on 6th order perspective-taking was slightly weakened ($F=2.581$, $p=0.058$), though participants with amygdala damage displayed decreased performance compared to NCs (mean difference = -0.149, $p=0.024$). Women may have also potentially tended to score higher than men on relatively easy items of 2nd order perspective-taking (mean difference = -0.076, $p=0.028$). To examine the effect of brain damage side, side was added as fixed factor in the original

MANCOVA. There remained no significant effect of group (F=0.759, p=0.690) and there is no significant effect of brain damage side (F=0.699, p=0.749). There was a possible weak trend toward a significant group by side interaction (F=1.403, p=0.111). This group by side interaction was potentially driven by a difference in performance on 5^{th} order perspective-taking (F=2.679, P=0.041), potentially due to poorer performance among those with left or bilateral amygdala damage (see Figure 48).

Second, between group differences were assessed for the content questions, which approximate the levels of difficulty of the perspective-taking items. However, given the 'non-reflexive' nature of these verbs, the items in which sentence complexity approximates 6^{th} and 7^{th} order perspective taking became easily falsifiable through identifying the single erroneous clause. As expected there were no group differences revealed by MANCOVA with age and education as covariates (F=0.799, p=0.702). There were significant effects of age (F=2.257, p=0.044) and education (F=2.560, p=0.024) in this model. Interestingly, there was a hint of a group difference where participants with amygdala damage show poorer performance on 6th order content questions compared to NCs (mean difference = -0.139, p=0.004), exactly the same pattern found for 6th order perspective-taking items. This seems to suggest that it is not any lack of ability to take the perspective of others that is potentially affected in participants with amygdala damage; rather, this potential deficit is more likely related to a subtle deficit in linguistic comprehension.

When including sex in the model, I again observed a trend toward a possible effect of sex (F=1.989, p=0.075), where women outperform men on 3^{rd} order content items (mean difference = -0.097, p=0.021) and a trend for 6^{th} order content items (mean difference = -0.060, p=0.077). With side as a fixed factor in the model, there was no main effect of side (F=0.960, p=0.492) though there was a trend to a significant group by side interaction (F=1.482, p=0.079), again driven by left and bilateral cases of amygdala damage (see Figure 49).

Third, the maximum level of correct (above chance) performance on both perspective-taking and content items was calculated for each subject. Group differences in maximum levels were assessed via MANCOVA with age and education as covariates. No group differences were observed ($F=1.287$, $p=0.265$). Next to assess the difference between maximum perspective-taking level and maximum content level, a difference score was calculate by subtracting maximum content level from maximum perspective-taking level. An ANCOVA with group as a fixed factor and age and education as covariates revealed no significant differences between groups ($F=1.595$, $p=0.195$). Pairwise comparisons however hinted at a potential difference between participants with VMPC damage and NCs where the difference between perspective-taking level and content level were greater for NCs than VMPCs (mean difference = -1.590, $p=0.034$). Similarly, a very weak trend was observed comparing VMPCs and BDCs (mean difference = -1.273, $p=0.103$). Sex effects were then included in this model, though there was no effect of group ($F=1.987$, $p=0.121$), sex ($F=0.070$, $p=0.791$), or side by group interaction ($F=0.960$, $p=0.415$). Pairwise comparisons hinted at a strengthened difference between participants with VMPC damage and BDCs (mean difference = -1.399, $p=0.078$) and NCs ($F=-1.752$, $p=0.022$). When side was included as a fixed factor in the analysis, there was no effect of side ($F=1.246$, $p=0.302$) or group by side interaction ($F=0.737$, $p=0.483$). There was however a weak trend for an effect of group when side of brain damage was included in the model ($F=2.479$, $p=0.093$). Again participants with VMPC damage displayed a trend of decreased difference between perspective-taking performance and content item performance compared to those with amygdala damage (mean difference = -2.267, $p=0.059$) and BDCs (mean difference = -1.555, $p=0.071$) (see Figure 50).

Social Network Index

Group differences in social network were assessed again using an ANCOVA with age and education as covariates. A trend toward a significant effect of group was observed on the size of one's social network ($F=2.182$, $p=0.095$). Instead of the VMPCs having a smaller social network size as predicted by the Social Brain Hypothesis, it was brain damaged comparison participants that report significantly smaller social networks compared to participants with VMPC damage (mean difference = -5.363, $p=0.045$) and amygdala damage (mean difference = -5.607, $p=0.038$) (see Figure 51). There was no significant effect of sex, when this variable was included in the model ($F=2.379$, $p=0.126$), nor was there an effect of brain damage side when this was included in the model ($F=0.543$, $p=0.584$).

Next, age and education were not correlated with the maximum level of perspective-taking, maximum content level, or the difference between these variables in the overall sample (minimum $p=0.099$ between education and maximum content level). Given this lack of correlation between age and education, these variables were not included in examinations of correlations between social network size and perspective taking measures within groups. There were no significant correlations between social network size and perspective-taking ability ($r=0.061$, $p=0.524$), performance on the content questions ($r=0.143$, $p=0.136$) (see Figure 52), or the difference between performance on perspective-taking and content items ($r=-0.120$, $p=0.213$) (see Figure 53). Likewise, there were no significant correlations in any of the groups.

Discussion

As predicted by the current hypothesis and contrary to the claims made by proponents of the Social Brain Hypothesis, all participants displayed similar perspective-taking ability, and there was no observed relationship with perspective taking ability and social network size. It did not seem as though increased group size was related to

increased cognitive difficult and thus larger brains may not be required to support larger human social groups.

It is possible that the current study was insufficiently powered to find the differences predicted by the proponents of the Social Brain Hypothesis. However, if the effect was indeed too small to be detected in our sample, this may indicate that such a weak effect may be unlikely to be a significant driving force in evolution given that it was not very strong in driving behaviour. Using procedures presumably similar to the Dunbar group for estimating the maximum level of perspective-taking attained, I do estimate a similar level of 5th order perspective taking as the maximum across all participant groups (see Figure 50). However estimating the maximum level conceals the observation that ability decreases progressively with increasing difficulty. There was not a precipitous decrease beyond 5th-order perspective-taking, nor is 5th order perspective-taking performed at a level similar to lower orders (see Figure 48).

There was a potential hint at poorer performance of smaller social networks in the BDC group compared to the other groups, which may provide a neural substrate to the social cognitive processes associated with larger groups. However it is very likely that the BDC group carries the burden of other deficits that may interfere with forming as large social groups, including effects on mobility given that many subjects have brain damage to somatosensory and motor regions of the brain, which may place realistic limits on social contact. Also there is the potential for language related deficits in this group given the proximity of some of these lesions to Broca's and Wernicke's areas, and deficits in language may interfere with real-world social functioning independent of actual social cognition. However, given that all groups had comparable scores on VIQ, language based deficits may not be an important factor.

There were some hints that participants with amygdala damage had poorer performance on perspective-taking items compared to other groups for 6th order items. However, these same participants displayed a difference for content items of 6th order as

well. Perhaps these participants display a subtle language deficit particularly in interpreting complex sentence structures.

A potential confound of this study, is that the Social Network Index relies on self reports of social network size. Perhaps certain participants lack the insight necessary to properly evaluate size of their own social networks. Potentially including evaluations by collaterals would yield more accurate, or at least different, estimates of an individual's social network size. This index was chosen in part due to its focus on more specific aspects of social network size, *i.e.*, focusing on different relationships and settings in which they occur, which may potentially minimize biases in estimating group size. In addition, perhaps participant's threshold for considering some one as close or not may differ. If this threshold differs systematically across groups a bias could be introduced into social network size estimates.

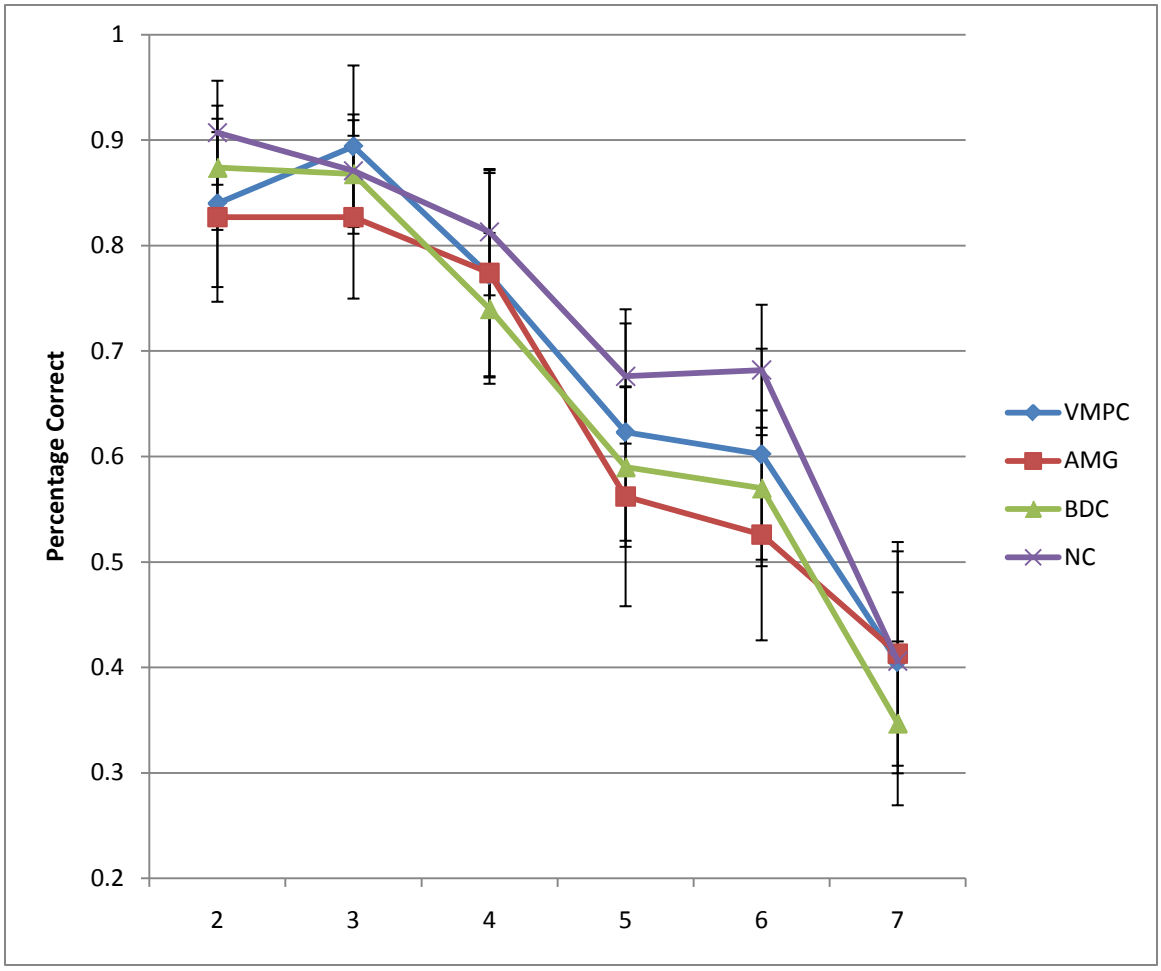

Figure 48 – Vignettes Task Perspective Taking Questions. Values on the horizontal axis represent the level of perspective-taking. Lines represent the % correct for each group. Note that performance drops consistently as difficulty increases. Error bars represent 95 % confidence intervals.

