Conflicting Evolutionary Pressures on Human Cognition: A Case Study of Autism

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Abstract

The current dominant view is that the evolutionary pressures leading to our large brain sizes were predominantly social. This study investigates the effects of both technical and social pressures on our cognitive evolution, to determine whether the pressures were more complex than social theories allow. This is assessed both between hominin species and within our species. Between species effects are determined by evaluating the evolution of human cognition in 4 stages. Archaeological evidence of behaviour and changes in brain structure are presented for each stage. This allows specializations to be identified, and permits us to suggest whether specialization in each species was in response to social pressures, or a more complex pattern of both technical and social pressures. The results of this evaluation support a more complex pattern of evolutionary pressures. Within species effects are assessed, using Autism Spectrum Condition (ASC) as an example of an alternate, more technically focused, adaptive strategy. This condition accentuates technical behavioural traits which would be advantageous to a Palaeolithic population. The genetics of the condition show that it is highly heritable, was likely present prior to 200ka, and under positive selection. Thus, these technical traits must have had an impact on past populations. A survey is conducted to assess whether characteristics and components of autism would influence individual’s engagement with material culture, in particular art. It found that the technical trait, high attention to detail, was associated with experience of art and susceptibility to pareidolic illusions. Previously it has been suggested that illusions such as this may be implicated in the origins of art. This provides an example of how individuals with enhanced technical traits within our species may have affected our cultural evolution. Thus, the role of technical pressures in our evolution and how they relate to social pressures requires more attention.

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Author’s Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Chapter 1: Introduction

1.1 Context and Significance

The evolution of the human mind is a topic with resounding importance not just for academics and medical practitioners but also for the general population. The human mind is viewed as the factor that ultimately separates us from all other species. It is generally perceived as what makes us human. The innovative creations it facilitated have allowed us to colonize the earth and tailor it to our needs. The evolution of the mind is predominantly viewed as the development towards ourselves.

The most prominent cognitive development highlighted in current research is our social ability. Theories of social evolution such as the Machiavellian Intelligence Theory (Byrne & Whiten, 1989), Social Brain Hypothesis (SBH: Dunbar, 1998; Dunbar, 1992), Cultural Intelligence Hypothesis (Donald, 2000; Hare, 2011; Herrmann, Call et al., 2007), and the Self Domestication Theory (Hare, 2007, 2017), posit that nature positively selected for social attributes which enhance collaboration. The Machiavellian Intelligence Theory argued that the ability to cooperate with and manipulate others was the primary pressure on our intelligence. The SBH provided data showing a relationship between neocortex size and group size in primates and humans, which supported the Machiavellian theory. Thus, as group size increased social mechanisms became more complex, leading to more intelligent primates. These mechanisms allowed social groups to form a Cultural Intelligence. Groups were able to transmit cultural knowledge through generations, leading to the accumulation of more complex material cultures. Thus, it is currently thought that social selection was the primary evolutionary pressure for our increased intelligence. This selection for prosociality is thought to be so extreme that humans began to show signs of Self Domestication, through a reduction in brow ridge size and increased facial feminization.

These theories have shown the impact of sociality on human evolution and will be explored further below. However, they do not recognize the importance of pressures for technical skills, such as perception, visualization, memory, and the systemization of information (see 2.1 for full definition). Thus, this project will evaluate the importance of non-social, technical evolution on the hominin lineage.

The conflict between these two pressures may also have had a significant impact within species, with some individuals being more technically adept but less social than others. Variation such as this may promote new ways of thinking and broadens the minds of individuals in a diverse population, which helps produce novel solutions to group problems (Phillips, 2014). It may foster specialization and innovation, which can enhance aspects of material and social life (Spikins et al., 2016). And, on a species level, it may produce individuals adapted to different ecological, or social niches - thus increasing the adaptability of both the species and populations (Wilson, 1994).

Autism Spectrum Condition (ASC) and variation upon the Autism spectrum is an example of cognitive difference within our species. Individuals who are high on the spectrum commonly have enhanced technical abilities, with a trade-off of social abilities. Some researchers claim that individuals with this condition are deleterious offshoots (Bednarik, 2013; Pickard et al., 2011). However, attempts have been made to argue that this variation may have been a factor leading to our evolutionary success (Kellman, 1998; Spikins, 2009; Spikins & Wright, 2016; Spikins et al., 2016; Spikins et al., 2017). This is a factor which is rarely touched upon. However, creating more inclusive theories of evolution that account for the entire species and not just neurotypical individuals is highly important; firstly, to fully understand human evolutionary processes; and secondly, to increase awareness that cognitive difference doesn’t equate to disability.

1.2 Aims

The aim of this dissertation is to assess the impact of non-social technical evolutionary pressures on the human lineage, and consider the whether the traits of ASC, a condition which leads to more focus on technical rather than social stimuli, may have significantly impacted human evolution.

This will be accomplished in 3 steps (see figure 1). Firstly, evolutionary pressures will be defined, and an overview of the current dominant theories presented. Secondly, the archaeological record will be evaluated to determine how social and technical pressures may have affected our ancestors’ development. Thirdly, the behaviour of individuals with ASC will be assessed and the impact of their traits on Palaeolithic societies considered, particularly their impact on artwork.

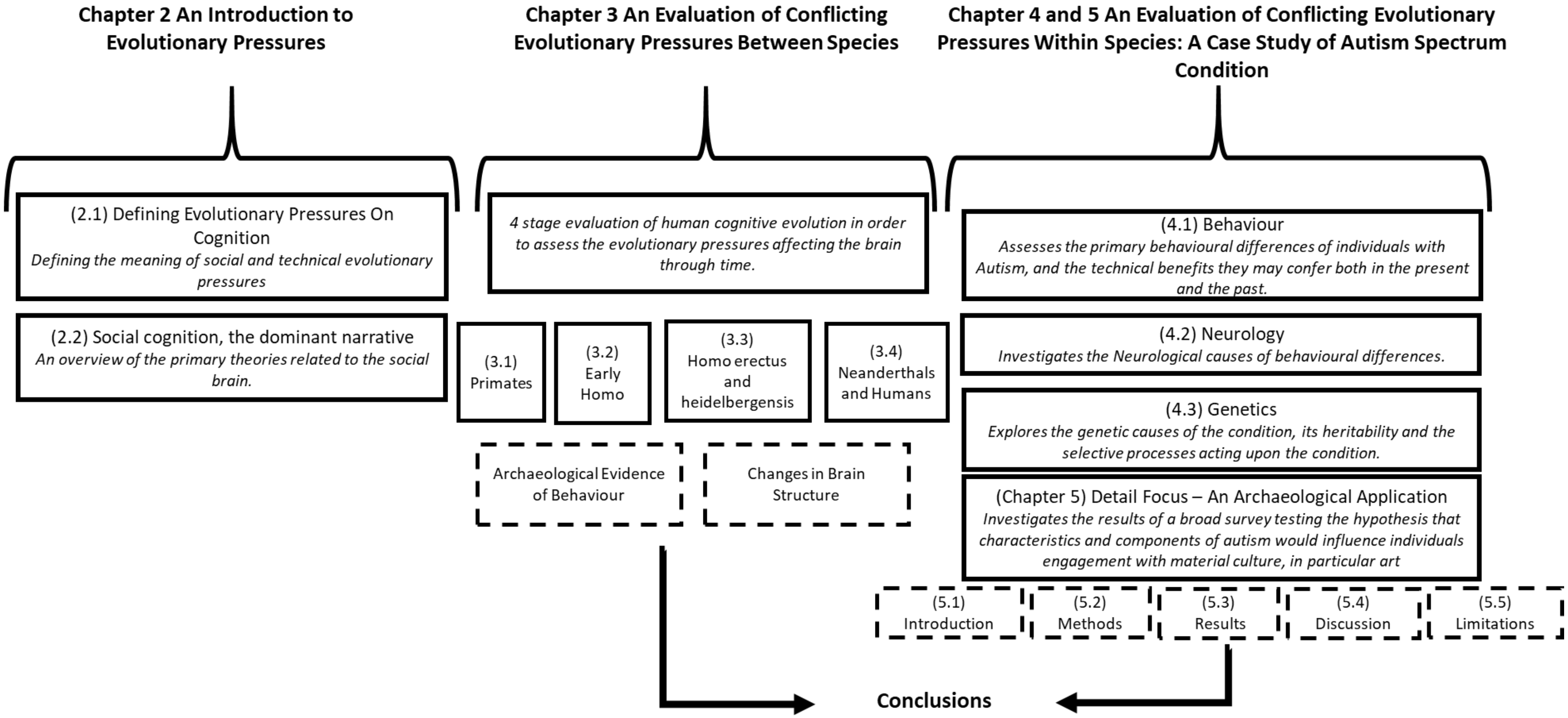


Figure 1. Chart of the dissertation's structure

1.3 Objectives

Firstly, I will explicitly define what social and technical evolutionary pressures are. Then I will outline theories which regard social pressures as the most influential in human evolution. I will evaluate how these evolutionary pressures have affected our ancestors' neurology, behaviour, and material objects. This will focus on several key changes. Firstly, the cognitive abilities of primates, in particular chimpanzees, will be assessed as an indirect measure for the possible capabilities of the LCA. Following this, I will assess the evidence of early *Homo* (predominantly *Homo habilis)*, the first species to exceed the primate brain size limit and increase reliance on tools. Then *Homo erectus* and *heidelbergensis*, our first ancestors to reach 1000cc brain size and display an imposition of specific shape upon tools. Finally, the differences between Neanderthals and anatomically modern humans will be assessed due to their similar brain size yet vastly different lifestyles.

I will then investigate the effect of the conflicting evolutionary pressures within our species, using Autism as an example of an alternate adaptive strategy. This will assess the impact autistic traits may have had upon Palaeolithic populations, and Palaeolithic artwork. I will review published research, reflect on debates, and then carry out my own case study.

The case study will test the theory that individuals with Autism or autistic traits may have created Palaeolithic artwork, using a broad survey. This theory was posited by Humphrey (1998) and Kellman (1998), who discovered many similarities between the artwork of autistic savants and Palaeolithic artists, almost 2 decades ago. However, it has been revived by Spikins and her colleagues in a different format, suggesting that autistic traits may have impacted not only art, but material culture, and the minds of those around them (Spikins, 2009; Spikins & Wright, 2016; Spikins et al., 2016; Spikins et al., 2017). This has been met with counter arguments by Bednarik (2013, 2016) and Pickard et al. (2011). Among their criticisms is that the theory has a lack of empirical support. Therefore, this survey attempts to test the theory using empirical data to rectify this issue. The survey will test the hypothesis that characteristics and components of autism influence individual's engagement with material culture, in particular art. If individuals with high autistic traits are better able to identify hidden figures in Palaeolithic artwork the hypothesis is supported. By assessing this I aim to emphasise the importance of analysing cognitive variation, which provides new avenues for interpreting prehistoric material culture, and explore whether technical traits have had a significant impact on our evolutionary trajectory.

Chapter 2: An Introduction to Evolutionary Pressures

This chapter will define social and technical evolutionary pressures, and will explain how they will be evaluated in later chapters (2.1). It will then outline the theories supporting the dominant view, that evolution for social abilities was the primary development in the hominin lineage, and how this view became so influential. This will also explore the faculties which are thought to have developed as a result of increased sociality: theory of mind, language, and due to facilitation from the previous functions, technological proficiency (2.2).

2.1 Defining Evolutionary Pressures on Cognition

There are two evolutionary pressures affecting cognition which are assessed in this study: social pressures, and technical pressures. While there are other evolutionary pressures, such as environmental stressors, which could be analysed, for clarity and due to limitations of space we will focus on these two.

Social pressures relate to the stressors of group living. When social group size increases, complexity increases. There are more individuals to interact, be wary of, and compete with. Nevertheless, large groups increase foraging success and mitigate predation (Dunbar, 2009). However, strategies must be developed to reduce the costs for the advantages to be worthwhile. These costs may be reduced by forming alliances, understanding others' minds, communicating, and tracking group dynamics. There are therefore many different functions and, consequently, areas of the brain which were affected by social pressures.

Technical pressures are an umbrella term used within this thesis to describe pressures related to functions such as perception, visualization, memory, hand-eye coordination, and the systemization of information. These traits may give many advantages. A better ability to perceive hidden figures, such as predators and prey, within the landscape. Enhanced abilities for visualizing a desired form within raw material. A greater memory for the past locations of vital resources. Greater systemization of the environment, and thus more accurate predictions of future resource locations, and a more structured use of the landscape. The defining feature of technical pressures and the resulting abilities, is that they are non-social and related directly to an individual's ability to functionally utilize the environment around them. Social functions may enable groups to utilize an environment more effectively, however they would have no effect on an isolated individual's survival. In comparison, technical functions would enhance an isolated individual's survival. Further, these skills would also benefit social groups.