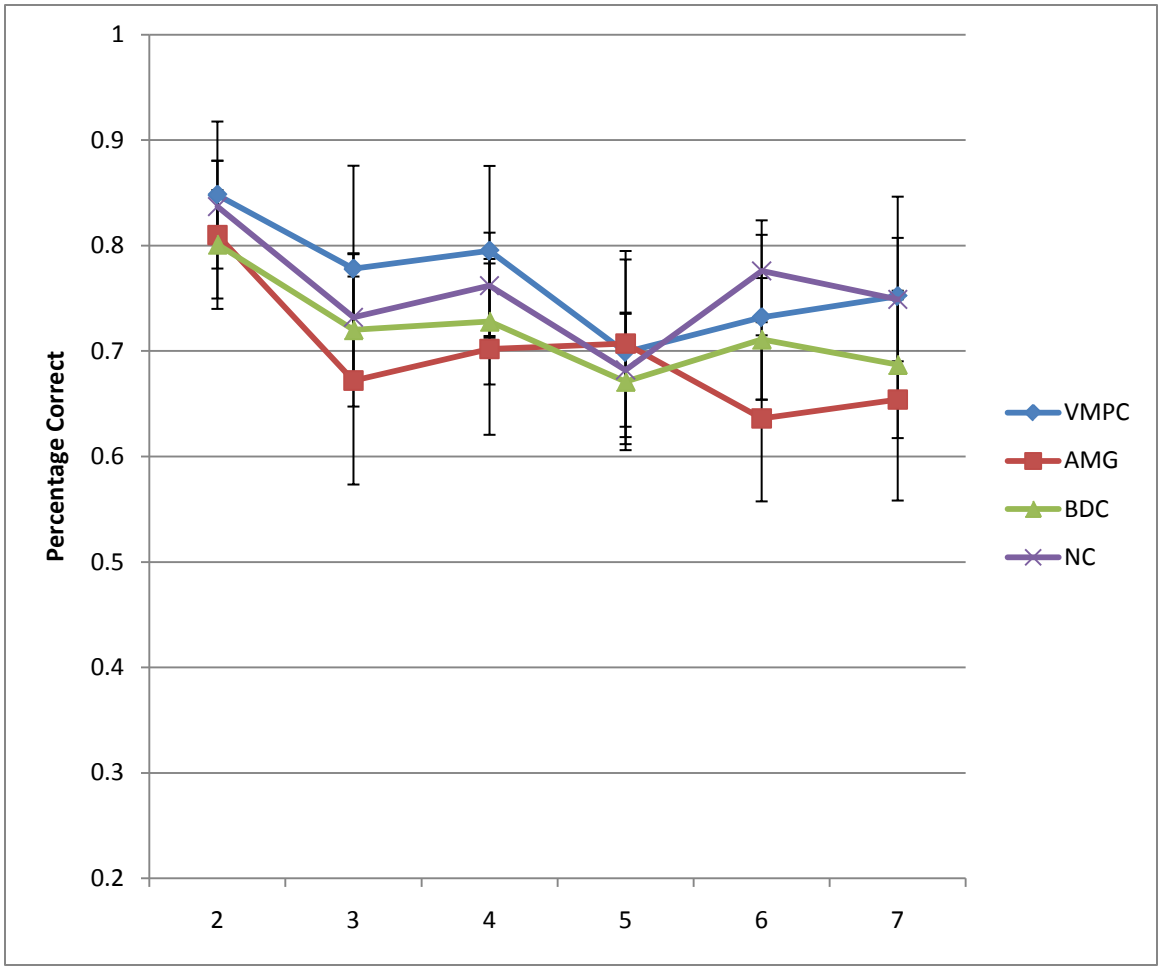

Figure 49 – Vignettes Task Content Questions. Values on the horizontal axis represent the level of perspective-taking. Lines represent the % correct for each group. Error bars represent 95 % confidence intervals.

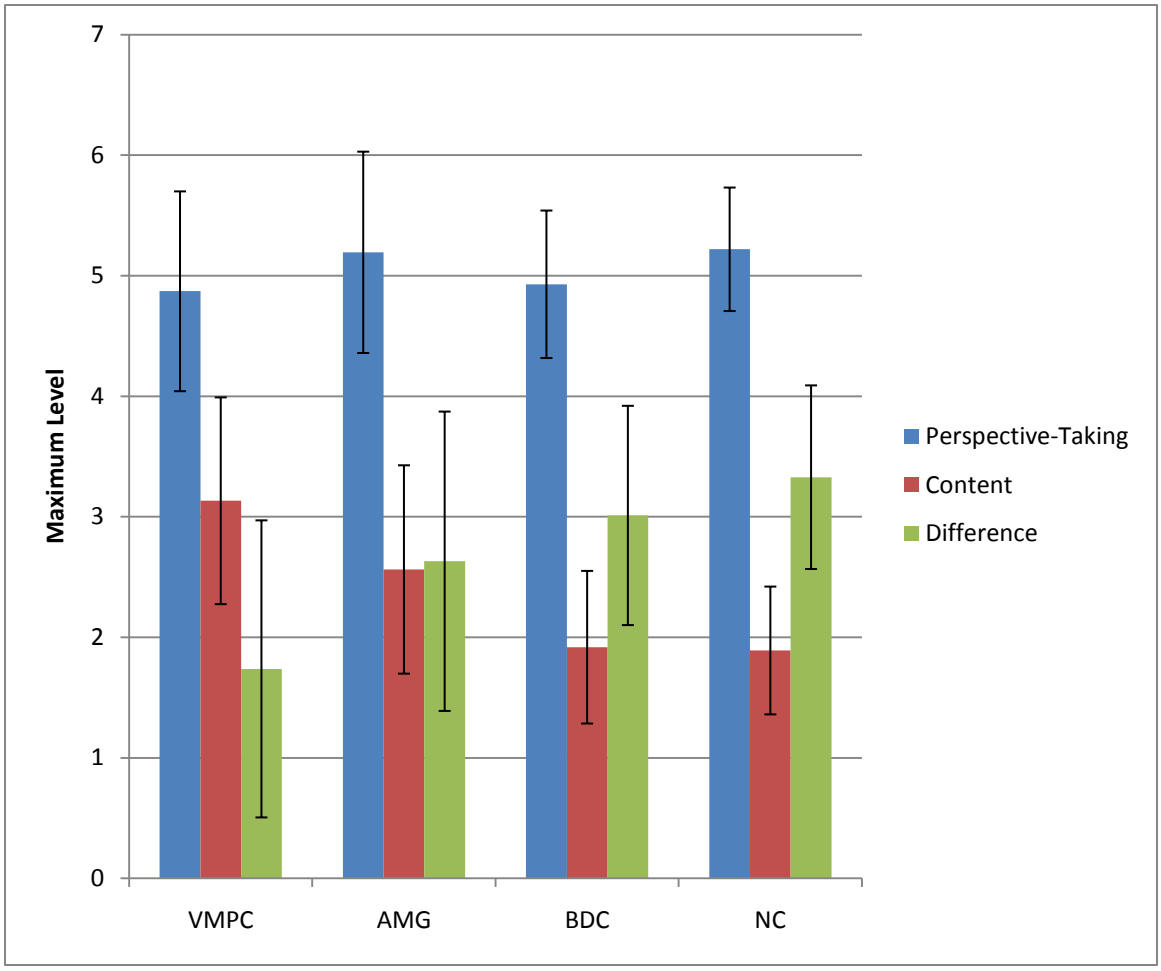

Figure 50 – Vignettes Task Maximum Level Attained. Bars represent the estimated marginal means for maximum difficulty of items that participants perform above chance. The difference bars represent the difference in difficulty between perspective-taking items and content items. None of the groups displayed significant differences. Error bars represent 95 % confidence intervals.

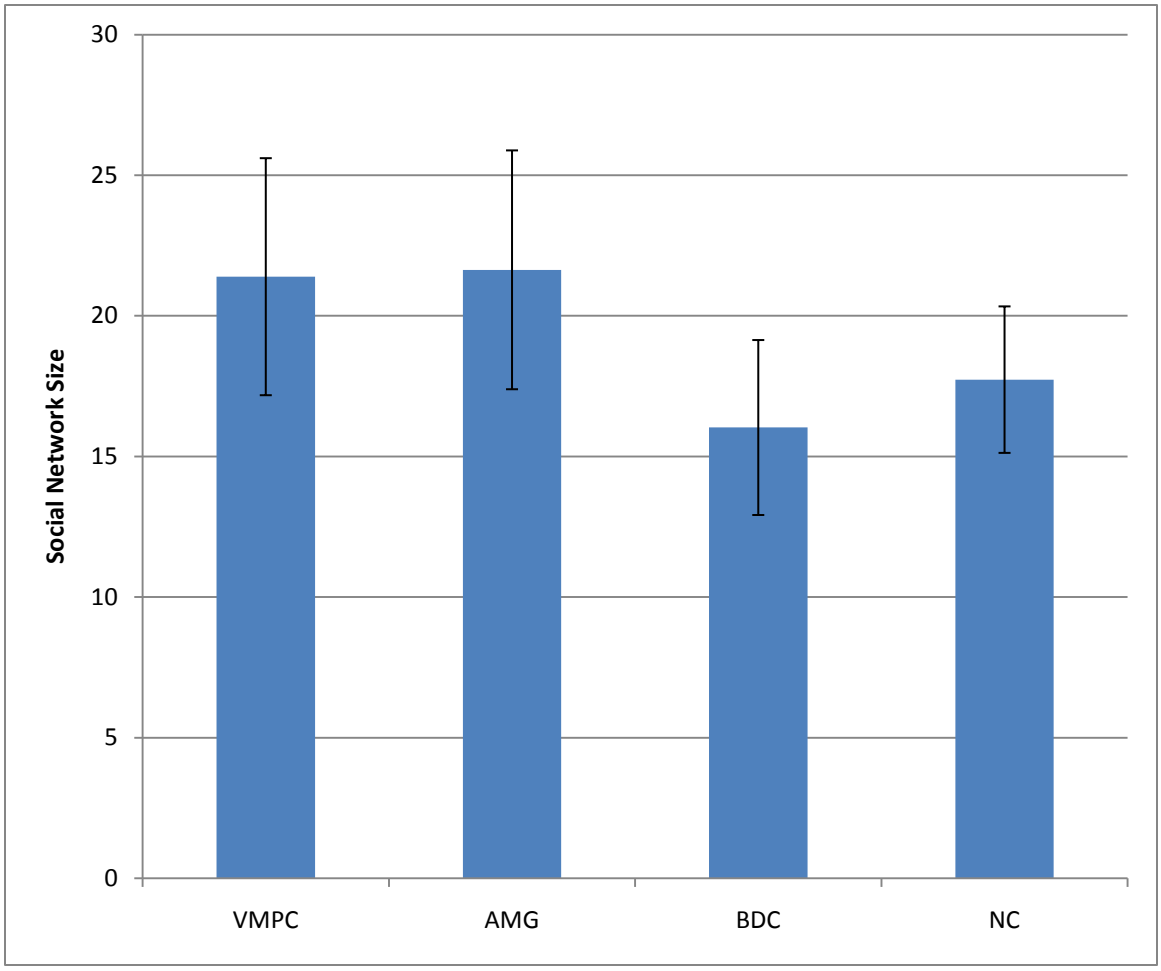

Figure 51 – Social Network Index. Bars represent the estimated marginal means for the reported size of participant's social groups. BDCs report significantly smaller group size than participants with damage to VMPC and AMG. Error bars represent 95 % confidence intervals.

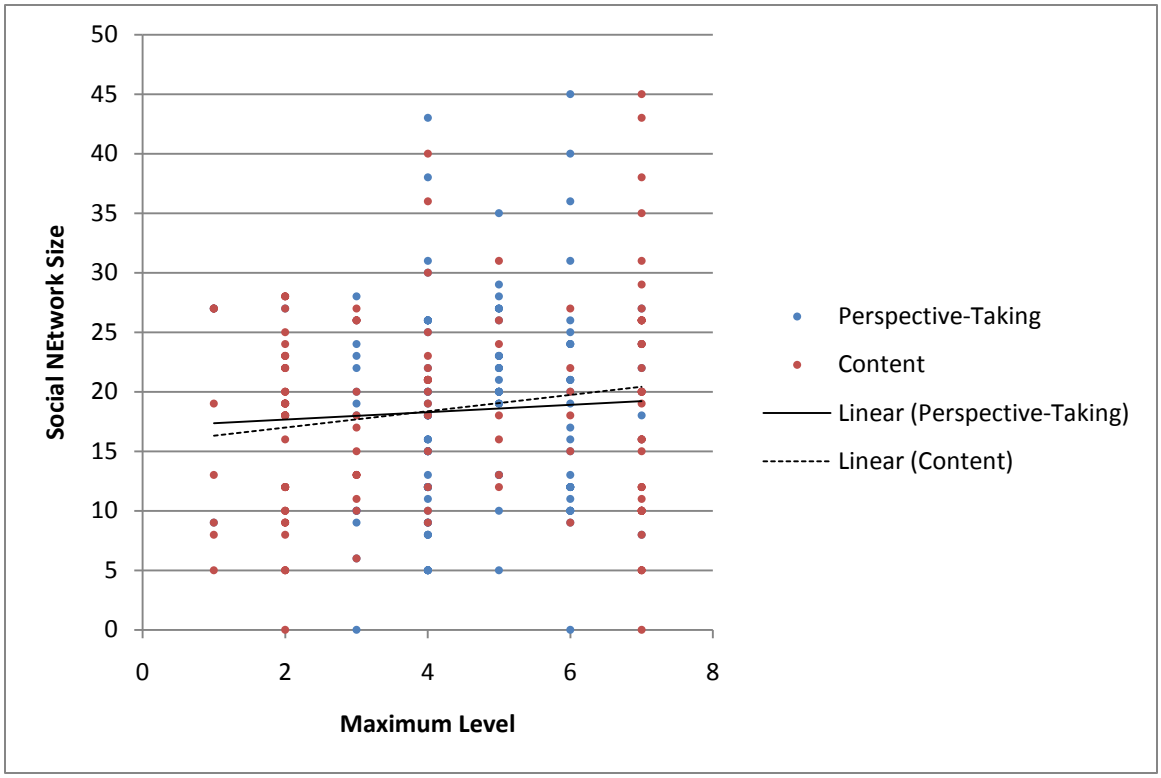

Figure 52 – Vignettes Task Performance vs. Social Network Size. This scatterplot depicts the potential relationship between performance on the vignettes task for both perspective-taking and content items and the participant's social network size.

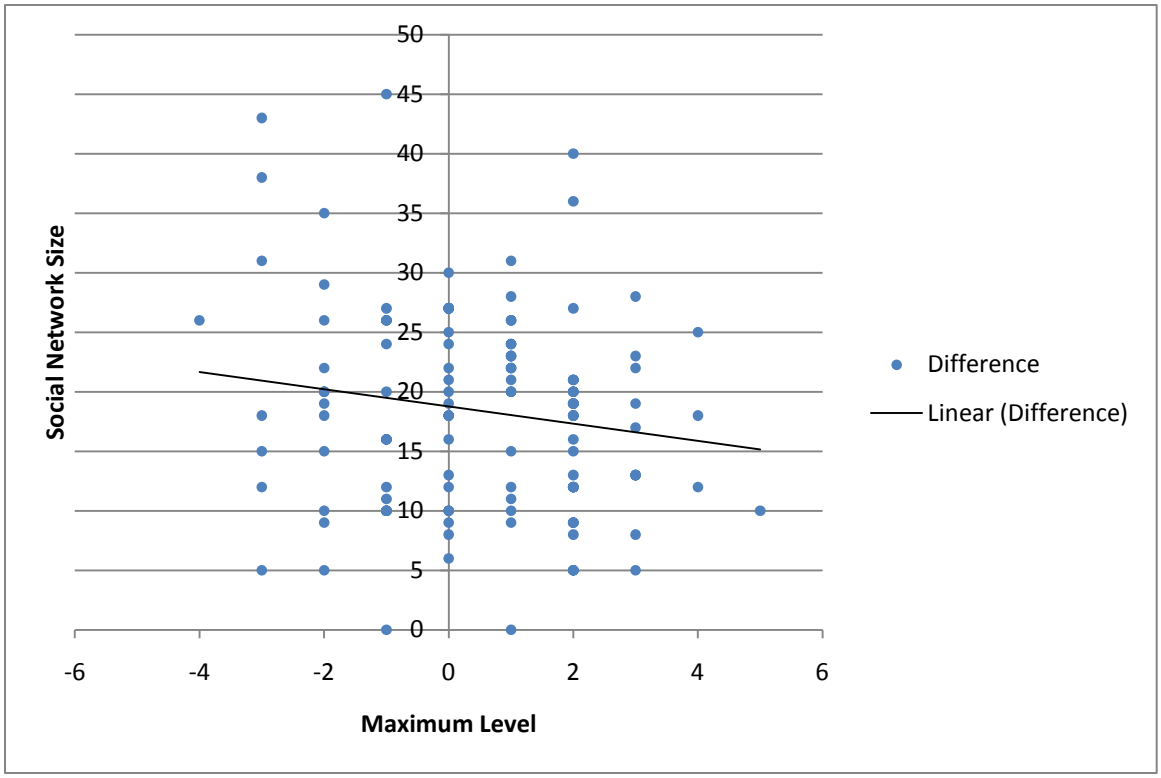

Figure 53 – Difference between perspective-taking ability and content performance and social network size for all participants.

CHAPTER 10

SOCIAL HIERARCHY

Logic

Another important aspect of adaptive behaviour in a social group is to understand social hierarchy positions. In human groups, there are multiple, interacting and interwoven hierarchies, for example the hierarchy found in the office may differ from and interact with a social hierarchy outside of work. Importantly, social hierarchies need to be inferred from experience. Previous research has suggested that participants with damage to the VMPC may be normal in determining dominance hierarchies from observing others (Karafin, Tranel, & Adolphs, 2004). However, the tasks employed with these patients were largely off-line and did not directly manipulate inference. The question remains open as to whether or not the target patients have a difficulty when they are actively engaged in the social hierarchy themselves.

Though examining the cognitions behind inferring social hierarchies is an interesting question on its own, this experiment will help to elucidate the cognitive processes behind many social decisions and processes. In order to determine social hierarchies, a person must be able to utilize 'transitive inference.' Since it is not always feasible, practical, or advisable to interact with every person in such a way as to know your place in the social group, people must infer where they fit in from the relations between others. The basic premise of transitive inference is that if A > B, and B > C, then it follows that A > C. The ability to do this type of reasoning is very common in the animal kingdom, given that fish can infer their social rank through observation alone (Grosenick, Clement, & Fernald, 2007). Given that transitive inference is necessary for many instances of social cognition, this experiment is designed to control for the possibility that the fundamental problem after damage to social areas of the brain, including the target regions, might interrupt ones' ability to use transitive inference in the

social domain. Furthermore, since the current hypothesis predicts that human cognitive performance has largely be driven by the complexity of inferential problems, then inferring information transitively may be a key pillar underlying much of social cognition, and participants with damage to the VMPC or amygdala will exhibit a performance deficit.

Experimental Design

This experiment was designed to test two ideas: whether or not participants with focal VMPC or amygdala damage have difficulty transitively inferring their place in a social hierarchy in which they are active participants, and whether or not any difficulty in transitive inference occurs outside of the arena of social processing.

Nim Tournament

Participants competed in a tournament of Nim (explained below). There were seven competitors, including the participant and six simulated players. Each player played against two others. Players 2 through 6 all won one game and lost another, player 1 won twice, and player 7 lost twice. Player numbers refer to their position in the tournament hierarchy. Player 2 will beat player 3, but lose to player 1; player 3 will defeat player 4, player 4 will defeat player 5, and so on. Players 1 and 7 were not included in the options from which the participants constructed their hierarchy. The participants, who were always player 4, competed against player 5 and won, and against player 3 and lost. Participants observed the rest of the tournament, such that a hierarchy can be constructed where player 1 > 2 > 3 > 4 > 5 > 6 > 7.

The reason to use the game, Nim, was because it is complex enough so that the participants could not infer the winning strategy easily (and even if they do it is too computationally complex to utilize),[43] wins can be virtually guaranteed, losses can also

43 Computing a winning strategy involves converting the number of items in each pile to its binary representation then calculating a bitwise-exclusive or function for these representations.

be guaranteed, it appears as if skill is involved, and it takes only about a minute or two to play a game. Furthermore, Nim has very simple rules. There are 'n' piles of 'x' objects. Players take turns removing items from one of the piles, until there are no items left. Players can take as many objects (from 1 to x_n) from only one pile each turn. The object of the game is to be the player who takes the last object(s) from play.

As described above, participants played two rounds of Nim with three piles of objects and observed the other players play two rounds each. Following this, the players were asked which player (of players 2 – 6) was best and which was worst. Finally, participants were asked to rank the players, including themselves, from best to worst. For each of these decisions, players could select from players 2, 3, 4, 5, and 6. Players 1 and 7 were removed from the selection as they did not have equal numbers of wins and losses as the other players, and thus transitive inference would not be required to select from these players.

Patterns Task

In this task, participants viewed black and white patterns and were to press a button in response to what they saw (similar to the protocol in: Acuna, Eliassen, Donoghue, & Sanes, 2002). They were presented with two objects at a time, otherwise they were asked to maintain fixation on a centrally located cross. Participants had two response buttons, one that corresponded to the image on the left of fixation and the other that corresponded to the image to the right of fixation. On each trial participants were presented with two objects and asked to choose the 'correct' one. The participants were required to infer which response is correct, from the feedback given. Testing consisted of two training blocks, and two test blocks. Correct responses were determined such that a linear hierarchy of 'correctness' of the 7 objects can be inferred. In the test block, novel combinations of objects were presented, in addition to memory trials which were identical to items in practice trials. See figure 54 for a depiction of item types.

Figure 54 – Patterns Task Item Type Schematic

Predicted Results

The current hypothesis predicts that participants with VMPC or amygdala damage will have difficulty utilizing transitive inference. It may be that target participants have a specific difficulty inferring social relationships, and would make sub-optimal decisions in the Nim tournament. However, if deficits in utilizing transitive inference are specific to social phenomena, there will be no deficit in the non-social task. Alternatively, it is possible that the target patients will have difficulty utilizing transitive inference at all and would thus show deficits on both the Nim tournament as well as the non-social task. In addition, the current hypothesis predicts that deficits in transitive inference should increase as inferential difficulty increases.

Previous research has used relatively small sample sizes to test transitive inferences, *e.g.*, in Acuna, *et al.*, (2002), 25 normal subjects were given the transitive inference task. I have simplified the task (7 objects from 11 objects in the previous study) and this proposed study has a similar sample size. Thus, I predict that this study will have enough power to test our hypotheses given these similar results. For the NIM tournament, given that there is an optimal response, any deviation from this response will be obvious; however it is difficult to perform a power analysis without a similar study to on which to base it.

Results

Nim Tournament

To analyze performance in the Nim Tournament task, a MANCOVA was used with age and education as covariates, brain damage group as a fixed factor. The dependent variables in this analysis were extracted from the participant's rankings of the players in the tournament. Since all players available for ranking have the same win-loss

record (1 win, and 1 loss), inferring the correct ranking requires the use of transitive inference. Thus the accuracy of the ranking given by the participants was taken as a proxy measure for the use of transitive inference to infer a social hierarchy and was given by a score calculated by finding the difference between the ranking given and the correct ranking determined by the tournament results. This yielded a 'ranking' score between 0 and 12, which was then converted to a percentage for easier interpretation. Group differences in the ranking score were analyzed via an ANCOVA with age and education as covariates. There was a significant effect of group in this model (F=3.481, p-0.019). Pairwise comparisons revealed that participants with VMPC damage actually were more accurate than the other groups in inferring the correct rankings compared to participants with amygdala damage (mean difference = -0.232, p=0.004), brain damaged comparisons (mean difference = -0.194, p=0.009) and normal healthy adults (mean difference = -0.124, p=0.063). Subjects with amygdala damage may have shown a very weak trend to performing worse than NCs (mean difference = 0.109, p=0.112) (see Figure 53). When sex was included in the model, I observed no significant differences of sex (F=0.526, p=0.470) or a group by sex interaction (F=0.383, p=0.765). Likewise, I found no significant effect of side (F=1.824, p=0.172) when this variable was included in the model nor a group by side interaction (F=1.246, p=0.304), the main effect of group however was noticeable stronger (F=5.707, p=0.006).