I will assess the impact of these pressures by evaluating the evolution of human cognition. This will be accomplished by investigating archaeological evidence for changing behaviour, such as site structure and material culture, and by assessing what structures of the brain have changed through time. This will enable me to propose what functions are developing, and thus what effect technical and social pressures have had on our evolution at a species level. This evaluation will focus on 4 stages: Primates (to estimate the capacities of the LCA), Early *Homo*, *Homo erectus* and *heidelbergensis*, Neanderthals and Humans. Following this, I will use Autism as an example of an alternate adaptive strategy, which causes enhancements in technical skills, but difficulties in social skills, to investigate the impact these pressures may have had causing variability within our species, and determine whether individuals with this condition may have had a significant positive impact on Palaeolithic groups.

Firstly, we will assess how social cognitive evolution became the dominant narrative and the current state of this theory.

2.2 Social Cognition, the Dominant Narrative

Currently, theories relating to our sociality are the most popular explanations for our large brain sizes and complex behaviour. Three ‘social theories’, as they will be collectively labelled, have become particularly prominent: The Social Brain Hypothesis, Cultural Intelligence Hypothesis, and Self-Domestication Hypothesis. However, prior to this boom of social literature, complex tool production, was considered the defining feature. At this time tool production was largely regarded as separate from sociality, and thus under this logic it was thought that technical pressures and skills led to its development.

Darwin (1888, pp. 26–64) stressed technology’s important role on evolution, and for the majority of the 20th century developments in tool production and subsistence strategies were considered to be the primary pressures of human evolution (Hill, 1982). It was thought that when tool use developed, it was so adaptive that the rate of evolution quickened, and the brain expanded to specialize in tool use (Lancaster, 1968; Oakley, 1954). This then allowed a transition from frugivory to meat eating and colonization of savannah habitats (Dart, 1934; Kortlandt, 1962). When classifying *Homo habilis* as a member of our genus, precision grip and the hominins association with stone tools was emphasised. This ultimately led to the species’ name, *habilis,* meaning ‘handy’ (Leakey et al., 1964). This demonstrates just how dominant the view of hominin technical specialization was.

However, it must be noted that even at this time there was an appreciation for the importance of sociality. Darwin (1888, pp. 26–64) understood that we are social animals with specialized cognitive skills (such as empathy) for this purpose. He believed that we developed to our current state through selection for intelligence in tool making and selection for sociality in tandem. While research continued to stress the importance of social selection, it was largely a secondary point. For example, Bruner (1965) and Lancaster (1968) highlighted the importance of cultural transmission and teaching to the development of material culture. Washburn (1960) stated that the areas of the brain most expanded in humans are those used for social functions. However, he still believed that specialization for tool production was the primary development. But more socially oriented theories were available. Etkin (1954) believed that tool use created pressure for increased intelligence. However, he believed that social functions initially facilitated the development of complex technology. Through analysis of lemurs, which showed that they may possess advanced social intelligence while having rudimentary technical intelligence, Jolly (1966) posited that sociality preceded technical ability. Similarly, Humphrey (1976) argued that social games of plotting and counter-plotting were responsible for the intelligences of primates and humans alike. During the 1980s, theories such as this became more prominent. Lovejoy (1981) rejected the idea that subsistence strategies and tool production were the primary pressures for human specialization. Instead he suggested that a unique reproductive strategy, with extended childhood, intensified parenting, and stronger social relationships was pivotal to the origin of our species. But it was Byrne and Whiten's (1989) Machiavellian Intelligence Hypothesis which brought popularity to the theory that sociality is responsible for our intelligence. This integrated the works of Jolly and Humphrey and suggested that the ability to cooperate with and manipulate others was the primary pressure leading to our intelligence (Byrne, 1995). Thus, suggesting that social complexity was the primary driving force of cognitive evolution.

The work of Dunbar and colleagues on the Social Brain Hypothesis (SBH) provided support for Machiavellian Intelligence. The human brain is approximately 3 times larger than expected for a primate of our size, with a neocortex 61% larger than expected (when humans are excluded from the regression line: Rilling & Insel, 1999). Dunbar (1992) found a quantitative relationship between relative neocortex size and group size in primates and humans (DeCasien et al., 2017; Dunbar, 1998). This relationship is robust, with 70% of group size variation being species relative and correlating with neocortex size (Sandel et al., 2016). This theory has been highly influential. The SBH has been used to suggest changes in social structure, ToM ability, language, and technology in past hominins (Cole, 2012; Dunbar, 2003, 2009; Gamble et al., 2011; McNabb, 2012).

The SBH depends on social group size as the feature that predominantly increases pressure on social cognition. There are two primary reasons why animals merge into large groups, either to aid foraging or to mitigate predation through group cooperation (Dunbar, 2009). A combination of these two pressures is most likely to be the motive for past hominins, particularly following the introduction of more meat into the diet, as foraging tactics would have been synonymous with increased predation risk (O'Connell et al., 1988; Treves & Naughton-Treves, 1999). Following the formation of larger groups, competition for food and harassment by others, which has been shown to decrease reproductive success in females, may have increased (Dunbar & Shultz, 2007). Therefore, coping mechanisms would have been necessary to overcome new social stressors. Among modern primates these pressures are reduced by forming alliances through grooming, which creates a sense of obligation to aid an individual who is under attack or struggling to find resources (Dunbar, 2004). Our closest relatives, chimpanzees, form their strongest bonds with individuals who are either maternally related or the same rank when grooming is shared equally (Mitani, 2009). However, more complex appraisals of the social structure of the group are also used. The most successful individuals form coalitions with individuals who do not have bonds with each other. This suggests that they are aware of the relationships of others and can utilize this knowledge to their own advantage (Gilby et al., 2013). Hence, for our closest relatives, grooming and the manipulation of social information are integral mechanisms to mitigate the negative effects of group living. Due to grooming clique size and other displays of social complexity (lower ranked males mating more successfully, juvenile social play, and use of deception) correlating with neocortex size in primates, it supports the notion that social Machiavellian functions are the primary cause of encephalization in both primate and human evolution (Byrne & Corp, 2004; Kudo & Dunbar, 2001; Lewis, 2000; Pawłowskil et al., 1998).

As brain size increased through the hominin lineage, the SBH posits that group size increased beyond the primate limit. Consequently, grooming times would have exceeded the primate maximum of 20% of their total day (Dunbar, 2004). For example, if modern humans invested in grooming to the same proportions as primates, our group size means we would spend approximately 43% of our day grooming (Dunbar, 2003). Therefore, alternative methods of sociality were needed. Theory of Mind (ToM) and language are posited to be the primary coping strategies hominins developed to manage increasing group sizes.

ToM is the ability to infer the thoughts and beliefs (mental states) of other individuals. This is measured in levels of intentionality. For example, intentionality level 1 is the ability to infer one's own beliefs, whereas level 2 is the ability to infer another individual’s beliefs or thoughts, level 3 is the ability to understand someone’s beliefs about another individual. Humans are thought to be able to reach level 5 intentionality. ToM is suggested to have developed in a stepped progression in hominin species through time as brain size and group size increased (Gamble et al., 2011; McNabb, 2012).

Language is another function hypothesised to have developed to mitigate the costs of increasing group size and allow a further increase in group size (Aiello & Dunbar, 1993; Dunbar, 2003, 2017). Contrasting to ToM, language is thought to be a recent progression. It is argued that wordless singing was adopted by *Homo erectus* (500ka) to replace grooming. This led to the establishment of the anatomy needed for language (Dunbar, 2003, 2017). However, the capacity to use the grammatical structure needed for language is thought to have developed between 300ka and 80ka, with no clear consensus on whether language is human specific or Neanderthals and possibly earlier hominins possessed the ability (Atkinson, 2011; Dunbar, 2003; Johansson, 2013). Dunbar (2004) suggests that language requires intentionality level 2 or higher and that this facilitates interaction with 3 individuals simultaneously, therefore allowing humans to spend social time more efficiently and increase group sizes. This also reduces the human social time to the expected 20%. Thus, the SBH views language as a cognitive function which developed because of increased group size and processing power to make sociality more efficient. This allowed group sizes to increase further, increasing selective pressure for sociality, which in turn increased the complexity of language (and other social functions).

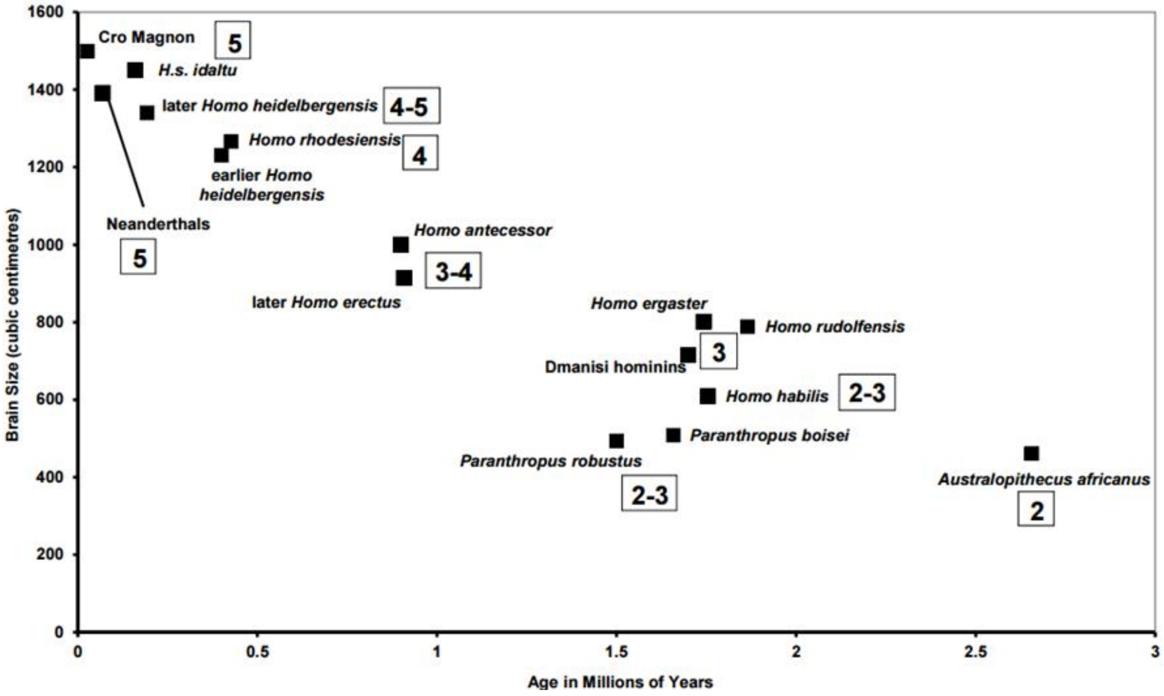


Figure 2. Hominin brain size plotted against time with orders of intentionality in numerals inside boxes (McNabb 2012).

Both ToM and language have been associated with technological proficiency. Hence, through association technological ability is regarded as a product of sociality, rather than technical pressures. ToM has been associated with technology in three ways. Firstly, the transmission of technological information is thought to be facilitated by mirror neurons, which are located in areas of the brain associated with ToM. These neurons activate when an individual performs an action. However, they also create an empathetic response when observing another's actions, and activate as if the observer was performing the action themselves. Development of the mirror neuron system is thought to have accentuated imitation ability, leading to an evolutionary progression from undirected emulation (seen in non-human primates), to high fidelity imitation, and finally intentional imitation utilizing ToM perspective taking. This is posited to be the cause of increased technological innovation through time as it facilitated a greater spread of new ideas and their integration into material culture (Hodgson, 2013). Secondly, increasing complexity in stone tool production has been related to increases in levels of intentionality, with it further being suggested that technology became social as well as functional when intentionality level 3 was reached (Cole, 2012). Thirdly, Acheulean handaxes are thought to require a minds-eye view similar to higher levels of intentionality (Gamble et al., 2011). The Cultural Intelligence Hypothesis argues that our enhanced ability to learn the collective skills of a social group and transmit knowledge through generations allowed the accumulation of material culture (Donald, 2000; Herrmann et al., 2007; Tomasello et al., 2005). Thus, the social abilities to share intentions, collaborate, understand other's minds, teach, and learn led to the complex technological knowledge of the hominin lineage (Hare, 2011).

Language has been suggested to relate to technology because lateralization of the brain for precise tool production involving two hands may have been the protoarchitecture needed for language (Ambrose, 2001). Further, the Broca's area (associated with the motor functions of language) is derived from areas related to fine motor hand control. It is suggested that as the frontal cortex expanded areas related to syntactic language became more pronounced and specialized, similarly as this took place areas related to object manipulation became more complex, allowing the production of more complex tools (Greenfield, 1991). Finally, it has been suggested that the production of lithic tools is directly comparable to the production of structured syntax, with both requiring production by conventional rules, anticipation of the next action needed, and an understanding of the overall goal (Stout & Chaminade, 2012). This has led to the suggestion that we may use the complexity of the material record to infer lingual complexity (Vieira, 2010). Further, I would argue this suggests that the evolution of technical abilities for tool production and social abilities for language coevolved.