The observation that VMPC subjects actually outperform the other groups is counter-intuitive. However, the performance level of the VMPC group was not significantly different from chance (50%) where the other groups perform significantly worse than chance, consistently.

Patterns Task

The patterns task was analyzed by calculating three separate scores based on performance during the test blocks of the task. First, a 'learned' score represents the

percentage of items that had been encountered during the training session that were answered correctly (items 1vs2, 2vs3, 3vs4, 4vs5, 5vs6, and 6vs7). Second, a transitive inference score was calculated as the percentage of items that were answered correctly that are not previously learned and involve a transitive relationship to the learned stimuli (items 2vs4, 2vs5, 2vs6, 3vs4, 3vs5, 3vs6, 4vs5, 4vs6, and 5vs6). Third, non-transitive score was calculated by the percentage of items answered correctly that exclude previously learned items but include items that were either always correct or always incorrect, thus not requiring transitive inference (items 1vs3, 1vs4, 1vs5, 1vs6, 1vs7, 2vs7, 3vs7, 4vs7, and 5vs7). These variables, learned, transitive and non-transitive scores, were entered as dependent variables in a MANCOVA with age and education as covariates to examine group differences. There was no overall effect of group in the model ($F=1.069$, $p=0.387$), however this was expected as none of the groups were expected to differ for non-transitive or learned items. This was confirmed by no effect of group on learned ($F=0.898$, $p=0.445$) or non-transitive items ($F=0.528$, $p=0.664$), but a trend toward a significant effect on transitive items ($F=2.439$, $p=0.077$) (see Figure 56). Participants with VMPC damage perform the worst on transitive items, significantly worse than NCs (mean difference = -0.163, $p=0.010$), but perhaps very weak trends of worse performance compared to BDCs (mean difference = -0.102, $p=0.130$) and AMG subjects (mean difference = -0.099, $p=0.184$). There were no main effects of sex ($F=0.153$, $p=0.928$) or group by sex interactions ($F=0.354$, $p=0.955$) when sex was included in the model. Similarly there were no effects of brain damage side ($F=1.079$, $p=0.934$) or interactions of side and group ($F=0.882$, $p=0.567$).

Discussion

Consistent with the predictions made by the current hypothesis, participants with VMPC damage display a selective deficit on items that require transitive inference on the Patterns Task. It is important to note that this deficit was selective; they were able to

learn the training items as well as the other groups and were able to answer the non-transitive items as well as the other groups as well. Previous research has posited a role of dorsolateral and parietal cortices for transitive inference (Acuna, et al., 2002). The current research presents the possibility that the networks identified using fMRI may indeed not be necessary for transitive inference instead the critical neural machinery may be within VMPC. However, in order to make this conclusion with any certainty improved neuroanatomical analysis is absolutely required, moreover, the sample tested here may not adequately represent the dorsolateral prefrontal and parietal regions identified in the fMRI study of transitive inference. Likewise this data is equivocal as to the role of the hippocampus, as cases of focal damage to this structure (that excluded the amygdala) were excluded from the sample in this study.

This clear result on the Patterns Task is seemingly contradicted by the results of the Nim Tournament. Participants with VMPC damage are significantly more accurate in inferring the social hierarchy within this tournament setting, where as there may be hint of amygdala subjects actually doing worse than normal healthy adults. A possible explanation of the results may be that comparison subjects may rank the players that beat them as better than they should have due to some sort of self-affirmation bias. This interpretation is supported by the observation that VMPC participants perform no different than chance at inferring the rankings in the Nim Tournament, where all other groups do significantly worse than chance. Suggesting that the VMPC subjects cannot use transitive inference to infer rankings after all given their chance performance, however, for some reason they are not susceptible to the same bias as comparison groups in doing worse than chance. More study is needed to see if participants with VMPC damage may differ from comparison subjects on other potential social biases. Perhaps a lack of using transitive inference actually made it less likely for participants with VMPC damage to the feel negative emotions in relation to others performing better than they themselves did and in turn perhaps this made it less likely for participants with VMPC

damage to engage in compensatory mechanisms to make themselves feel better. On the other hand the other groups may appropriately attribute wins and losses to the other players, however this may threaten them in some way which then distorts their rankings of others to make themselves feel better This is a rather convoluted explanation, however future study could examine whether or not self-preservation biases are abnormally deployed in VMPC participants.

Another interpretation of the odd results in the Nim Tournament might relate to the findings reported in the Investors Game. Perhaps when the participant observed individuals competing in the Nim Tournament there were systematic ways in which the participants attributed wins and losses to individuals. Moreover, there may be systematic attribution biases associated with participants observing others compete and when actively competing against others.

The results on the Nim Tournament may also be affected by the fact that a large proportion of all subjects did very poorly in inferring the social hierarchy. Perhaps participants were not engaged enough in the task to properly infer the tournament hierarchy. Also given the number of participants among the NCs that ranked the players in the exact opposite of the correct ranking, perhaps there was some confusion as to which direction the rankings were supposed to be completed, however the anchors were clearly labeled on the screen.

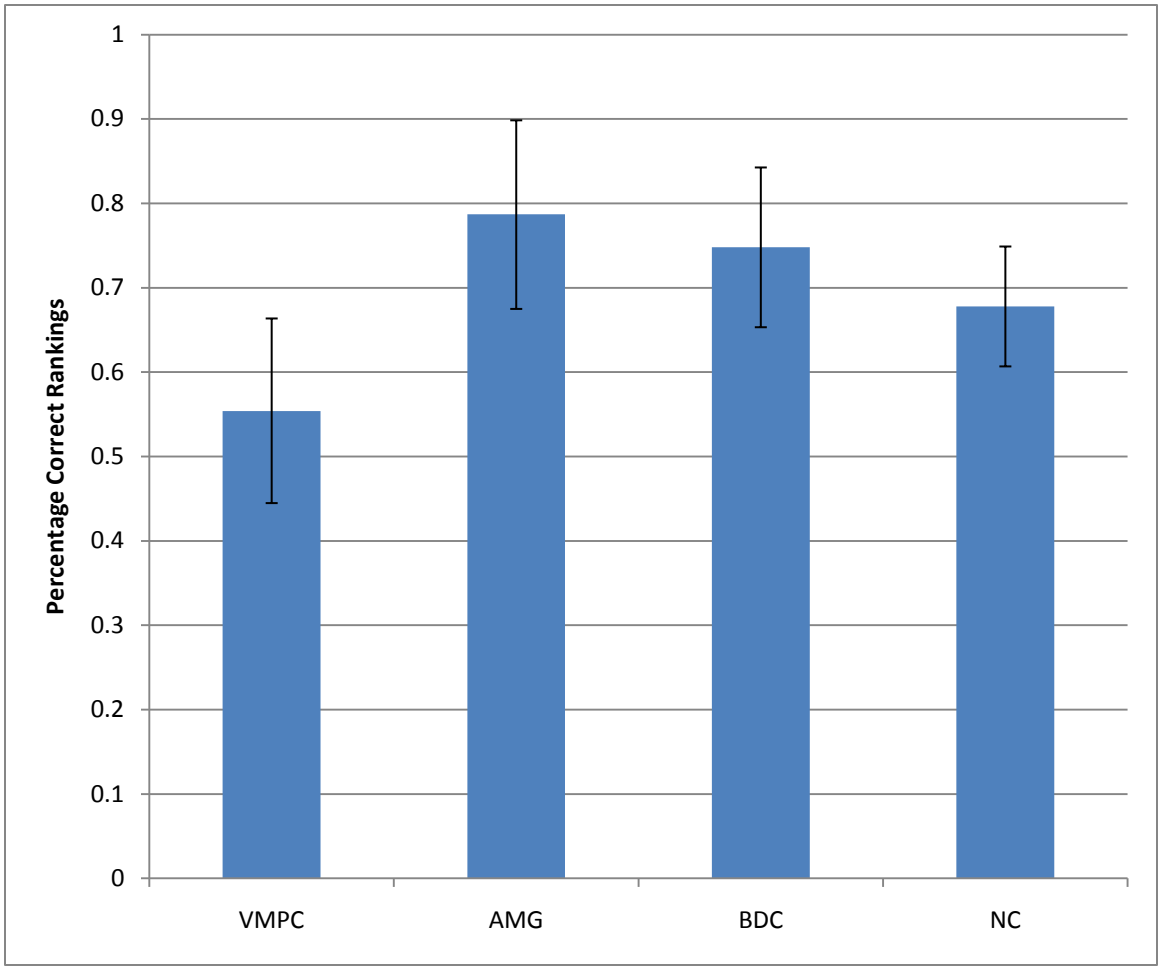

Figure 55 – Nim Tournament Performance. Bars represent the ability of participants to infer the correct ranking of players in the task, where lower score represent better performance. VMPCs tend to outperform the other groups. Error bars represent 95 % confidence intervals.

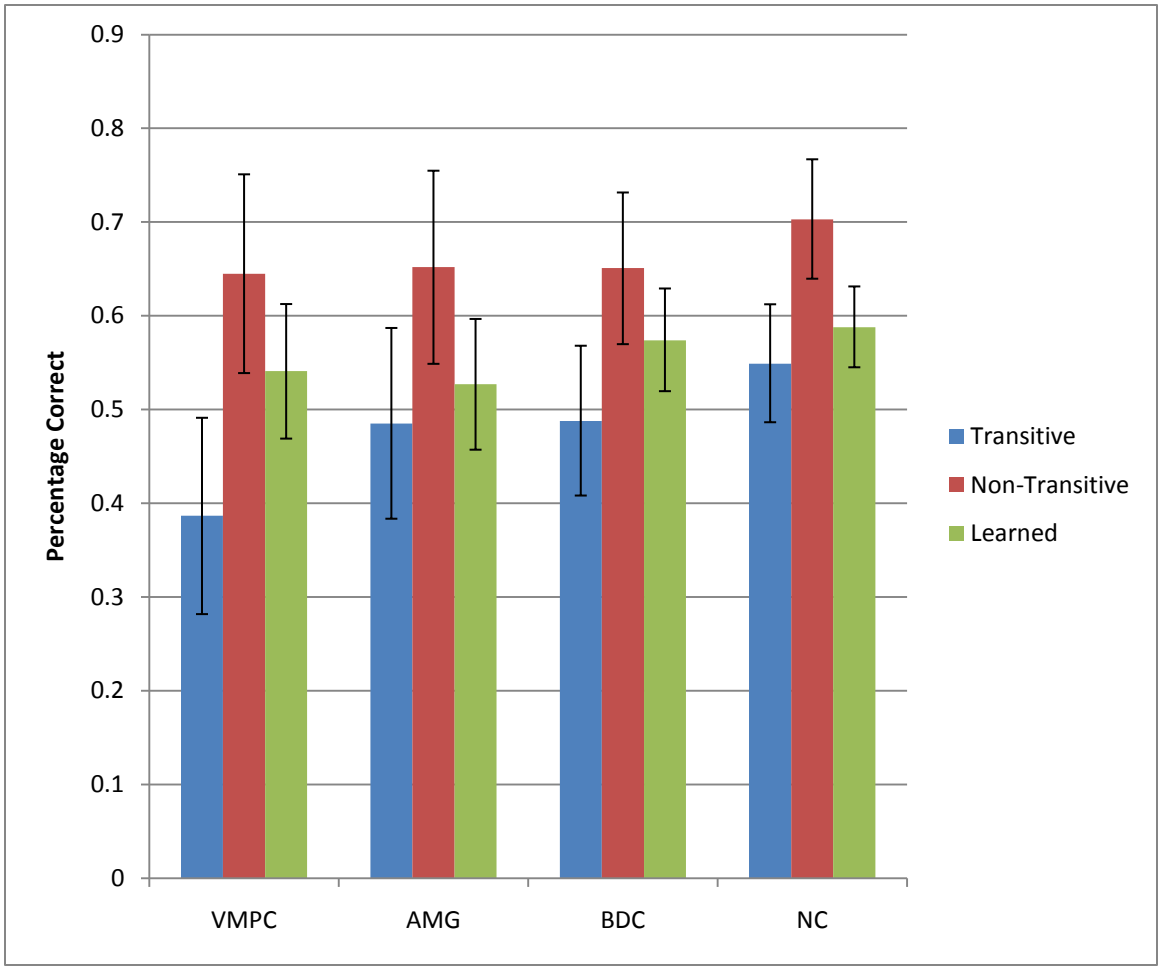

Figure 56 – Patterns Task Performance by Item Type. Bars represent the percent of items answered correctly on test blocks of the patterns task. Participants with VMPC damage perform significantly worse than the other groups for transitive items only. Error bars represent 95 % confidence intervals.