The selection for prosociality is suggested to be so extreme that humans began to show features of domestication syndrome (Hare, 2007, 2017). From the Middle Pleistocene onwards, our ancestors had more feminized and trustworthy faces, with smaller brow ridges, suggesting reduced testosterone and increased social tolerance (Cieri et al., 2014). Our uniquely white sclera has also developed to reveal gaze direction and increase both the ability to share attention to cooperate, and the ability to trust another individual (Hare, 2017). Thus, the impacts of social pressures are now seen to account for, not only the development of technology, but changes in bodily features. While the impact of self-domestication has been recognized since Darwin's (1888, pp. 26–30) reflections upon the topic (Washburn, 1960), it has only recently gained traction within the context of the current focus on human sociality.

To sum up, there has been a shift in thought away from the view that pressure for increased technical ability are responsible for our cognitive evolution. The current dominant view is that social pressures, due to increasing group sizes and complexity, are responsible for our intelligence. Primates cope with increased social stressors by creating alliances through grooming and may use information on the social dynamics of the group to form more profitable alliances. However, in the hominin lineage group size (as inferred from brain size) increased beyond the primate limit. Therefore, alternative strategies were needed to mitigate increasing social pressures. ToM, language, and increased tolerance are suggested as efficient adaptations that allowed social group size to continue to increase. It is argued that ToM developed in tandem with group size, language developed within the last 300ka, and tolerance gradually developing since the Middle Pleistocene, with the latter two facilitated by enhanced ToM abilities (Gamble et al., 2011). Further, these abilities have been associated with technological proficiency in a number of ways. Thus, it is now considered that social pressures are responsible for our intelligence.

To test how well this theory explains changes in the archaeological record, hominin encephalization will be evaluated in 4 stages, utilizing the three stages identified by Gamble et al. (2011):

(1) *Primates*: specifically focusing on our closest relatives, chimpanzees, and their ToM abilities to infer the skills of the last common ancestor (LCA).

(2) *Early Homo*: when hominin brain size first exceeded the primate limit and the earliest stone tools were produced.

(3) *Homo erectus and heidelbergensis*: when brain size exceeded 1000cc, migration increased, and tool shape became standardized with social functions.

(4) *Neanderthals and Humans*: when brain size reached modern sizes, focusing on the differences between Neanderthal and human social and material culture.

This will allow the strengths and flaws of the theory, and the impact of technical pressures, to be identified. Following this, the theory will be assessed in relation to Autism, a condition associated with social differences which may cause difficulties, but also leads to many technical advantages which would be beneficial to a hunter gatherer group.

Chapter 3: An Evaluation of Conflicting Evolutionary Pressures Between Species

This chapter will evaluate what impact social and technical pressures have had on our evolution at a species level. Firstly, we will investigate the social and technical abilities of primates, in particular chimpanzees, and assess whether they have theory of mind. This will give an estimate of the capabilities of the LCA, and provide a beginning for how these skills may have developed in the hominin lineage (3.1). We will then assess the archaeological evidence of behaviour and changes in brain structure, for Early Homo (3.2), Homo erectus and Homo heidelbergensis (3.3), and Neanderthals and Humans (3.4), to determine the impact of both social and technical evolutionary pressures on these species.

3.1 Primates

By using primates, and in particular chimpanzees, as an indirect way to assess the capabilities of the LCA, it is hoped that this will provide a beginning for how social skills and in particular ToM have developed in the hominin lineage. However, it must be recognised that chimpanzees have also been developing and specializing for the past 6 million years. This is highlighted by their stark behavioural differences from bonobo’s, with whom they diverged 2-3Ma. Therefore, although this provides an approximate theory of the capabilities of the LCA, divergent and convergent evolution during the past 6Ma do not allow a clear picture to be developed. However, when cautious some inferences may be made.

As shown above, primates may use social information to create the most profitable alliances. ToM and the virtual appraisal of group dynamics are thought to be integral to human complex sociality. However, while it has been suggested that great apes may possess these abilities, there is a clear difference between ape ability and human ability. Many researchers therefore conclude that these skills have become accentuated through the hominin lineage. To investigate how social skills may have developed in the hominin lineage we must first determine how they operate in primates.

As social group size increases, structural complexity and group dispersal must increase due to limited resources. This means that changes within the group may not be visually seen by all group members and more complex mechanisms are needed to appraise the state of the group. Changes must instead be mentally represented, based upon brief meetings, mental representations of those who aren’t present, and inferences based up other’s behaviour. Consequently, in fission-fusion societies, such as chimpanzee groups, mental simulations of group dynamics are paramount to understanding the social state of the group and assessing the value of alliances, an ability shown above to increase reproductive success and the probability of increasing in rank (Barrett et al., 2003). The Social Brain Hypothesis argues that group size increased through time (Dunbar, 1998). Therefore, the ability to simulate group dynamics would have been under high selective pressure. Barrett et al. (2003) argue that this virtual appraisal may be a precursor to ToM. From this it is clear that chimpanzees have mental abilities abstract from the present that allow the simulation of group dynamics. This provides a beginning for the development of ToM and advanced social skills. However, it does not display the extent of chimpanzees mentalizing abilities or answer Premack and Woodruff's (1978) question, 'Does the Chimpanzee have a Theory of Mind'.

Premack and Woodruff (1978) first answered their question by concluding that chimpanzees understand desires, intentions, and affective attitudes but not the knowledge an individual holds. As this subject developed the mind attributed to chimpanzees and the wider primate clade has become much more complex. Hare et al. (2001) have shown that they understand what others see and that this information can be used socially. This has been corroborated by observations of wild subordinate chimpanzees deceptively hiding their genitals from more dominant males while still keeping them in view of females (Byrne & Whiten, 1992). This form of deceptive behaviour has been shown in all anthropoid primates. However, rates of deception correlate with neocortex size and only great ape deception suggests mentalizing, with monkeys showing only learned associations (Byrne & Corp, 2004; Byrne & Whiten, 1992). Call and Tomasello (2008) have conducted a meta-analysis of 30 years of studies in this subject and concluded that, due to lack of evidence of the ability to attribute false beliefs, chimpanzee cognition is 'perception-goal' oriented rather than 'belief-desire'. However, previous observations of wild chimpanzees calling selectively to individuals who are ignorant of a danger shows that in a natural setting they may be able to understand the false beliefs of others and use this information to ensure group safety (Andrews, 2017; Crockford et al., 2012). Recent laboratory experiments have also yielded positive results for the ability to understand false beliefs. By using eye tracking technology and a more amusing false belief test scenario than usual to capture the apes attention, Krupenye et al. (2016) have shown that chimpanzees, bonobos and orangutans anticipatorily look in the direction where the agent falsely believes an object to be, rather than its true location. This suggests at least an implicit understanding of false beliefs (de Waal, 2016; Kano et al., 2017; Krupenye et al., 2016). Buttelmann et al. (2017) have also shown, using two false belief helping tasks compared to true belief and ignorance conditions, that great apes can understand false beliefs and that this alters their helping behaviour. Therefore, showing that in a laboratory setting information of other's beliefs can be used socially.

However, the evidence for ToM in great apes is still unclear with many suggesting either that they do not possess full ToM or that they possess no ability to attribute mental states and that positive results are due to the use of learned logical associations (Penn et al., 2008). For example, Hare et al. (2001) used a competitive feeding paradigm, and found that subordinate individuals approached the food more often when the dominant chimpanzee was uninformed, suggesting that they understood what the dominant knew. Penn and Povinelli (2007) critiqued these results by suggesting that this response was equally likely to be due to rules developed from past experience, 'Don't go after food if a dominant who is present is oriented towards it' (Penn & Povinelli, 2007). They believe that the ability to infer mental states is human specific. In their view, humans have evolved beyond the abilities of chimpanzees in both the ability to infer goals from behavioural cues and by developing a second 'representational system', which interprets behavioural cues in an abstract mentalistic way independent of the task being performed (Penn & Povinelli, 2013). They and many other researchers believe that the current experimental methods do not possess the ability to distinguish between mentalizing and goal oriented behavioural reading (Lurz, 2011; Penn et al., 2008; Penn & Povinelli, 2007, 2013).

Call and Tomasello (2008) have attempted to rectify this issue by suggesting that being able to infer a goal despite the agent making mistakes shows a division between behaviour reading and attributing mental states. Penn and Povinelli (2013) disagree, arguing that the intention could be logically determined behaviourally. These contradictions make it impossible to progress in the subject. If no current test can distinguish between attributing mental states and behaviour reading, then neither theory can be nullified or verified. All positive results for ToM can be attributed to behaviour reading, and all negative results can be credited to not understanding the behaviour. For example, the false belief test has been suggested to be the defining test, as it is the only test able to reliably display that an individual understands the mental view of others (Penn & Povinelli, 2013). The inability of primates to pass false belief tests (before now) has been viewed as evidence of lacking a ToM. However, put within the contradiction above this is either the case, or they do not understand the behaviour the same way as humans. This has been noted by Andrews (2017) who suggested this is similar to Vinden's (1999) results, which showed using three non-western populations that they may have a different ToM that isn't activated by western false belief tests. Further, as is shown in studies of Autism, when the task is understood hacking strategies reliant on understanding behaviour and perception that don't require ToM may be used to pass the test (Frith et al., 1991; Happé, 1994). Even when positive results have been found, such as Krupenye et al.'s (2016) study, they have been critiqued in the same way by Heyes (2017), who has suggested that visual aspects of the scene, rather than mentalizing, dictated the apes eye movements (when the individual with the green shirt appears the primates looked where the object was last time that colour was present because it acts as a cue). Such contrasting views have led to a stalemate, due to the individual biases of researchers.

Currently, we may not confidently conclude that chimpanzees possess or lack a full ToM as no unbiased method is currently being used by either side of the debate. However, we can conclude that chimpanzees utilize complex social mechanisms to both mitigate the costs and enhance the benefits of group living. They may: (1) understand what another individual has seen or heard in the present and the near past and use this information both competitively (Byrne & Whiten, 1992) and collaboratively (Crockford et al., 2012), even if this is not linked to a mentalistic attribution of knowledge or even what object within their gaze they are observing (Hare et al., 2001; Hostetter et al., 2007; Melis et al., 2006; Povinelli et al., 2000; Tomasello et al., 2003); (2) attribute goals to other individuals, either through an understanding of the other's mind during the activity and in relation to other activities (Call et al., 2004; Call & Tomasello, 2008; Uller, 2004), or through systematic reasoning of the behaviour (Lurz & Krachun, 2011; Penn & Povinelli, 2013).

Either way it is clear that this facilitates complex social behaviour. Further, I would argue that many negative results for ToM are a product of the abstract methods used in labs to test for them. The social complexity of wild chimpanzees outweighs what has been observed in labs. For example, contrary to what has been stated by Penn and Povinelli (2013) chimpanzee mothers from Taï have been seen to teach their young how to crack nuts (Boesch, 1991). In one case an adult chimpanzee noticed a juvenile struggling with an oddly shaped hammer. The adult took the tool and slowly rotated it for a full minute into the correct position. The adult then cracked several nuts and gave back the tool. The juvenile continued to crack nuts using the position it had been shown. Even when the juvenile had further difficulties it did not alter how the tool was gripped. This example shows the teacher understood the goals of the juvenile even though they were making mistakes. Further, active teaching shows that they may share joint attention and enforce attention upon an object. This is an essential prerequisite to ToM (Baron-Cohen, 1991). They have then used this to convey a meaning. When the chimpanzee rotated the tool, the action was slowed to aid the understanding of the juvenile. A mentalistic interpretation of this action would be that the adult chimpanzee understood that the juvenile wouldn't understand the action unless it was slowed down and the importance amplified - thus making allowances for an uninformed mind. A behavioural interpretation of this would be that through past experience the chimpanzee has realised that demonstrations need to be slowed or the juvenile won't be able to imitate. Either way, this is more complex behaviour than what has been shown in a lab setting and it has been suggested by Penn and Povinelli (2013, p. 71) in their denunciation that chimpanzees don't teach, that this would show, 'an ability to reason about others' goals as internal representational states'. This is convincing evidence for at least the beginnings of ToM in wild chimpanzees.