CHAPTER 11

GENERAL DISCUSSION, FUTURE DIRECTIONS, AND CONCLUSION

General Discussion

The results of some of the experiments were somewhat equivocal. On one hand it is clear that the VMPC and amygdala may not be integral in the perception of reproductively relevant signals given the equivocal results of the mate choice paradigm. On the other hand it is also clear that VMPC damage results in deficits in the types of social inference, as shown by the correspondence bias and transitive inference tasks, as is predicted by the current hypothesis. It may be that the VMPC is only involved in inferring social value and not its perception; that the brain regions once necessary for chemosensory discrimination are exapted for inferential social processes not perceptual ones. It appears that inference is the key, in that when social inference is needed specifically then participants with VMPC damage display a deficit, otherwise their performance appeared more or less normal. Interestingly this framework may help explain the deficits that these participants show on the Iowa Gambling Task. Perhaps they have a specific deficit in inferring from experience the values of individual decks and thus they continue to make many choices from the bad decks. Rather than there being a specific effect of punishment or reward magnitude or frequency, instead there may be a specific inability to infer the link between feedback and outcome across time.

More precise analysis of the brain lesions is required to pin down exactly which brain regions are critical for the results observed in this study. As mentioned above there may be subtle differences in anatomy between different etiologies of brain damage. For instance meningioma resections may preferentially affect area 10 in polar regions of prefrontal cortex where aneurysm ruptures may preferentially affect areas 11 and 14, which represent more caudal and medial regions of prefrontal cortex.

Despite the equivocal nature of some of the results as mentioned above, there does seem to be broad support for the Inferential Brain Hypothesis, but also that it needs some clarification. Specifically the respective roles of the amygdala and the VMPC are clearly different. The amygdala does not appear to be clearly involved in social inference at all. This may reflect a difference between bottom-up processes implemented by the amygdala, consistent with its role in rapid, on-line evaluation of the valence of incoming information. On the other hand the observed role for the VMPC in social inference, particularly extracting information via transitive inference, may reflect a role for this region in top-down processes acting on highly-processed sensory information in order extract the most relevant information given situational goals. In addition, the role of the VMPC needs to be clarified. It does not seem to be involved in perception of the biologically relevant information necessary for making-mate choices. However it does seem to be clearly necessary for social inference. It may be that this inference is the necessary component, which is again consistent with the role of the VMPC in top-down processing. In contrast other brain regions may be necessary for perception for biologically relevant information, such as the superior temporal sulcus given its role in extracting biological motion information. Given the present framework, it seems logically that since perceptual abilities were shifted from chemosensory to visual, these perceptual processing steps have been moved to areas more closely associated with vision and visual association and the VMPC (or old chemosensory cortex) is involved with inference from this information specifically.

Table 14 – Summary of Main Findings and Implications for the Inferential Brain Hypothesis

Protocol	Experiment	Main Result	Implications for Hypothesis
Mate Choice	Profile/Interview – Preferences	No significant group differences	VMPC may be involved only when inference is necessary.
	Mate Choices	No significant group differences	
Social Attribution	Quiz Game	No significant group differences	VMPC damage results in deficits in social attribution under some conditions.
	Investors Game	VMPCs do not show the Correspondence Bias.	
Perspective-taking	Vignettes	All groups show gradual decline with additional iterations.	Inconsistent with claims from Social Brain Hypothesis.
	Social Network Index	No group differences in social network size.	Deficits in social inference do not apparently affect social group size.
Social Hierarchy	Nim Tournament	VMPC perform at chance in identifying the social hierarchy.	VMPC damage results in a deficit in social inference.
	Patterns Task	VMPC show selective deficit for transitive items	VMPC damage results in deficit in inference in non-social settings

Future Directions

Given the data presented here there are several directions for further that these findings indicate. Likewise the extensive search and exploration of background information have pointed to certain areas in which the current state of the art in the literature leaves large unknowns and hint at what types of data should be collected in order to answer some of the difficult questions related to human abilities in relation to the abilities present in the animal kingdom.

In general, a different analytic approach to the current data set might yield interesting results that might be obscured by the peculiarities of MANCOVA analyses as well as the highly variable nature of behaviour and outcomes in brain damaged individuals. Instead of comparing across groups as was done in the current analyses, essentially starting at brain damage and the comparing behaviour; it would be insightful to look at the interesting and extreme behaviours exhibited by the subjects and the going in the reverse direction to look at what brain regions are involved. Perhaps the more extreme behavioural phenotypes are more likely to be associated with different groups or sites of brain damage.

Another extension of the current analyses would be to examine the effects of age on the variables examined here. Since the group of neurologically normal adults was recruited with the intent of getting a relatively representative sample of adults of different ages, it is possibly to probe this dataset for differences across the age span. Age was included as a covariate in the MANCOVA analyses that were conducted, however it would be interesting to extend the results explore possible correlations among the different experimental results and age. Particularly relevant may be the effects of age on social networks, not only social network size but also social network types, as ageing may simultaneously alter social goals but affect social networks due to limitations imposed by mobility or other factors that could increasingly interfere with sociality with age.

In relation to the Mate Choice paradigm, the evidence presented above suggests that the VMPC and amygdala may only weakly affect mate related decisions under the conditions of the protocol that was used. As mentioned in the discussion at the end of Chapter 7 on mate choices it is mentioned that the design of the experiment may not have been targeted specifically enough to the predictions of the Inferential Brain hypothesis. Specifically, there was no need to infer social values of potential mate choices, instead these values were consistently given. If the target regions are truly involved in inferring social value, this experiment may not have been adequately targeted to this aspect of mate-related decisions. This set of experiments did however provide valuable insight into the fact that the VMPC and the amygdala may not be critical for making mate choices under conditions when information is explicitly given. The question remains open as to whether or not damage to these areas is necessary for inferring social values for making mate decisions in the first place. Future studies are needed to address this possibility. Instead of being given direct access to biologically relevant factors, the paradigm used here could be tweaked in such a way that these same variables are inferred from observation of behaviour across time and space. This could not only illuminate the role of the VMPC and amygdala in social inference, but could potentially be done in such a way as to increase the ecological validity of the task, since these variables are often not directly observable in real-life. Likewise, variables such as physical attractiveness and socioeconomic status could be examined in more detail without the context of a mate-related decision such that an individual's ability to perceive differences in value and infer values from indirect sources could be more directly compared.

In relation to the study of the Correspondence bias present in Chapter 8, there are several questions raised by this work pointing to avenues of future research. First, an interesting extension of the Investors Game would include conditions under which participants are presented with negative information. The protocol presented above

restricted dispositional and situational information to being positive in nature only, due to logistical constraints on testing time and the concern of frustrating and losing the attention of participants. By examining presence or absence of the correspondence bias in relation to negative information, this paradigm could provide a test of the predictions of Error Management Theory and potentially help explain why participants with VMPC damage who do not show the correspondence bias have disorders of social conduct. For example, comparison groups would be expected to show a decreased investment with both dispositionally and situationally associated investment partners. Since they would decrease investments for both types of information, essentially treating situational information as diagnostic as dispositional information, they would display the correspondence bias under conditions which might protect them from loss. If on the other hand, VMPC subjects only decrease investments for dispositionally associated and not situationally associated ones, i.e., not displaying the correspondence bias, then this may place them at risk when investing under negative conditions.

Another aspect of the correspondence bias that warrants further scrutiny is the observation that the differences between groups of the presence or absence of the correspondence bias appeared to be transient. Perhaps this means that these ephemeral relationships like the ones in the Investors Game, do not affect long-term social behaviour. However, the transient nature may be a consequence of the limited nature of the interaction and experimental control exerted over the stimuli. It would be very informative to evaluate the role of the correspondence bias in a more naturalistic setting in which the formation of longer term relationships might be affected by the correspondence bias. This too could provide insight into how participants with VMPC damage have disorders of social conduct. In addition, it may also provide a means of rehabilitation of maladaptive social behaviour in these individuals, if a means of assisting them in biasing their attributions could be created, perhaps through extensive and focused training to link situational variables to dispositions.

Parametric manipulation of the correspondence bias would likely be a fruitful approach to quantifying the factors that influence whether or not individuals exhibit the correspondence bias. A particularly important parameter that could be considered as mentioned very briefly in the introduction to the correspondence bias in Chapter 8, is diagnosticity. It has been noted in the literature that individuals across different cultures appear to display the correspondence to greater or lesser degrees depending on how diagnostic the information provided is of someone's behaviour. By manipulating the degree of diagnosticity, it could provide insight into the possibility that VMPC damage differentially affects the correspondence bias under conditions of low to high diagnosticity. The information in the Quiz Game is lower in diagnosticity than the information given in the Investors Game, and this factor may indeed provide an explanation for the differential display of the correspondence bias among participants with VMPC damage. Another interesting parameter that could be manipulated would be reliability of the information needed to make the correspondence bias. It would be interesting to see how individuals differ in their display of the correspondence bias when information is associated with varying degrees of uncertainty. The Inferential Brain Hypothesis would predict that the higher the uncertainty, and thus the higher demand on drawing inferences, the less likely they would display the correspondence bias. On the other hand, if the correspondence bias is a heuristic to solve difficult problems while avoiding costly errors, then normal healthy adults should be more likely to display the correspondence bias under uncertainty. There are of course many other possible parameters that could be manipulated to see how they affect the correspondence bias including emotional content, even the direction of valence. Future studies could shed light on the role of the VMPC in exactly which factors influence its role in displaying the correspondence bias.

Another interesting twist on the correspondence bias stems from the fact that the sex of the individuals represented in the stimuli of both the Quiz Game and the Investors

Game were strictly controlled. In the Quiz Game, all participants observed same sex confederates. In the Investor Game all subjects interacted with male investors. Given that men and women may have different goals in same-sex compared to opposite-sex interactions, it might be reasonable to expect differences in attributions based on sex. Indeed, in the Investors Game, women tended to show a greater difference in investing with dispositional and situational information, possible suggesting that the correspondence bias is even weaker following VMPC damage for opposite-sex individuals. Likewise perhaps the lack of effect on the Quiz Game is due to the fact that same-sex confederates were used. Perhaps the biases are more important for relationships between men and women where biological adaptiveness for reproductive purposes places a premium on minimizing errors.

From the results of the transitive inference tasks, it seems clear that participants with VMPC damage have a selective deficit in utilizing transitive inference. However, from the Nim Tournament it is apparent that there are other biases such as a need for positive self-appraisal are potentially affected by VMPC damage. Future studies might benefit from examining inferential abilities in relation to one's own behaviour compared to the behaviour of others. Similarly an investigation of a positivity bias not present in participants with VMPC damage may be informative as well. In addition to other potential biases, it would be interesting to test brain-damaged patients for different reasoning and inferential processes. Perhaps, these processes can be assigned to different regions, where each region process incoming information in different ways (irrespective of the type of information that comes enters a module, the module process it according to the logical rules that it implements).

In addition to the future directions suggested by the observations of the protocols employed here, through extensive search of scientific literature from multiple different disciplines from comparative anatomy, to paleontology, to molecular and cognitive neuroscience, it is abundantly clear that there is a dearth of comparative information

available. There are only a very limited number of species studied in detail and what data do exist for many species, suitable for comparative studies, includes only relatively gross measures. Compounding this problem is the almost complete lack of any standard measure of comparison of function across a large sampling species. There are complicated problems of determining homologous brain structures and connections across species, let alone determining changes in relative importance or change in functional significance of brain regions. One particular reason for the lack of high-quality comparative data is the ethical considerations that preclude invasive study of so many species. What is needed is a method whereby non-invasive techniques suitable to studying humans without harm are applied to the study of as many other species as possible. Such samples of species are potentially readily available in zoos around the world, and non-invasive techniques are present that would allow not only detailed anatomical analysis and comparison of brains across species but also potentially of a form of brain function across species. Resting-state functional connectivity MR imaging could potentially be used to create a rich dataset ripe for phylogenetic comparison of brain structure and function. The benefits of this type of imaging are obvious in that functional relationships can be extracted even while an individual (or potentially an animal) is sedated and is task-independent. This means that harm to animals would be minimal and the constraints associated with developing species-specific tasks would be relaxed. Methods such as this could be used to elucidate brain evolution in unprecedented detail. The Inferential Brain Hypothesis presented here would make several predictions, particularly relating to the decline of chemosensation and enhancement of vision in primates.

Conclusion

Further study is required to confirm the overall validity of the current hypothesis. It does seem to be the case that social inference is a critical feature of the VMPC however

the results are less clear for the involvement of the amygdala. It is also probable, given the results presented here that the role of the VMPC in evaluating the social world is of a higher-order than low-level perceptual processes, involved in inference not social perception. Furthermore, this research project has pointed in several directions in which to continue testing and evaluating the roles of the VMPC and amygdala in social behaviour. Ultimately, this line of research will hopefully make at least a small contribution to our understanding of how and why the human brain evolved and provide insight into ways in which we can fix or improve our brains, cognitions, and behaviours.

APPENDIX A

DEFINITION OF TERMS

Amniote – The group of four-legged vertebrate animals with terrestrially adapted eggs. This group includes all mammals, birds, dinosaurs, reptiles, turtles, *etc.*, but excludes amphibians including frogs, toads, salamanders, *etc.*

Anthropoid – The group of true primates that include all the haplorhine primates excluding tarsiers. Anthropoids include New and Old World monkeys, apes and humans.

Biome – Climatically and geologically defined communities of organisms, basically synonymous with th term ecosystem.

Carnivoran – Animals of the Carnivora order. This group includes cats, dogs, bears, seals, *etc.*

Catarrhine – The group of true primates that includes all Old World monkeys and apes, including humans. They are characterized by downward pointing nostrils.

Clade (also **phylogenetic clade**) – A group that consists of an organism and all of its descendents.

Cynodont – An ancestor to all modern mammals (all mammals are cynodonts). Appeared during the Permian period. They are named after their dog-like teeth, and likely had fur and were endothermic.

Diapsid – The group of amniote animals that includes all living reptiles and birds and extinct relatives including the dinosaurs. In the context presented here the term is differentiated from the term sauropsid by excluding reptiles and turtles which have modified skulls that no longer contain two temporal fenestra that characterizes the group, leaving only birds and dinosaurs. Though it should be noted that this is not the accepted or widespread use of the term.

Endocast – A fossilized impression of the interior space of the skull. These can be either discovered, having been generated through fossilization of material entering the cranial cavity, or artificial generated by either making a physical impression of the intracranial space or digitally via CT scanning.

Endothermy, endothermic – the capability of an organism to internally regulate and maintain their body temperature, irrespective of external temperatures in the environment.

Euprimates – True primates, including all modern primates and extinct relatives, though excluding plesiadapiformes.

Eutheria, eutherian – The group of mammals that includes all placental animals and there extinct relatives most closely related to them than other non-placental mammals. This term is almost synonymous with Placentalia or placental which excludes certain extinct members of Eutheria.

Frugivory, frugivorous – A diet consisting of fruits.

Haplorhine – true primates that include all living primates excluding lemurs and other strepsirrhines. This group is characterized by a dry nose. This group includes tarsiers, New and Old world monkeys, apes, and humans.

Hominid – The group of true primates that includes gorillas, chimpanzees and humans. Similar to hominoids excluding gibbons.

Hominin – The group of true primates that includes humans and their extinct relatives more closely related to them than chimpanzees.

Hominoid – The group of true primates that includes gibbons, apes, and humans, excluding all Old world monkeys.

Hylobates – The true primates that include only gibbons.

Insectivory, insectivorous – a diet consisting primarily of insects.

Metatheria, metatherian – The group of mammals that includes all marsupials and their extinct relatives more closely related to them than to other mammal types.

Monotremata, monotreme – The group of mammals that includes egg-laying mammals (platypus and echidna) and their extinct relatives, excluding Eutheria and Metatheria.

Panin – The true primates include all species of orangutan, chimpanzee, and gorilla.

Platyrrhine – The group of animals that are the true primates that make up the New World monkeys, and include all South and Central American primates. They are the only primates with prehensile tails.

Plesiadapiformes – A group of extinct animals closely related to modern Primates.

Plesiomorphy, plesiomorphic – when features are primitive, i.e., structurally similar/identical to the primitive form. In other words, a feature that is plesiomorphic for a set of species indicates that this feature was also present in their last common ancestor.

Preadaptation, preadapted – a situation where a species uses a preexisting structure inherited from an ancestor that presumably used this feature for an unrelated function.

Prehensile – adapted for grasping, such as the hands and feet of most primates, and the tails of New World monkeys.

Sauropsid – The group of amniote animals that includes all reptiles and birds as well as extinct species more closely related to them than to mammals, including dinosaurs.

Strepsirrhine – The group of true primates that includes lemurs, lorises, and galagos. They retain a characteristic wet nose.

Synapsid – A group of amniote animals more closely related to mammals than other amniotes, including reptiles, birds, and dinosaurs. These animals are characterized by the presence of a single, low temporal fenestra. This group includes mammals and mammal-like reptiles.

Temporal fenestra – large holes in the side of the skull. Mammals and mammal-like reptiles, collectively the synapsids, have a single characteristic lower temporal fenestra. Modern mammals have highly modified fenestra such that the hole is no longer present, though its presence is still visible in the human skull, behind the orbit and above the bony ridge, the zygomatic arch, where the upper portion of the jaw and skull meet.

Therapsid – A group of synapsids that includes cynodonts and thus all mammals. They have adaptations including differentiated types of teeth and limbs that extend beneath the body rather than to the side like reptiles.

APPENDIX B

REGIONAL BRAIN DIFFERENCES ACROSS PRIMATE SPECIES

If the Inferential Brain Hypothesis is correct then one would predict a distinct pattern of regional brain changes superimposed on existing primate trends. Specifically three trends would be readily observable. 1. The olfactory bulbs will be substantially reduced in size, reflecting a decrease in importance of the chemical senses (the absence of the accessory olfactory bulbs in many primate species is well known and is thus excluded from any analysis here). 2. The decreased size of the chemical senses (olfactory bulbs) will be decoupled from the cortical regions that process this type of information. The brain regions in non-human mammals that are necessary for chemical communication predicted to have been exapted for human forms of social evaluation independent of the chemical senses. These brain regions will be expanded or at least spared the decrease observed for the olfactory bulbs in humans only, as they are exapted for social inference.

Luckily, there is a set of comparative data published by Stephan, Frahm, and Baron (1981) that contains measurements of regional brain volumes for many species of insectivore and primates. To test these hypotheses, relative brain volumes were calculated for each species available in the Stephan, et al. data by dividing each of the values by the volume of the medulla. To control for differences in overall brain size it is innapprorpiate to use overall brain volume as a control variable as this is known to differ across species independently from differences in body size. Given that the functions of the medulla represent more basic functions for moment-to-moment survival, it may be reasonable to use medulla volume to control for overall changes in brain size that are due to non-species specific changes due to differences body size. Brain measures that were analyzed include: olfactory bulb volume, neocortex volume, striate cortex, piriform cortex, paleocortex, and amygdala. Piriform cortex includes paleo cortex and amygdala.

Paleocortex includes retrobulbar cortex (anterior olfactory nucleus), prepiriform cortex, lateral and medial olfactory tracts, internal olfactory tract, anterior commissure, olfactory tubercle, substantia innominata, and the basal nucleus of Meynert.

As you get phylogenetically closer to humans relative olfactory bulb volume steadily decreases and neocortex volume increases. Volume of striate cortex appears to increase as you get phylogenetically closer to the cercopithecines, from there it reaches a plateau to be approximately equal in relative volume across cercopithecines, panins, and hominins. Volume of piriform cortex suggests that humans have relatively large 'piriform lobes' as defined by Stephan et al. compared to the predicted value from primates. This effect seems to be largely driven by the volume of paleocortex, which decreases as you get phylogenetically closer to humans (though there is not data on panins), however humans have a much higher volume of paleocortex than would be predicted from the primate trend. This lack of decreased paleocortex volume is within the high-end of the range observed for strepsirrhine primates, and close to range of non-primate mammals. Interestingly, the amygdala shows no trend of change in volume from non-primates to humans, where all species appear to maintain a similarly sized amygdala relative to their medulla size.

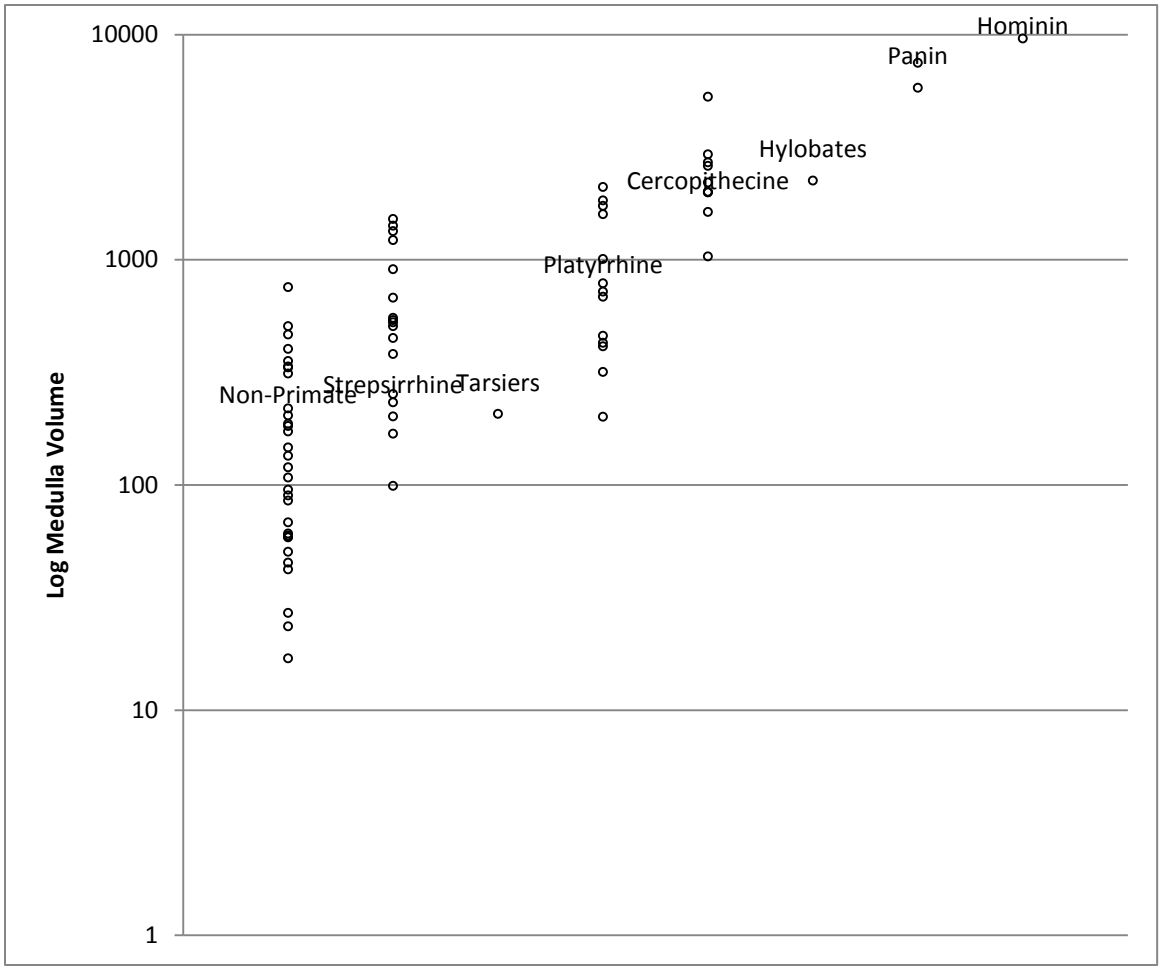

Figure B1 – Medulla Volume across Species. Medulla volume is used to control for overall differences in brain size that are due to differences in body size and – non-specific differences in brain size. Data are plotted on a logarithmic scale.