The evidence is becoming more convincing despite opposition. However, what is clear is that there are two systems that facilitate complex sociality, a behavioural system (a complex form of systematic behaviour reading), and a ToM system. This is similar to Apperly and Butterfill's (2009) suggestion that understanding beliefs relies upon two systems, one inflexible and efficient (behavioural system), the other flexible yet inefficient (ToM). This is consistent with Bermúdez's (2003) suggestion that the majority of our sociality is a product of primitive structures rather than ToM. However, the inflexibility of this structure is thought to be overestimated and it is suggested that some form of multi-system architecture utilizing executive function is most likely to be the precursor to ToM (Bermúdez, 2003; Christensen & Michael, 2016). I believe Central coherence is also likely to be vital to this system as it requires the integration of a wide range of information to form a view of another's behaviour.

Clearly, chimpanzees are highly proficient in using the behavioural system for understanding other's actions. However, it is unclear whether they possess a ToM due to biases in the subject. Based upon the current evidence it may be suggested that while they may not possess a full ToM they possess some form of lesser mentalizing ability which is rarely used and cognitively demanding. This mentalizing may be an extension of the behavioural system which allows a faint and imprecise view of another individual's mind.

Chimpanzee's technical abilities are also relatively complex. As shown above, they are capable of using tools. However, their ability is more complex than commonly assumed. Apes in comparison to monkeys have a greater understanding of cause and effect when using tools, thus making them more adept at tool use tasks (Visalberghi et al., 1995). Further, the chimpanzees from Fongoli, Senegal have been shown to use spears produced in a 5-step procedure to hunt bushbabies (Gibbons, 2007; Pruetz & Bertolani, 2007). I believe this shows that chimpanzees are able to keep a desired goal in mind for an extended period of time, while completing steps to achieve the objective, suggesting a greater working memory than has been suggested by some authors (Read, 2008). Thus, their complex tool use is facilitated by complex technical abilities, as well as the social transmission outlined above. They have also been shown to use long term spatial memory to enhance foraging ability, by remembering and approaching particular high yield trees in a goal directed manner in separate seasons and years (Janmaat et al., 2013). Chimpanzees may also have a better spatial working memory than humans (Inoue & Matsuzawa, 2007). Although, this has since been critiqued, suggesting that when under the same test conditions humans outperform chimpanzees (Cook & Wilson, 2010). Finally, it has been shown that chimpanzee and human short-term memory is similar. Each can remember no more than 5-7 objects. However, humans may use language to expand the functional use of this limited space. For example, by remembering 5 phrases, rather than words (Premack, 2007). We can suggest from this, that while chimpanzees have complex technical skills in certain areas, largely they are more accentuated in humans.

It is likely that the LCA had many of these technical and social abilities, and a highly sophisticated behavioural system. However, as noted at the start of this section, 6 million years separate chimpanzees from the LCA and further behavioural evolution is likely to have taken place. Therefore, while we may make inferences about the LCA based upon chimpanzees and other primates, it is important to note that these are tentative rather than definitive conclusions. What is most important to recognize from this section is that understanding other individual’s minds is a large adaptation which may not have occurred in one motion, but may have gradually developed with the cognitive demand lessening, interpretations of other minds becoming clearer and the frequency of use increasing through evolution until a clear level 2 intentionality was formed. Further, interpretations based upon behavioural reading rather than ToM can lead to complex sociality. Therefore, this comparison with primates provides a beginning to understanding the linear adaptation of ToM as a gradual progression derived from behaviour reading that was likely starting to form within the LCA, and highlight the vast social developments our lineage has made. We must also recognize that the technical abilities of the LCA were likely complex, with sequential tool production already established and advanced spatial memory supporting foraging. However, many technical functions, including those assessed here, were greatly accentuated within the hominin lineage.

3.2 Early *Homo*

Archaeological Evidence of Behaviour

Early *Homo* is not the earliest user of stone tool technology. Stone technology likely has a longer history, as is seen by the chimpanzee and capuchin use of unmodified stone tools (Proffitt et al., 2016), the sophistication of the Oldowan technocomplex which suggests prior experience, and hand morphology suggesting hominin tool use was possible by 3.2Ma (Panger et al., 2002). However, early *Homo* was more reliant on stone tools and used more complex technology. This likely facilitated greater access to meat or a more versatile diet, which would have allowed higher energy budgets and increased selection pressures for more technologically and socially adept groups (Plummer, 2004). Gamble et al. (2011) highlight several further examples of technological complexity. Selection and transport of particular materials to increase flaking success (Stout et al., 2005). Use of prepared cores which have been shown to increase cutting edge and reduce waste (Brantingham & Kuhn, 2001; de la Torre et al., 2003). Possible inclusion of meat shown by high $\delta^{13}C$ values in hominin enamel (Lee-Thorp et al., 2010; Sponheimer et al., 2013; Sponheimer & Lee-Thorp, 1999).

I argue that these examples suggest increased pressure for technical ability. The use of prepared cores suggests the beginnings of a ‘mind’s eye’ to visualize the final form of a tool. Further, although it is unclear from isotopic data due to lack of evidence (Lee-Thorp et al., 2007), greater reliance on tools may suggest increased meat consumption, or at least a more versatile diet relative to Australopithecines (Ungar et al., 2006). Meat consumption would put hominins in competition with predators and put pressure on the ability to identify hidden figures in the environment, spatial memory of where prey and predators are frequently located, and understanding the systems of the environment. However, these examples also suggest increased social complexity. Increased and complex tool production suggests greater social learning and social cohesion to find resources. Meat consumption would suggest a greater emphasis on cooperation to overcome predators during scavenging or hunting (O’Connell et al., 1988; Treves & Naughton-Treves, 1999), and sharing during consumption (Plummer, 2004). This would allow higher energy budgets and permit brain sizes to increase. Further, if meat consumption did not increase, a more versatile diet would have led to a more seasonally stable energy intake which has been shown to enable increased brain sizes (Navarrete et al., 2011).

At this time there was a shift to more open C_4 grassland replacing C_3 woodland, with smaller scale fluctuations causing variability within this (Lee-Thorp et al., 2007). To adapt to this *Homo habilis* and *Australopithecines* became more generalist feeders, as stated above. This is shown by the high individual variability in $\delta^{13}C$ which indicate different levels of C_4 plant consumption (Lee-Thorp et al., 2007, 2010; Sponheimer & Lee-Thorp, 1999; van der Merwe et al., 2008). Contrasting to this, chimpanzees in savanna areas with predominantly open C_4 grassland feed almost exclusively in smaller forested or wooded areas, consuming C_3 plant foods, showing high reliance on particular resources, and little consumption of meat (Sandberg et al., 2012; Schoeninger et al., 1999). An increase in dietary breadth would have allowed the two hominin species to survive more comfortably in these highly variable environments.

Resource acquisition skills, as show at Gona (2.6Ma) by the selection and transportation of stones of a particular quality for tool production (Stout et al., 2005), would have been easily transferable for foraging and scavenging. This would be particularly useful in more arid conditions, when resources would be sparser, and selective stone acquisition would act as a form of practice during more humid periods. Thus, the technical ability to acquire spatial knowledge of the environment and recognize desirable resources for foraging, was not only under natural selection, but also under artificial selection during times when resources were plentiful. Additionally, the increase in dietary breadth to incorporate C_4 foods suggests selective pressure on long-term memory to remember what resources are edible.

Social pressures would also affect this last point, with increased cultural knowledge being imperative for groups to collect the more generalized diet, in a similar way to how later hominins would collect knowledge of material inventions. The transition to more open environments has also been argued to increase fission when searching for resources (Gamble et al., 2011). As shown in the previous section, this increases pressure on social aspects of the brain to simulate the dynamics of an invisible group.

Finally, increasing predation as the environment became more open would further intensify social selection.

Hence, the archaeological evidence suggests that both social and technical abilities were under intense pressure to develop.

Changes in Brain Structure

At this time brain size increased to approximately 600cc. From this increase in brain size we may infer several interpretations. Physiologically, we may infer that an alternative diet, reduction in digestive tract, less adipose depots, or a smaller locomotor impact of adipose depots must have developed to account for the increased energetic cost as the number of neurons in the brain increased (Aiello & Wheeler, 1995; Fonseca-Azevedo & Herculano-Houzel, 2012; Herculano-Houzel, 2011; Navarrete et al., 2011). Behaviourally, according to the SBH we may infer that *Homo habilis* reached group sizes of between 70 and 100 individuals (Gamble et al., 2011). If social bonding was formed through grooming when group sizes reached this size, *Homo habilis* would have exceeded the maximum limit that primates allow for grooming, 20% of their daily time (Dunbar, 2004). Therefore, different strategies must have been utilized to reduce social time. As seen in modern primates this may be achieved through increased vocalization and fission (Lehmann et al., 2007). Therefore, following the social theories, rearrangements in social and neural structure must have taken place in early *Homo* to facilitate larger group sizes and the skills outlined above.

Several visible neural rearrangements took place early in the hominin lineage. Firstly, the lunate sulcus (between the primary visual cortex and the parietal cortex) was reconfigured. This increased the size of the parietal and temporal association cortices and decreased the visual cortex and indicates an improvement of visuospatial and sensorimotor abilities used in object manipulation (Holloway, 2015; Sherwood et al., 2008). This change is also significant because the junction between these two areas, the temporo parietal junction (TPJ), is consistently activated by ToM, empathy and testing internal predictions (Carrington & Bailey, 2009; Decety & Lamm, 2007; Samson et al., 2004). Expansion of these two areas may have enhanced internal representative abilities. Secondly, the frontal lobes and temporal poles, linked to general social cognition, facial recognition, the mediation of social behaviour and ToM, began to expand (Mychack et al., 2001; Olson et al., 2007; Saxe & Powell, 2006). Particularly, Brodmann’s area 10 in the medial prefrontal cortex, associated with abstract thinking and planning future actions based upon past experiences (particularly in a social context), expanded (Euston et al., 2012; Falk et al., 2000). This suggests that more complex cognitive mechanisms abstract from the present reality were beginning to form. Thirdly, the Broca’s and Wernicke’s areas enlarged with an overall shift to more human-like asymmetries (Gibson, 1991; Tobias, 1987, 2009). This has prompted debate over whether language was present in *Homo habilis*. However, due to the positive allometric relationship between grey matter and white matter (Rilling & Insel, 1999), it is likely that a brain of 600cc did not have the integrative mechanisms necessary for language. Nevertheless, expansion of these regions may have facilitated more complex vocalization than is seen in modern primates.

Additionally, modern FMRI studies of individuals knapping Oldowan technology have shown activation of visuomotor elements of the parietal cortex, the right hemisphere homologue of the Broca’s area, and the medial prefrontal cortex, suggesting co-evolution of language and tool production (Stout et al., 2011; Stout et al., 2008). These areas have been shown above to be expanded in *Homo habilis*, therefore providing support and a neural mechanism for the species having enhanced technological abilities.

The neural changes presented here show that the overall cortical architecture of hominins at this time was becoming increasingly more human. Following McNabb’s graph (2012: figure 1), it is suggested that this period represents the time when hominins were approaching level 3 intentionality. A level which suggests the ability to create and accept social norms (Dunbar, 2003). A more conservative estimate is presented by Gamble et al. (2011) of level 2 intentionality being reached at this time.

These changes would have facilitated the more complex sociality needed for an expanded and dispersed group and would likely have allowed allogrooming times to decrease to the expected 20%. Further, these new skills may have begun to replace allogrooming, due to selection for hairlessness to reduce ectoparasite load (Pagel & Bodmer, 2003; Rantala, 2007). Therefore, complex socio-cognitive adaptations were a major change at this time.

However, due to the association of many of the expanded regions to technology, and the expansion of regions related to object manipulation it is clear that the selective pressures were not wholly social, and were perhaps more complex than the current literature allows, with a significant impact from technical pressures.

To sum, increased C_4 grassland and environmental variability led to greater social and technical evolutionary pressures. This provoked many behavioural changes in early *Homo*, ranging from an increased reliance on tools, to greater social cooperation. The neurological changes which took place to facilitate this behaviour, show expansions in areas related to object manipulation, ToM, and broader social cognition. However, many of the areas related to social cognition, and in particular language, are also associated with tool use. This suggests that both technical and social pressures were significant in cognitive evolution at the time, and that as well as modules of the brain specializing for either social or technical abilities, they could also coevolve for both.

3.3 *Homo erectus* and *Homo heidelbergensis*

Archaeological Evidence of Behaviour

The shift to *Homo erectus* and *Homo heidelbergensis* is characterized by an increase in brain size to 1000cc, an increase in population sizes and densities (inferred from site distributions and material densities), larger body size, increased dispersal, standardization of tool shape, stasis in material culture, and exaggerations of size and symmetry in stone tools that go beyond function.