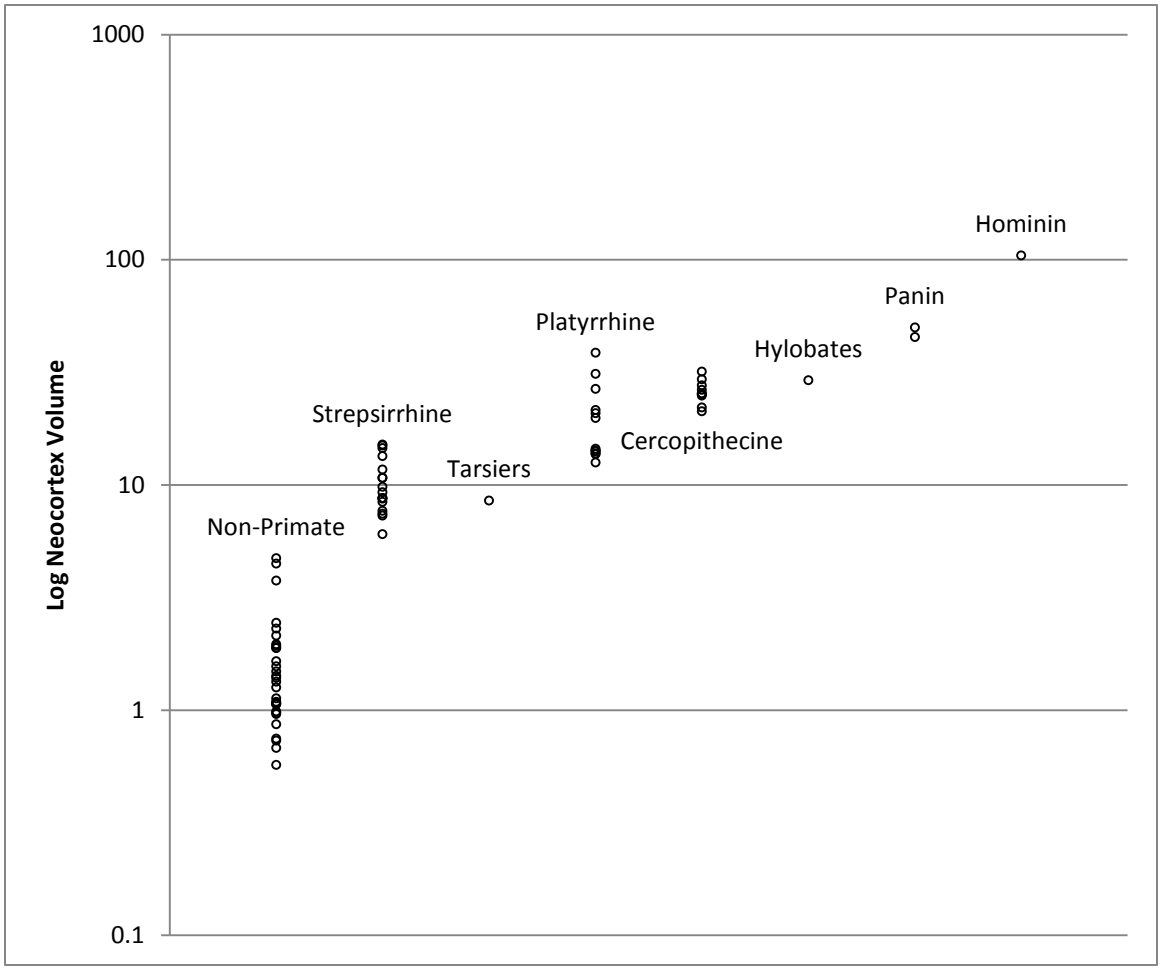

Figure B2 – Relative Neocortex Volume across species. There is a clear trend toward increased neocortex size among primates as you get phylogenetically closer to humans with the largest increase in neocortex size. Data are plotted on a logarithmic scale.

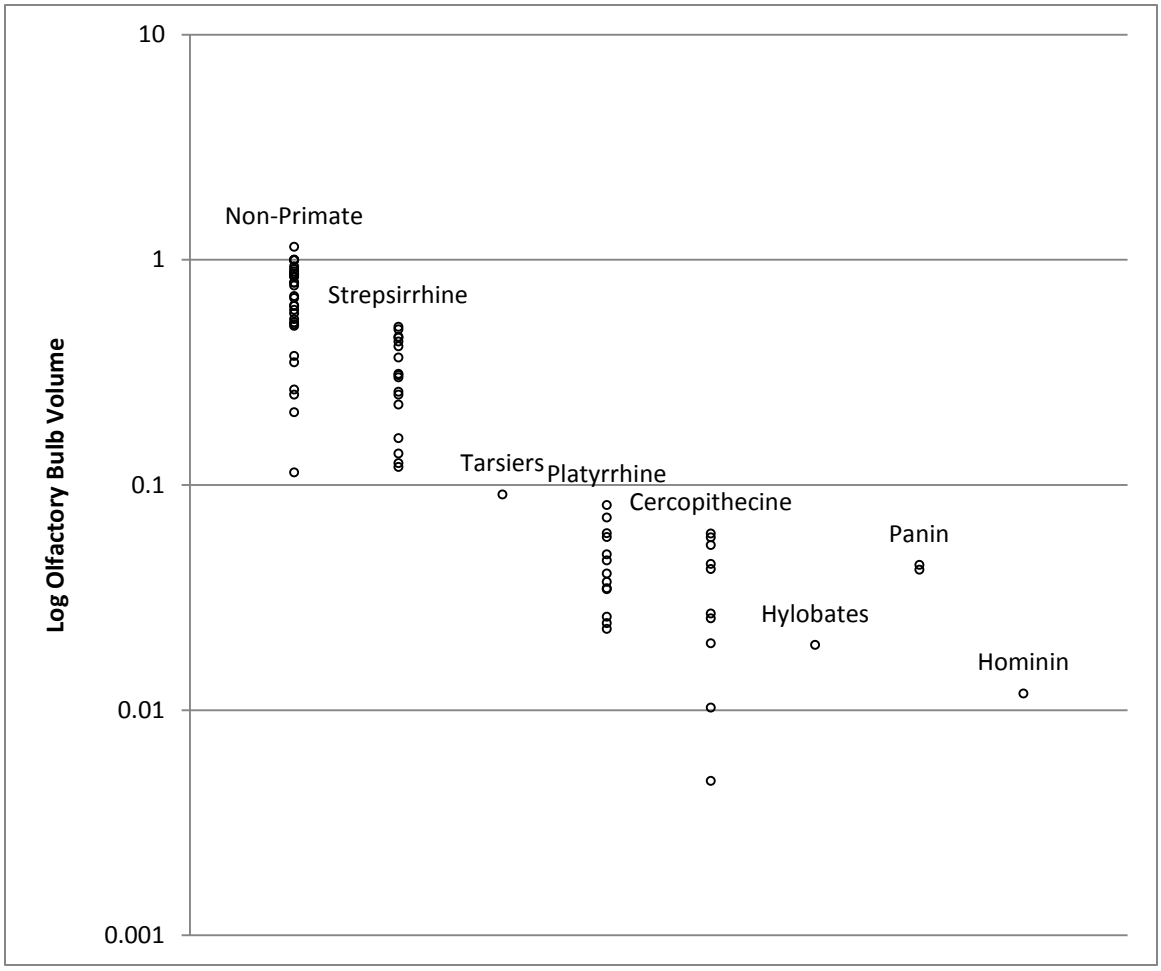

Figure B3 – Relative Olfactory Bulb Volume across Species. There is a clear trend of decreased olfactory bulb volume across primate species, where humans and closely related primates are outside of the minimum range of the measure non-primate mammals. Data are plotted on a logarithmic scale.

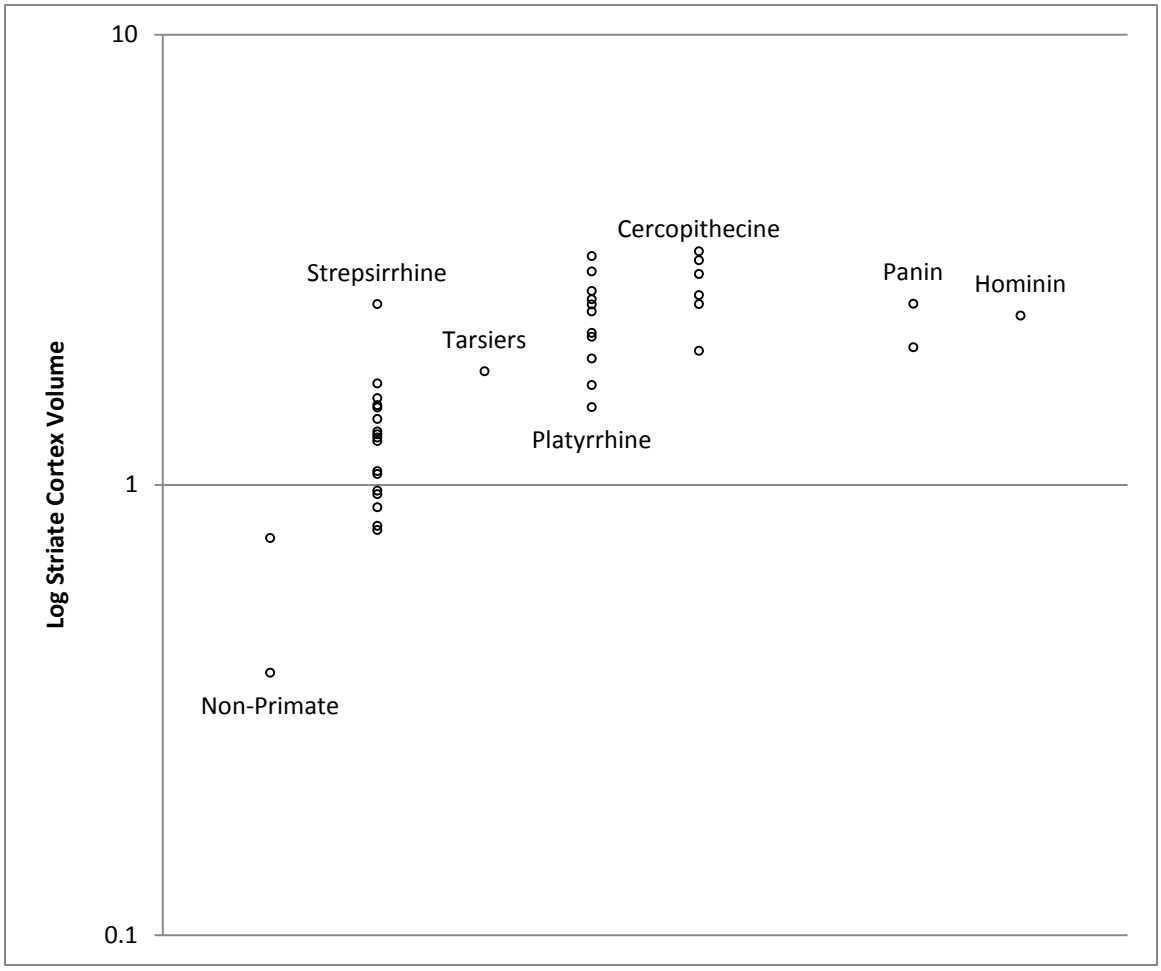

Figure B4 – Relative Striate Cortex Volume across Species. Striate cortex appears to increase in primates up to a plateau among Catarrhine primates. Data are plotted on a logarithmic scale.