Site distribution and material densities suggest an increase in both group and population sizes (Hawks et al., 2000; Klein, 2009), which put further pressure on social abilities. The SBH identifies this population expansion, with estimations of population density correlating with brain size (Bailey & Geary, 2009), and a large increase in brain size at this time suggesting an increase in group sizes to 100-120 individuals (Gamble et al., 2011). Social theories suggest that increased group sizes at this time forced the brain to rapidly evolve. Larger groups would have to disperse further to find resources (Gamble et al., 2011). Consequently, putting more pressure on the ability to simulate group dynamics, thought to be a precursor of ToM (Barrett et al., 2003), and may explain some of the exaggerated features of stone tools.

At this time the environment became more arid, and by 1.6Ma open grassland dominated (deMenocal, 2004; Lee-Thorp et al., 2007; Maslin et al., 2014). Due to these environmental stressors, as well as disease and parasitic stressors, *Homo erectus* began to disperse sporadically into Europe and Asia (Bar-Yosef & Belfer-Cohen, 2001; Larick & Ciochon, 1996). In order to survive in new, open, and varied environments they would have required a more generalized toolkit, with new inventions. For example, the use of projectiles as seen at Boxgrove would enable hunting in more open regions (Roberts, 1997). It must also be noted that *Homo erectus* is physically more suited to open air habitation than previous hominins with complete terrestriality, longer and stronger hind limbs (Ruff, 2009), and endurance running (Bramble & Lieberman, 2004). This likely greatly facilitated migration. Home ranges could be increased due to more efficient mobility, enabling the aggregation of resources from a wider area and less reliance on individual sources. Particularly important for the finding of water in an increasingly arid environment (Finlayson, 2014, pp. 69–83).

I believe their survival in more varied, open, and arid habitats, increased movement out of Africa or within Africa, and increased population sizes are likely to have required stronger social cohesion and enhanced social abilities, which are thought to be the drivers of further encephalization leading to *Homo heidelbergensis*. Groups which were previously tethered to more vast and permanent sources of water were now required to search for more seasonally ephemeral bodies of water. They were required to disperse further on a local (group) and global (species) basis to find resources and were forced to be less selective for familiar foods or easier prey, likely leading to the hunting of larger game (such as at Boxgrove). This increased risks from predation, but also starvation and dehydration if they travelled to the wrong areas (Finlayson, 2014, pp. 69–83). Such stressors create conflict between groups for resources, which further requires collaboration and social skills to overcome competitors, trust in others suggesting where to go for resources would be needed, technical spatial abilities to find and remember the seasonal layout of the environment would be imperative, and alternate social mechanisms would be necessary for a group which would be highly fragmentary for a large proportion of time as they searched for resources.

These developments are reflected in the material culture, which transformed dramatically at this time.

Tool shape became standardized by *Homo erectus* 1.5 million years ago. This standardized toolkit was characterized by large cutting tools (LCTs) such as bifaces, picks, and cleavers, which dominated until 300ka (Ambrose, 2001). The standardization of these forms suggests that the maker holds a mental image of their desired tool and how it will be formed during production, an advanced technical ability. There are alternative explanations for their forms, such as rates of reduction. However, the theory that toolmakers have a predetermined goal is currently the most accepted view (Dibble, 1995; McPherron, 2000).

This strict adherence to form is beyond functional and therefore is present for a different most likely social reason (Machin et al., 2016, 2007). It has been argued that highly symmetrical handaxes may be used for sexual display as an indicator that the maker has good health and intellect (Kohn & Mithen, 1999). This was refuted due to a lack of support for aspects of the theory: an absence of evolution in handaxe form as different anatomical features were being selected as sexually attractive in the toolmakers; evidence for cooperation in handaxe production showing that it may not be an indicator of individual ability; better indicators of health being available (Machin, 2008). However, it was applauded as the first attempt to explore the social element of this material. Hodgson (2009) proposed a more technical theory, suggesting the ritual production of symmetrical objects provides comfort. He argued that the affinity for symmetry developed prior to the production of symmetrical objects to increase detection of living organisms (highly symmetrical) among inanimate objects, as symmetry prompts further scrutiny of visual stimuli. Through time the ventral 'what' system located in the inferior parietal lobe, and dorsal visuo-spatial systems located in the superior parietal lobe became increasingly integrated. This allowed increased motor planning, increased mental rotation abilities, and more interest in 'what' objects are and hence their categorization. Consequently, as the parietal lobe increased in size and intra-connectivity between 1.6Ma and 300ka, these skills allowed the predisposition to symmetry to be acted upon (Hodgson, 2009, 2005). Even if the production of handaxes is determined by a preadapted predilection towards symmetry it is clear that, as well as representing a neurological change in areas associated with technical ability, it is a wide social change, possibly signifying the earliest symbolic cultural thought (Le Tensorer, 2008). Perhaps the affinity to symmetry merely dictated the form that the symbol took. Whether this symbol was a competitive sexual display, or a collaborative display of trust as suggested by Spikins (2012), it clearly represents a fundamental change, socially, technically, and neurologically.

At this time physiological changes are suggested to promote social changes. Increased body, brain sizes and their associated energetic costs imply a greater reliance on nutrition dense foods such as underground storage organs and meat (Aiello & Key, 2002). Greater cooperation would be required to obtain the large amounts of energy needed either through active hunting, scavenging, or competing against predators for carcasses. *Homo erectus* clearly accentuated the gathering and hunting skills of *Homo habilis*. However, evidence for more extreme forms of cooperation than attaining food are evident at this time. The transportation of meat to areas of group occupation suggests that sharing may have occurred (Isaac, 1978). Individualistic hunting or reward based upon hunt participation do not account for the energetic costs of *Homo erectus*. Aiello and Key (2002) suggest that when pregnant or nursing, mothers would be unable to provide themselves with the energy they needed. Therefore, cooperation was key and was managed in several ways. Grandmother's and older siblings helped to care for children, and males provided resources to increase their likelihood of mating (Lovejoy, 1981). This collaboration decreased interbirth intervals and increased efficiency (Aiello & Key, 2002).

However, this collaboration requires individuals to reduce their own gain in order to help another. While food sharing is seen in chimpanzees it is largely in response to begging by reciprocating allies, close kin, harassers or to increase the probability of mating (Silk et al., 2013). It is reasonable to suggest that sharing functioned in this way in Australopithecines with slight developments in *Homo habilis*. However, *Homo erectus* and *Homo heidelbergensis* show more selfless prosocial forms of sharing. KNM-ER 1808, a *Homo erectus* individual from Koobi Fora (1.6Ma), suffered from hypervitaminosis A, a condition caused by over ingestion of liver which led to abnormal bone growth up to 7mm thick over all long bone shafts and reduced bone density (Walker, 1981). The condition likely reduced mobility and led to dependence on others. In order for the individual to survive long enough for the illness to be present on the bones, they would have needed care from others for weeks or possibly months (Spikins et al., 2010). A second example is the Dmanisi hominin from Georgia who lost all but one tooth several years before death and would have required care (Lordkipanidze et al., 2005). Evidence of a herniated disc in the lower lumbar region of a *Homo erectus* from Nariokotome (1.5Ma), which occurred several months before death suggests social care (Haeusler et al., 2013). The final examples are from Sima de los Huesos (approximately 500ka), where late ancestors of Neanderthals cared for a child with craniosynostosis, an elderly individual with locomotive difficulties, another individual with ear hyperostosis which likely caused deafness, and one with a severe dental abscess (Bonmatí et al., 2011; Gracia et al., 2009; Meyer et al., 2016; Pérez et al., 1997). Examples such as these have been used to suggest that hominins were becoming more compassionate at this time (Spikins et al., 2010; Spikins, 2017).

Reduced sexual dimorphism through the hominin lineage may also support this suggestion (see figure 3), as lower dimorphisms suggest less male-male competition and pair bonding. Further, following the Self-Domestication Hypothesis, increased feminization suggests lower testosterone levels and increased tolerance (Hare, 2017). However, studies may exaggerate dimorphisms in Australopithecines due to small and fragmentary samples sizes, imperfect sexing, and inaccurate proxies for calculating body weight (Larsen, 2003).

Combining this increased evidence of sharing, care, and collaboration with the suggestion that handaxes were a social display of trust (Spikins, 2012), it may be concluded that handaxes had multiple functions. Firstly, they fulfilled an aesthetic predilection to symmetry as the parietal lobe became more connected and provided comfort. Secondly, they were a display of social trust that the maker had the patience to care for something or someone without the prospect of return. Thirdly, this display of care likely increased the probability of mating due to females preferring males who would aid them during pregnancy. Importantly, the first two functions are not male specific. Therefore, while it may be more profitable for males to produce handaxes, it would still have been profitable for females to produce them.

The comfort provided by a highly symmetrical handaxe may have also functioned in another way. Spikins et al. (2010) suggest that with modern humans objects began to be cared for as symbols of supportive relationships. A 10-fold increase in the home range sizes of *Homo erectus* relative to Australopithecines may have caused this mechanism to develop earlier than thought (Antón et al., 2002). Spikins (2012) suggests that handaxes may remind others of an individual’s trustworthiness. I argue this would be most effective if the handaxe was gifted to another individual, so that while they were away from the maker the object was a source of comfort in times of stress or loneliness and reminded them of the maker. An increase in raw material transport distances from ≤1 km to ≤15 km at this time has commonly been used to suggest extensive planning prior to stone tool use (Marwick, 2003). However, the extensive transportation of hand axes combined with their elaborate form and *Homo erectus'* large home range may support their use as comfort objects. This would enable social bonds to be strengthened and reaffirmed even when an individual was absent, a method which may be made even more efficient if multiple individuals helped produce a single handaxe. This would have provided an alternative to language to aid increasing group sizes and helped stabilize a dispersed group.

As can be seen, hominins at this time would have been under high pressure to adapt technically and socially. The increasingly open environment and arid conditions would have led to selection for individuals with a better understand of the systems in the natural environment and enhanced spatial abilities to find and remember the seasonal layout of the environment. Further, the ability to detect hidden predators and prey may have been even more selectively advantageous. This intense pressure may have led to the predilection to symmetry described above (to detect animals), which was then acted upon when producing handaxes. At the same time, greater group sizes, dispersal, energy requirements, and predation would have increased social pressures. This likely led to increased collaboration, a better ability to visualize group dynamics, and new methods of socializing utilizing material culture to strengthen bonds. But what neurological changes took place for these skills to develop?

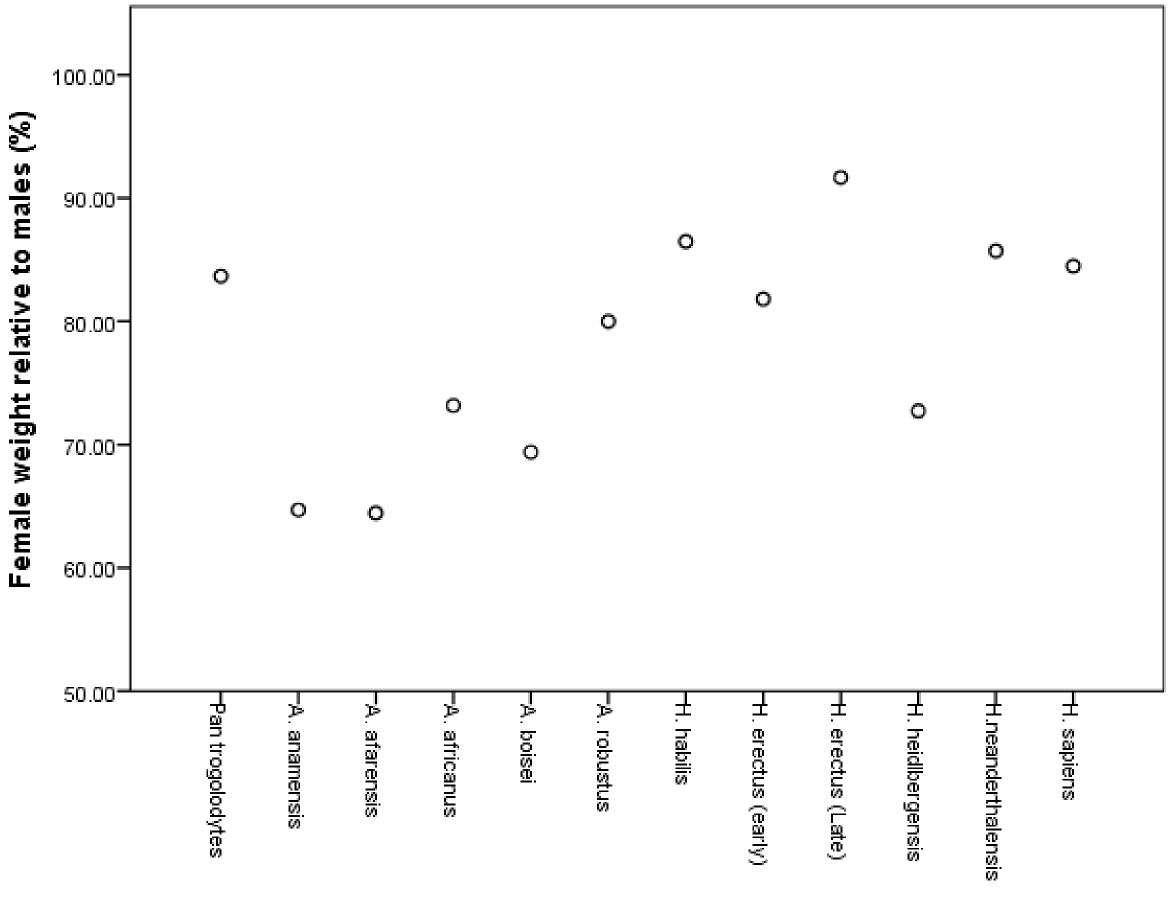


Figure 3. Hominin female body weight as a percentage of male body weight, higher percentage suggests less dimorphism (data from Leonard & Robertson 1994; Leonard et al. 2003; McHenry & Coffing 2000; Sorensen & Leonard 2001).

Changes in Brain Structure

With the speciation of *Homo erectus* brain sizes reached an average of between 800-1000cc (Bruner et al., 2015). Due to their increased body size, they had a similar relative brain size to *Homo habilis*. This has been used to suggest that they had similar intelligence levels (Wynn, 2002). However, relative brain size remained fairly constant until the speciation of *Homo sapiens (*Kappelman, 1996*)*. Therefore, unless a unique change occurred in the hominin lineage we would have to suggest intellectual progression was static for 2 million years, a conclusion which contrasts with the material record.

Several advances in comparative neurology rectify this issue. Deaner et al. (2007) conducted an analysis of primate intelligence and found a greater relationship with absolute rather than relative brain size. This is due to intelligence correlating with number of neurons and their conduction velocity (Roth & Dicke, 2005). The density and velocity of which remains the same through the primate clade, including in humans (Azevedo et al., 2009; Herculano-Houzel, 2009, 2012). Therefore, increases in brain size through human evolution correlate with intellectual capacity. Due to the high expense of additional neurons, great apes usually trade an increased brain size, for a decreased body size (Herculano-Houzel, 2011). As can be seen in figure 4, brain size increases consistently through time (B). Meanwhile body size decreases through time until *Homo erectus* when body size shows a sharp increase (A), indicating that this was the time when body size and brain size became disconnected (chimpanzees are used as a proxy for the LCA). The separation between the two was likely facilitated in two ways. Firstly, cooking, as seen at Gesher Benot Ya'aqov (790kya), and indicated by a smaller jaw size, and energy requirements for female *Homo erectus* suggesting that they would have had to chew raw meat for 5.7-6.2 hours per day (Alperson-Afil & Goren-Inbar, 2006; Fonseca-Azevedo & Herculano-Houzel, 2012; Wrangham & Conklin-Brittain, 2003). Secondly, by reducing gut size, a highly expensive tissue (Aiello & Wheeler, 1995). This would have been facilitated by eating higher quality food, likely through cooking. As shown by figure 4B this untethering sped up encephalization and allowed intelligence to increase exponentially.

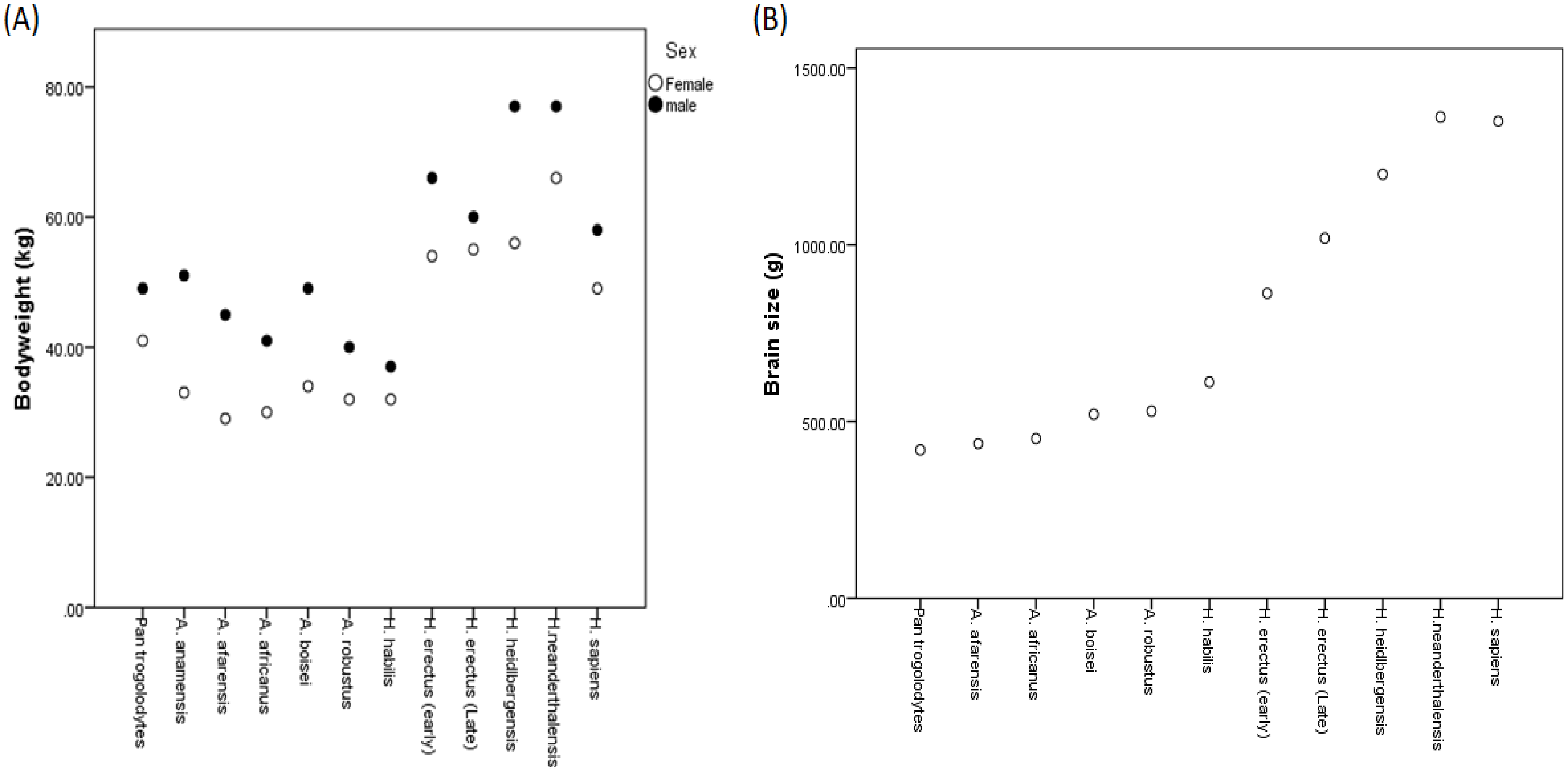


Figure 4. (A) Hominin average body weight (kg) separated by male and female. (B) Average Hominin Brain size (g). (data from Ben-Dor et al. 2011; Leonard & Robertson 1994; Leonard et al. 2003; McHenry & Coffing 2000; Sorensen & Leonard 2001).

Enlargement of the brain from *Homo habilis* to *Homo erectus* was predominantly allometric (Holloway, 2015). However, there are some differences between *Homo erectus*, older hominins and later hominins which are highly relevant for this evaluation.

As stated above the frontal and temporal poles began to expand with *Homo habilis*. However, with the speciation of *Homo erectus* they were still flatter and narrower than in modern humans (Bruner et al., 2015; Wu et al., 2006). Initially, in earlier individuals, the frontal lobes were not an area of great change. However, evidence from Java suggests this species progressed. Earlier fossils from Trinil and Sangiran display narrow and flat frontal lobes. Whereas, Later fossils in Java, such as at Ngandong and Sambungmacan, have wider frontal areas suggesting a progressive evolution of this component. This population was isolated and has been suggested to represent a distinct taxon, *Homo soloensis* (Bruner et al., 2015). Nevertheless, this is a distinct change which has been caused by ecological constriction of the population leading to enhancement of the primary social area of the brain. This was likely exacerbated by an environmental shift from open savanna and forested areas to more closed rainforest environments, further limiting habitable space (Bettis et al., 2009; Finlayson, 2014, p. 61). Relating this to the general evolution of the frontal lobes, it is currently unclear due to lack of evidence whether the proportions of cortical areas changed significantly in *Homo heidelbergensis*. Nevertheless, overall neural rearrangements were progressive towards a more refined human layout, with the same regions as in *Homo habilis* undergoing evolutionary change, with no perceivable outliers (Holloway, 2015). The frontal lobes continued to broaden in width until in *Homo sapiens* it also began to expand in height (Albessard et al., 2016). The overall expansion of the frontal lobes was allometric to overall brain size since the LCA, thus internal changes must have occurred which led to higher levels of cognition (Broadfield et al., 2001).

Non-allometric enlargement of the prefrontal cortex, with increased gyrification has taken place, however when this happened isn’t discernible on the endocasts (Buckner & Krienen, 2013; Sherwood et al., 2008). More directly, it has been shown using endocasts that the Broca’s area increased in size through the hominin lineage. Balzeau et al. (2014) used the third frontal convolution, where the Broca’s area is located, to create a quantitative method of analysing the evolution of this area. They found that the relative size of convolution was highly variable between individuals, that it increased in size through the hominin lineage, and that contrary to common belief the convolution had an extended length on the right side relative to the left. The left area is smaller, compact, and more defined than on the right. It is currently unclear what implications this has for the evolution of language, but the primary conclusion should be that the evolution of this area was continuous through time towards larger third frontal convolutions and a more defined Broca’s area. The result of this is that the convolution was becoming more functionally lateralized, with the left specializing in lingual processing of the direct structures and sounds of speech, while the right specialized in contextualizing what is said and the tone in which it is spoken (Stout & Chaminade, 2012).

The lateralization of the brain is also related to handedness, with increased lateralization leading to right handed populations. It is clear from the striation patterns from Sima de los Huesos that the population predominantly used their right hands, with all individuals (N=20) in one study showing right oriented striations (Lozano et al., 2009) and 16 out of 21 showing right handedness in a second study (Poza-Rey et al., 2017). However, research into the lateralization of the Broca's area and the petalias are less definitive suggesting a proportion of 4/6 right handers to left handers rather than 9/1. This suggests that while handedness was becoming established, the lateralization of the brain and neural specialization was still in development. Therefore, the motor abilities both for tool production and speech, as well as the ability to process more complexly structured forms of each (Stout & Chaminade, 2012), continued to develop in *Homo erectus*. They had more control and precision in tool production, as evidenced by the material record described above, and more advanced (yet still limited) lingual abilities (Klein, 2017).

Due to the movement of the lunate sulcus in *Homo habilis*, the parietal lobe increased in proportional size. The lobe continued to increase in size allometrically with the rest of the brain, but with an extra-allometric increase in width of the inferior parietal areas (Bruner et al., 2015). As stated above, the integration of the inferior and superior parietal cortices may have led to the development from Oldowan to Acheulean technology (Hodgson, 2005, 2009). I agree with Hodgson, that selective expansion of the lower parietal areas may have stimulated the categorization of objects, while the integration of this area with the superior parietal cortex would have enabled visuospatial abilities to be used to create more complex, symmetrically appealing, categorized objects. This interpretation is supported by limited activation of the inferior parietal lobe during Oldowan tool production when compared to Acheulean tools, which suggests shape production was not a primary aim or that the area was not developed enough to be capable of such production (Stout et al., 2000; Wynn, 2002). Wynn (2002) has shown that through this period the affinity to symmetry became more accentuated and complex. Firstly, bifaces were produced with two-dimensional bilateral symmetry of the edges. Then as the brain (and inferior parietal cortex) expanded, in particular with the speciation of *Homo heidelbergensis*, symmetry in stone tools became three dimensional. Spatial abilities were increased, individuals could simultaneously integrate multiple perspectives of an object and create near identical symmetry. The selective pressures for this are outlined above, however the biological determinants remain unclear due to a lack of evidence from endocasts (particularly *Homo heidelbergensis*). I suggest that the increase in the inferior parietal lobe and intra-connectivity of the entire lobe likely had a large impact. This is particularly significant as the inferior parietal cortex expanded significantly more than the superior parietal cortex and it was only with *Homo sapiens* that the superior cortex began to expand more rapidly. The attention to shape enabled by the inferior parietal cortex increased planning capabilities, and the ability to visualize a wanted object on the blank material (Hodgson, 2009; Stout et al., 2000). Further, this area has been implicated in taking others perspective, understanding the intentions of others and has been shown to be part of the mirror neuron system (Brüne & Brüne-Cohrs, 2006; Chong et al., 2008; Fogassi et al., 2005). This is likely connected to ToM and imitative ability, giving it a social element. However, I argue this provides an explanation for how *Homo heidelbergensis* in particular was representing multiple perspectives of an object at once. If an individual can represent the perspective of another individual (particularly one they haven't experienced themselves) then representing a perspective they have just seen would be a simple task and may be the starting point for true metarepresentational abilities.