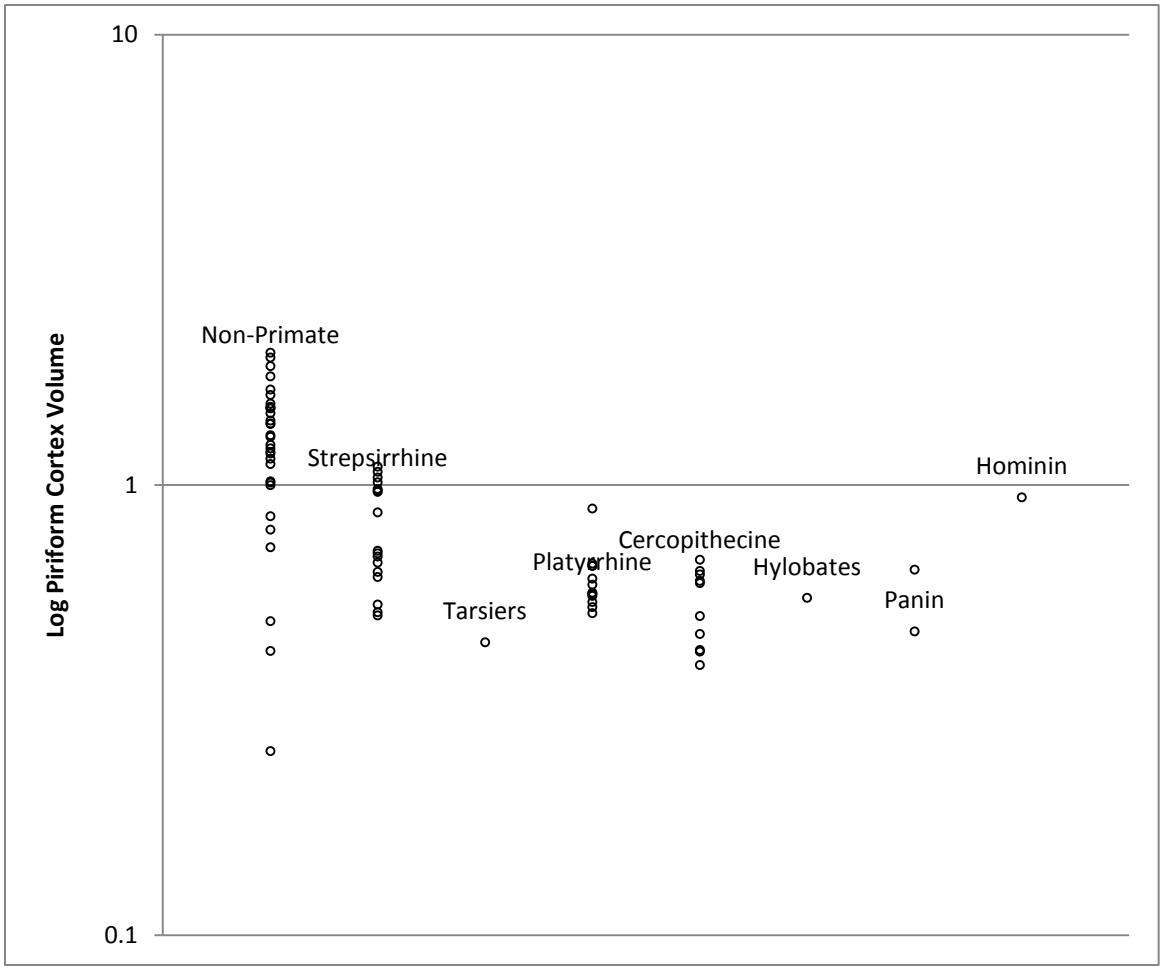

Figure B5 – Relative Piriform Cortex Volume across Species. There is a clear trend of decrease in piriform cortex volume across species, where panins have the smallest relative size. Humans are an exception, having a piriform cortex size greater than the maximum for all primates except some strepsirrhines. Data are plotted on a logarithmic scale.

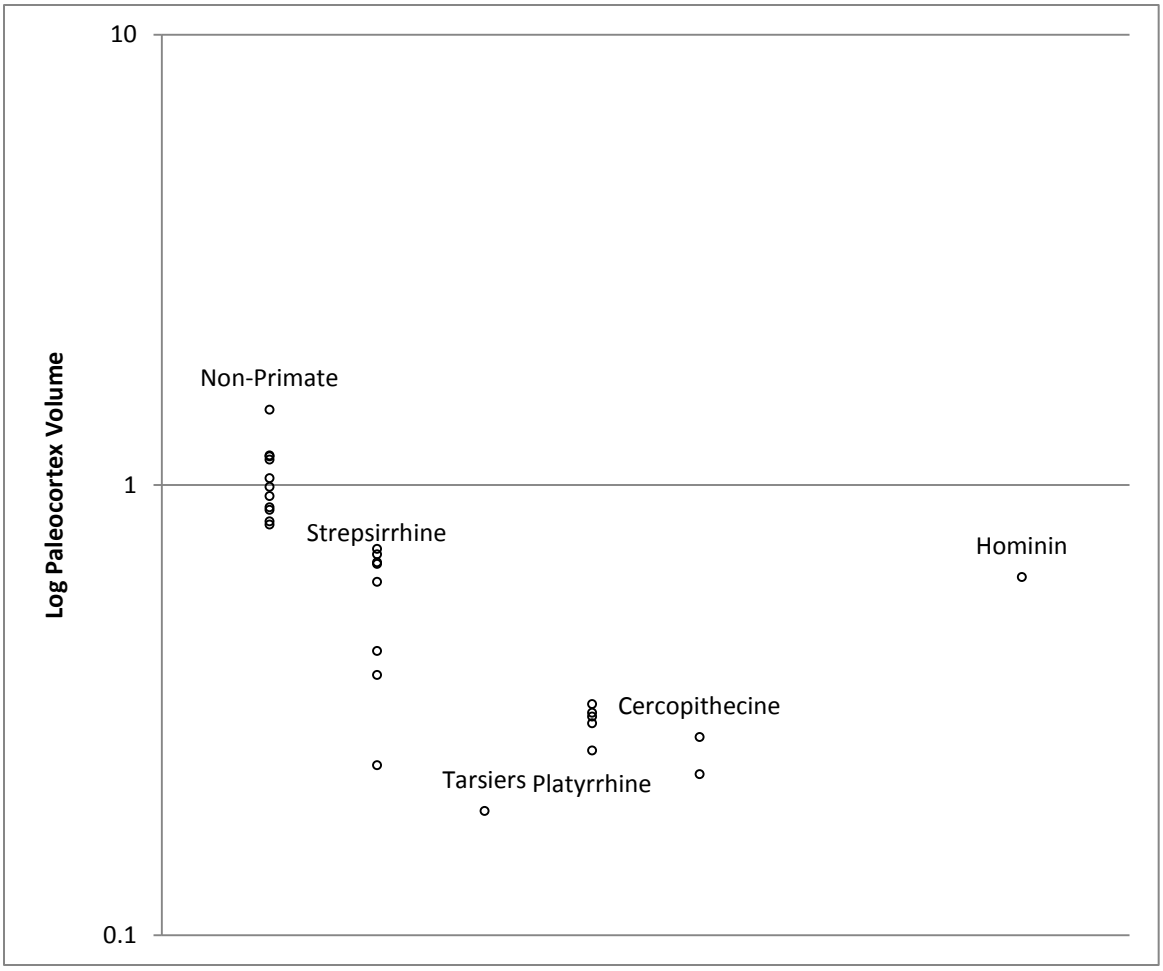

Figure B6 – Relative Paleocortex Volume across Species. There is a clear trend of decreased paleocortex size from non-primate mammals to primates. Humans however present a clear exception to this trend, having a relative volume near the maximal end of the primate range and minimal end of the non-primate range. Data are plotted on a logarithmic scale.

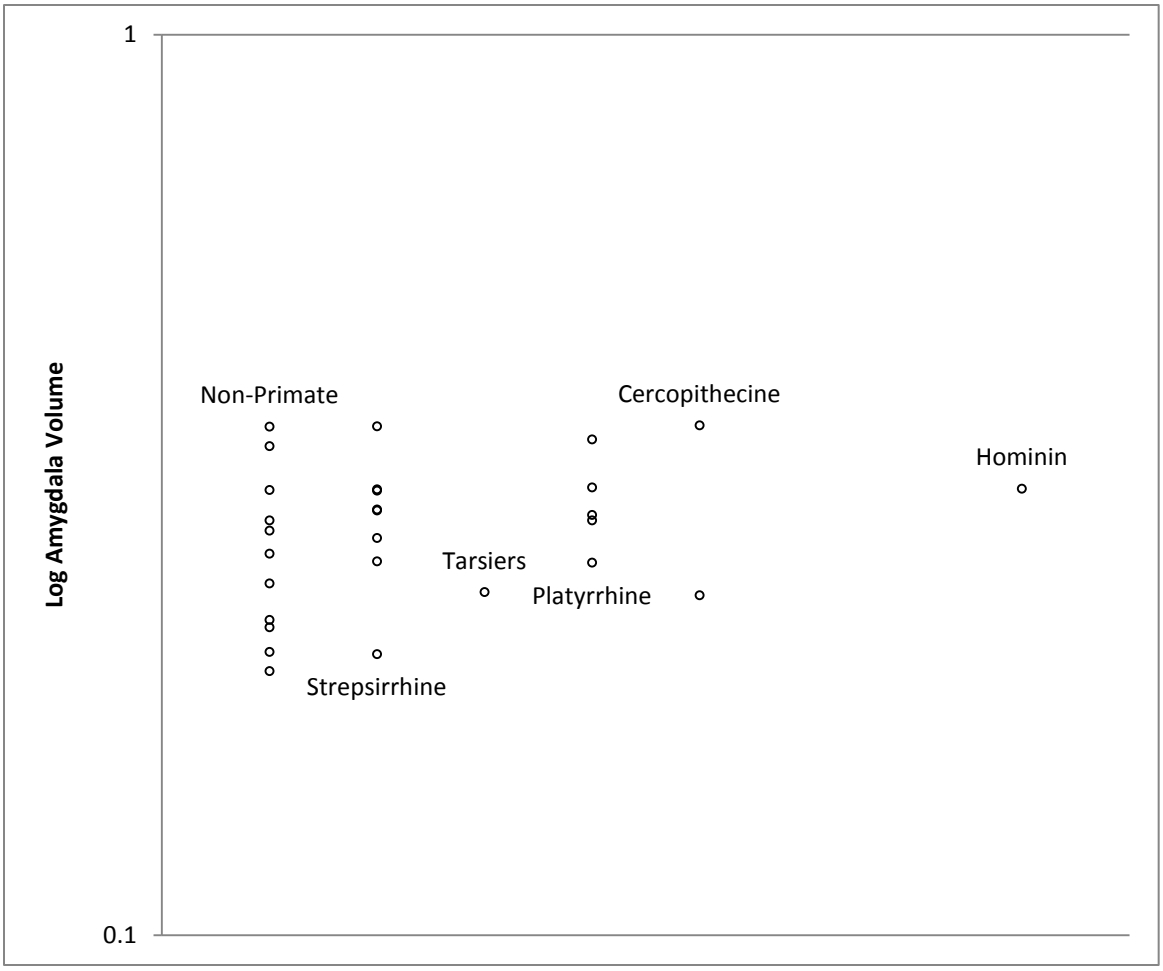

Figure B7 – Relative Amygdala Volume across Species. Relative amygdala volume appears to be consistent across species, perhaps this is indicative that amygdala-mediated processes are vital for the mammalian condition thus its size is maintained. Data are plotted on a logarithmic scale.

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