The parietal lobe was increasing in overall size, with allometric expansion of the superior parietal cortex and non-allometric expansion of the inferior parietal cortex. The lobe became more intra-connected allowing the integration of visuospatial and shape recognition information and the production of more consistent, symmetrical, and aesthetically pleasing tools. The expansion of this area also had social implications for imitative abilities and empathic neural responses. Therefore, I suggest that fitness in this area of the brain and hence symmetrical, congruent tool production may have a more direct neural affiliation with trustworthiness and compassion than first suggested by Spikins (2012). Although, it must be noted that these social functions employ multiple modules. Thus, the evolution of the parietal cortex is unlikely to be solely responsible for this change.

The human temporal lobe is larger than expected for a primate of our size, with significantly more white matter. Due to the displacement of object recognition areas ventrally and laterally by lingual areas which are highly connected to the prefrontal cortex, it has been suggested that this enlargement and increase in white matter was to facilitate lingual abilities (Rilling & Seligman, 2002). Homo erectus compared to earlier hominins had wider temporal lobes (Bruner et al., 2015). Therefore, we may speculate that they had more enhanced lingual capabilities. An increase in white matter in this lobe, particularly the posterior regions, further enhanced its associative abilities. This would aid in both linguistics and tool production, leading to an alternative form of sociality and the creation of the Acheulean technocomplex. By increasing the intra-connectivity of the posterior temporal cortex and its inter-connectivity with the frontal and parietal lobes the abilities to imbue objects and sounds with functional meaning, process more complex hierarchically structured information (such as how to produce a tool or structure a sentence), and integrate visuospatial and sensorimotor information to produce congruent pleasing tools and sounds to be categorized with specific functions, would have been enhanced (Stout & Chaminade, 2012). Thus, this enhanced both technical abilities, process more complex hierarchical information, and social abilities, imbuing objects and sounds with meaning. Further, by enhancing connections between these areas mind reading abilities are likely to have improved, as the temporoparietal junction, superior temporal sulcus and inferior parietal cortex are significantly active during tests of ToM (Brüne & Brüne-Cohrs, 2006; Carrington & Bailey, 2009; Lewis et al., 2011; Shultz & Dunbar, 2012).

These abilities, both technological and social, would not be directly comparable to human abilities due to the reduced width of the frontal cortex, size of the prefrontal cortex, the flattening of the parietal cortex and lower laterality. Further, the *Homo erectus* brain is 72-84% its maximum size at 1 year of age, similar to chimpanzees. This suggests a shorter-range connective layout in the brain than in modern humans and later hominins (Coqueugniot et al., 2004). Thus, it is highly improbable that they would have reached the higher levels of intentionality attained by humans. Compared to earlier hominins, however, they were more capable of understand the minds of those around them, and most probably reached intentionality level 3.

At this stage it is suggested by McNabb's (2012) predictive graph that *Homo erectus* had level 3 intentionality and *Homo heidelbergensis* reached level 4 intentionality. This overlaps with the modern human male mean of 4.41 (Stiller & Dunbar, 2007). Therefore, unless we suggest that *Homo heidelbergensis* possessed advanced human-like social abilities we must suggest that the species possessed a different degree of clarity, accuracy and processing ability when inferring mental states at level 4 (as described above for chimpanzees) or that they had a lower level of intentionality. Due to the standardization of technology, it is clear that social norms were being adhered to, therefore intentionality level 3 must have been reached (Dunbar, 2003). Reinforcing this, Gamble et al. (2011) suggest that the ability to manipulate multiple factors of flint when producing a handaxe and utilize a ‘mind’s-eye’ during production requires similar skills to higher levels of intentionality. Nevertheless, for level 4 to be reached there must be signs of ritual or religion (Dunbar, 2003). Controversially, this may be present at Sima de los Huesos, Atapuerca, where the ‘ritual’ burial of 28 individuals (commonly attributed to *Homo heidelbergensis*) with the earliest grave good, a highly symmetrical quartzite handaxe, took place (Carbonell & Mosquera, 2006). However, it is unclear whether this was religious as many other explanations exist for this artefact. McNabb (2012) concluded that despite the predictions of figure 1, the Acheulean toolmakers were unlikely to have a full theory of mind, but nevertheless had a more defined sense of self and other. I would add to this and suggest that they did understand the minds of others, perhaps not to the level of modern humans but the cases of compassion and advanced cooperation without sign of a direct personal gain suggest that a network of moral judgement was in place. For such a system to operate understanding how others view you is a prerequisite.

In conclusion, site distributions and material densities at sites suggest an increase in overall population and group size at this time. This increase in population put stress on an already depleting environment and therefore required individuals to disperse further. Dispersal occurred both locally and globally. Individuals within groups increased their home range and groups migrated across Europe and Asia as they adapted to more marginal environments. These conditions required enhanced social and technical abilities. Particularly as environments would have been more open, leading to increased predation, and more difficult and competitive resource acquisition. The social evolution that took place was the origin of compassion and cooperation, which led to hominins being more effective at finding resources and being able to gain access to more novel resources such as meat. Cooperation also allowed more expensive energy budgets to be reached, particularly important for pregnant females. But such a collaborative social system requires trust, particularly in marginal, arid, and open environments with high predation. Handaxes may have had multiple functions to aid in this environment, by providing comfort, displaying an ability to care for another through caring for the object and reminding individuals of, or even enhancing their bonds with, others while they are away. This final point may have been imperative in highly dispersed groups. Nevertheless, they also represent a considerable change in technical ability. They display an ability to process more complex hierarchical information, visualize multiple perspectives of an object, and produce a predetermined visualized usually symmetrical form. This predilection to symmetry in material objects may also signify an enhanced ability to identify symmetrical objects in the landscape, thus enhancing individual’s ability to detect hidden animals. Thus, the hominins of this period were likely under complex evolutionary pressures, not only social but also technical, and adapted accordingly.

Further research using *Homo heidelbergensis* endocasts would greatly benefit the study of cognition during this period.

3.4 Neanderthals and Humans

Archaeological Evidence of Behaviour

This period was characterized by a further transition in technological culture, the habituation and extinction of Neanderthals in Eurasia, the speciation of *Homo sapiens* and their movement into the Eurasian plains, a human specific ‘revolution’ in social material culture including the advent of representational art, the existence of a hominin species with a larger brain size than modern humans, and the advent of true language. This section will assess whether Neanderthals and Anatomically Modern Humans (AMH) adapted differently to the social and technical evolutionary pressures of the time.

The Palaeoenvironmental record at this time in Europe is punctuated by 5 oxygen isotope stages (OIS: see figure 5)

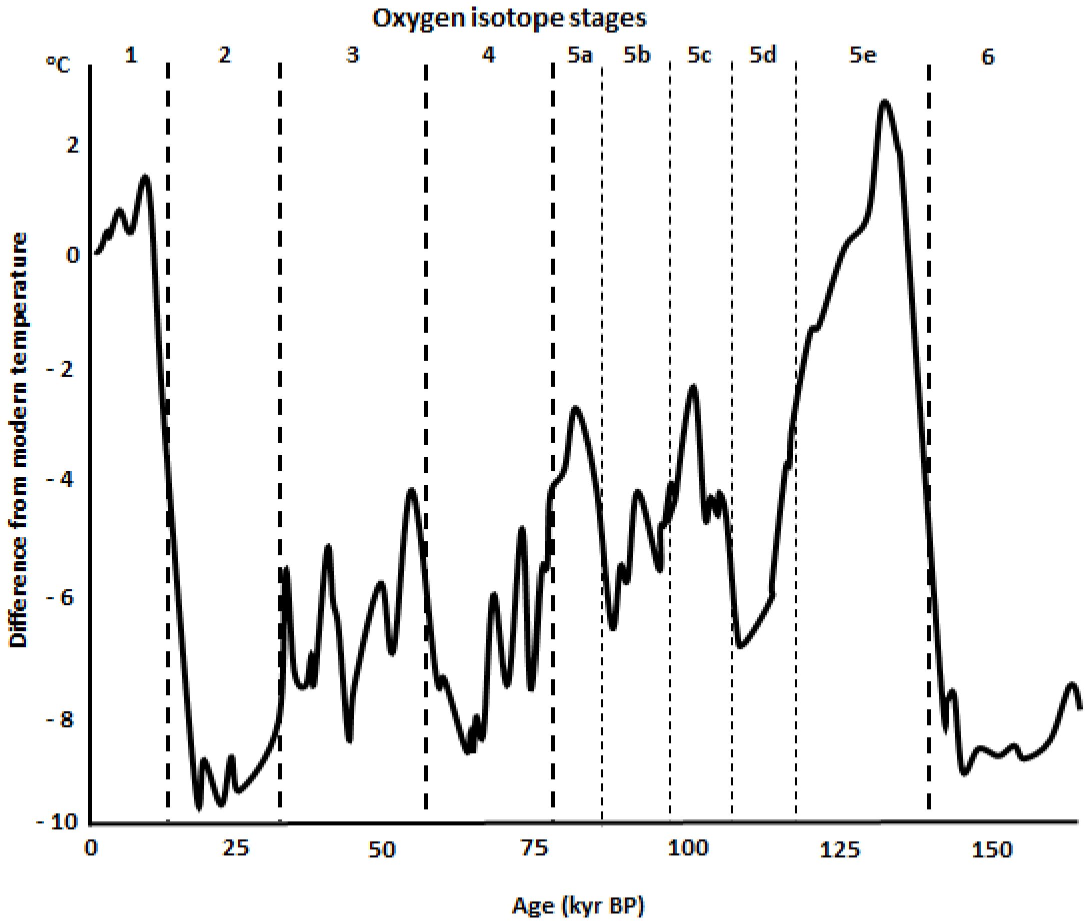


Figure 5. Estimated variations in temperature during the last glacial cycle using oxygen isotope and deuterium ratios from the Voztok ice core, with oxygen isotope phases marked (After Jouzel et al. 1987).

This rapid environmental change would have required extensive adaptability. Social and technical mechanisms would have been under more pressure than in previous time periods, and hence cortical areas would have been forced to adapt. Interestingly, the two species of Homo present at this time appear to have distinct adaptive strategies for coping with this change. AMH are argued to have adapted socially, which allowed increased material invention, specialization, and more structured landscape exploitation. Whereas, Neanderthals are suggested to have been more static at this time in both technological and social innovation, relying on the biological suitability of environments rather than culturally adapting to conditions (Finlayson, 2004, pp. 125–128; Kuhn & Stiner, 1998; Lewis-Williams, 2004, pp. 69–101; Pearce et al., 2013).

These differences are proposed by many authors to be responsible for the extinction of Neanderthals and success of AMH (Banks et al., 2008; Bar-Yosef, 2013; Gilpin et al., 2016; Horan et al., 2005; Wynn et al., 2016). By assessing the social, technical, and neurological differences between the two hominins we will explore how they each adapted to the complex evolutionary pressures.

The social structures of Neanderthals and AMH differ largely. Group size estimates for Neanderthals are highly variable ranging from as high as 143 when averaging Aiello and Dunbar's (1993) data utilizing overall cranial capacity or 115 when accounting for the larger size of the Neanderthals visual cortex (Pearce et al., 2013), to as low as 8-10 based upon the sleeping area size at Abric Romani, El Sidron, and Barakaevskaya (Hoffecker, 1999; Lalueza-Fox et al., 2011; Vallverdú et al., 2010). These estimates likely define the term 'group' differently, with the first referring to the whole social network and the second representing a single family or hunting/foraging party, henceforth referred to as a 'group'. However, the lower figure has been used recently by Nakahashi (2017) to estimate innovation rates, and it was suggested that communication with more than 10 individuals would be difficult. I believe this conclusion greatly underestimates the sociability of Neanderthals. As stated above this figure likely represents a single hunting party. Further, with skeletal damage indicating severe injury on almost every reasonably complete Neanderthal skeleton (Berger & Trinkaus, 1995), I argue it is unlikely they would have been able to survive in such small groups. If they did, provisioning care for someone unable to contribute would be a substantial sacrifice - particularly if it was long term, as the 'Old man of Shanidar' would have needed (Spikins et al., 2010). Likewise, Aiello and Dunbar's (1993) and Pearce et al.'s (2013) estimations based upon the SBH overestimate the sociability of this hominin. The SBH estimates are supposed to encompass a collection of individuals that you would expect to complete a personal favour (Dunbar, 2003). The population density of Neanderthals has been estimated to be between half the size and ten times lower than that of Aurignacian AMH (Bocquet-Appel & Degioanni, 2013; Mellars & French, 2011). The latest estimate suggests a much higher population size in the tens of thousands. However, the authors found high rates of genetic drift, suggestive of a small population size. Therefore, they suggested that the large metapopulation consisted of small isolated populations with little contact (Fabre et al., 2009; Rogers et al., 2017). Hence, I argue Neanderthals would have had much less contact with other groups and group sizes would have been much lower than those of AMH. This is particularly demonstrated by the inbreeding seen in the Altai Siberian Neanderthal genome (Prüfer et al., 2014).

Contrary to this evidence, Hayden (2012) has assumed, based upon generalizations from ethnographic evidence, that Neanderthals must have had connections with 450 other individuals in order not to die out. He states that Neanderthal groups must have been between 12-24 people and had connections with 10-20 other groups in order to survive. If these bonds did form they are unlikely to have been as intimate as those affecting the development of the social skills, as is displayed by a lack of long distance (>100km) down-line trade in finished objects (Féblot- Augustins, 2009), a common feature in AMH social networks, and the genetic evidence for isolation cited above. Nevertheless, I agree that connections must have existed in some form between groups, at least intermittently. Perhaps this took the form of immigrations for mating as is seen in chimpanzees (Luncz & Boesch, 2014). Due to a lack of material evidence these connections are currently difficult to understand.

The ability to have long distance bonds is likely to have been affected by environmental conditions. Féblot-Augustins (1993) suggests that mobility was higher in areas of harsh climatic variability and high prey mobility, which provoked intergroup interaction. However, in the northern latitudes and in eastern Europe, populations were subject to bottlenecks causing a decrease in population density (Hawks, 2013; Hoffecker, 1999). An increase in distance between groups combined with more difficult travel conditions may have made inter-group collaboration impossible leading to increased inbreeding. I would suggest that inbreeding in these regions would decrease during interstadials and increase during stadials. This is supported by the Altai Neanderthal who, although not directly dated, is thought to have lived prior to 50ka (Prüfer et al., 2014). This puts the individual within the glacial conditions of OIS 4 (or at least the recovery stage leading to OIS 3) and may be an example of a group heading towards extinction due to isolation. This hypothesis may be confirmed or negated with further DNA analysis of directly dated individuals. The broader social relations of Neanderthals likely varied greatly depending on environmental conditions. Group sizes of Neanderthals are also likely to have been affected by ecological variation. When the carrying capacity of the land decreased it is likely that group size also decreased and vice versa. Therefore, I believe that in the low resolution record we have of Neanderthal social structure, social network, and group size they are likely to have varied greatly in response to environmental change, as supported by the regional extinction hypothesis (Eller et al., 2009; Hublin & Roebroeks, 2009).

Overall, the common consensus is that Neanderthals lived in small group sizes with high local residential mobility within limited boundaries (Ambrose, 2010; Churchill, 2014; Conard et al., 2012; Féblot- Augustins, 2009; Finlayson, 2004, pp. 94–134; Lieberman & Shea, 1994). Increases in the density of stone tool artefacts from 6.6 to 17.6 tools per m^2 per 1000 years from the Middle Palaeolithic to the Upper Palaeolithic have been used to suggest an increase in population density (Mellars & French, 2011). However, it may also indicate an increase in sedentism and radiating mobility at sites, therefore suggesting a change in subsistence. This was characterized by greater specialization in prey and is supported by an increase in storage, bulk harvesting of resources, and a change to using tools such as projectile points that are manufactured for reliability while performing a specific task rather than maintainability and versatility (Churchill & Rhodes, 2009; Churchill, 2009).

Neanderthals largely lacked these changes. There is only evidence of three storage pits both of which were absent of bones, and evidence of enamel hypoplasia has been used to suggest a lack of winter storage (Churchill, 2014). Although, when directly compared, rates of hypoplasia were similar to Inuit groups (Guatelli-Steinberg et al., 2004). Lack of specialization in hunting can be seen in the faunal assemblages which represent the natural ecological distribution of animals (Burke, 2004). Ambrose (2010) has even suggested that Neanderthals made unplanned random movements through the landscape reacting opportunistically to encountered resources. Although, this may be questioned due to archaeological evidence which shows that they were capable of planned seasonal exploitation of recurring resources, as is seen at Jonzac, a site characterized by short term seasonal visits to exploit migrating deer (Britton et al., 2011; Niven et al., 2012). Further, Neanderthals at El Esquilleu are argued to have specialized in hunting solitary ibex and chamois in difficult terrain (de los Terreros et al., 2014). Hence, while there are still many unanswered questions and disagreements regarding Neanderthal mobility and subsistence, the most plausible interpretation is that they were likely to have a more structured use of the environment than preceding hominins, but were unlikely to have a developed system in the same way as AMH to harvest the home range in bulk.

These differences in subsistence strategy have led Finlayson (2004, pp. 94–134) to conclude that Neanderthals acted as ‘groups’ merely cooperating to achieve a goal, whereas AMH were acting as ‘teams’ with specific tasks and recognition of other’s roles. Due to small group sizes many of these features of modernity may not have been possible or needed, but it still marks a change in strategy which is often quoted as due to cognitive differences. Further, the larger energetic costs of Neanderthals may have prohibited large group sizes, aggregations, and the travel needed to maintain an extended social network. This may have led to intimate kin-based groups, which may have been resistant to external ideas, leading to decreased innovation (Spikins et al., 2017). From this, it is clear that Neanderthals didn’t put as much emphasis on extended sociality as AMH. They lived in smaller group sizes with limited interactions with other groups and showed little evidence of social networks. Their subsistence strategies were more opportunistic and didn’t require as much forethought, particularly when compared to the extensive evidence of Upper Palaeolithic storage (Hoffecker, 2005). From this we may infer that Neanderthals, a hominin with comparable brain size to humans which survived twice as long on earth as we have, evolved along a different path to humans. One that may not have put as much emphasis on sociability.

Material culture was greatly affected by this difference in sociality. As stated above, Neanderthal material culture was largely static in comparison to AMHs. Compared to earlier hominins the Levallois technology of the Neanderthals represented a shift towards a more diverse array of tools. This shows that Neanderthals were more capable of imitating and maintaining different forms of tool through their cultural history (Foley & Lahr, 2003). They produced scrapers, points, notched and denticulated tools, blades, and backed knives, as well as continuing to make the highly standardized bifacial tools of the Acheulean (Mellars, 1995, pp. 95–140). Evidence of hafted and composite tools in the Middle Palaeolithic has been used to suggest that Neanderthals were capable of constructive memory and even language (Ambrose, 2010; Rots, 2013). Therefore, it is clear that Neanderthals show increased complexity technologically. Further, contrary to previous assertions (Ambrose, 2001; Mellars, 1995, pp. 95–140), regional differences in tool shape suggest culturally determined imposition of form (Ruebens & Sykes, 2016). Although, tools were less standardized than in Upper Palaeolithic contexts (Pastoors & Tafelmaier, 2010). However, decreased attention to style in these artefacts may not indicate inferiority. Rather, it has been suggested that Levallois technology is ‘incomparably’ more difficult to produce, and much more economically efficient (Brantingham & Kuhn, 2001; Eren et al., 2008; Hayden, 1993, p. 118). Hence, this is a sign of difference not inferiority.

A further difference is the scarcity of ivory, bone, and antler artefacts (Davies & Underdown, 2006; Hoffecker, 2011). Extending psychological work that suggests the human mind has multiple domains (or modules) which are specialized for particular topics, Mithen (1998, pp. 129–170) has suggested that the Neanderthal mind was domain specific. Neanderthals possessed a highly complex knowledge of the social, natural, and technical world, however he suggests they were unable to integrate this knowledge as they were in separate domains (Mithen, 1996, 2014). In contrast to the fluid nature of AMH cognition where modules are able to interact, this caused a number of differences. Metaphorical thought wasn't possible, and as a consequence neither was shared visual symbolism; innovation in technology was stinted due to an inability to form complex associations, for example between how a tool may relate to the prey hunted or to the environmental context in order to produce specialized implements; and social developments such as language and consciousness could only be used in a social context (Mithen, 1998, pp. 129–170). Mithen has suggested that the lack of bone, ivory and antler artefacts is practical evidence of this theory. The materials were part of nature and therefore they were unable to be used technologically. This theory also accounts for the complexity of Levallois flake production in contrast to a lack of tool specialization. However, at Pech de l'Azé and Abri Peyrony bone tools suggested to be specialized for removing hides have been found (Soressi et al., 2013). Thus, if the Neanderthal mind was modular, the divisions may not have been as clearly defined as Mithen suggests, allowing knowledge to permeate into other domains in special cases.

This separation of cognitive domains is most visible in the difference between the explosive prevalence of AMH and the absence of Neanderthal social material culture. AMH are associated with a plethora of symbolic and socially determined artefacts, ranging from the standardization of tool form stated above, to the production of beads, pendants and ultimately art. In contrast, Neanderthals are associated with the use of raptors and corvid feathers (Finlayson et al., 2012; Morin & Laroulandie, 2012), pigments (d'Errico et al., 2003; Zilhao, 2012), perforated shells and the highly controversial Chatelperronian culture (Zilhao, 2012). The Neanderthal evidence has not been universally accepted as evidence of social symbolism. Some researchers believe that this is due to a double standard being applied to the evidence (Zilhao, 2012). However, as Mithen (2014) has noted, not all decoration is symbolic and may merely be to enhance an individual's or object's appearance, making them look more attractive without any underlying symbolic meaning. Mithen (2014) applied this view to the use of pigments, however it is just as easily applied to all of the evidence listed above, excluding art. Therefore, unless art that is used to symbolize a form or a meaning is found in Neanderthal or even early AMH assemblages it could be concluded that there is no evidence for shared symbolic meaning. Furthermore, the use of feathers and shells does not contradict the 'domain specific' theory, as they were only used scarcely for food (Hardy & Moncel, 2011; Pearson, 2007). It is possible that these materials were part of the social rather than natural domain. Perhaps Acheulean handaxes and the 'symbolic' materials of Neanderthals listed above represent individual exceptions integrated into the general (cross domain) knowledge of the multi-module theory. This would suggest that development towards a domain general brain may have been more progressive. Following this evidence, I suggest that the majority of social material culture Neanderthals had was largely decorative with no evidence of an underlying deeper meaning.

This conclusion echoes the views of Lewis-Williams (2004, pp. 89–96), that Neanderthals may have adopted body decoration but associated it with a different or no meaning. Thus, while Neanderthal sociality developed in producing decoration, this form of activity can be seen as superficial in contrast to the highly symbolic products of art. However, it does represent a change. By using external objects for decoration, even if it does not symbolize the hierarchy of a group or any deeper spiritual meaning, the social self has been extended to external objects. Items that were previously exclusive to other domains have been accepted as socially important. The same may be said with the initial standardization of bifaces. Therefore, from the Acheulean onward particular objects have been selected which create emotional reactions in others and incorporated into the social world. The most probable interpretation is that an appreciation for aesthetics implies a level of ToM, as it requires understanding other's views of an object and a shared ascribed value (McNabb, 2012). With the full integration of the domains in the Upper Palaeolithic this created a wealth of symbolic meaning. With social consequences being implemented in the broader standardization of lithic technology. The use of animals and the fusion of animals with people to create social or functional symbolic meaning, such as the Trois Frere Sorcerer or the Lion Man from Hohlenstein-Stadel. The use of elements of nature symbolically for social purposes, such as the early example of Qafzeh 11 who was buried with antler (90-100 ka BP) or the later Natufian 'shaman' burial with 50 tortoise shells (15,000-11,500 BP).

While the differences in Neanderthal cognition severely impacted inventiveness, low group size and population density would also have had a significant effect. Horizontal transmission (between peers) in Neanderthal groups would be restricted, therefore leading to less innovation (Hodgson, 2013; Nakahashi, 2017). When innovation rates were modelled to assess reactions to the environment it was found that those in more variable locations with uncertain resources consistently invented new subsistence methods in hope to find a more efficient way of coping (Pereda et al., 2017). Neanderthals were unable to be as reactive to the environment and were more vulnerable to extinction events, as is seen by frequent population bottlenecks (Bocquet-Appel & Degioanni, 2013). Hence, the social complexity of humans greatly impacted both their technology and adaptability.

Changes in Brain Structure

Clearly there were some fundamental neurological differences between Neanderthals and AMH. This is interesting because the behavioural evidence explored above indicates non-social specialization in Neanderthals, which directly contradicts the social theories.

Neanderthals reached similar brain sizes as humans through different non-allometric expansions. The three primary areas of differences between Neanderthals and AMHs are the visual cortex, parietal cortex, and the overall connectivity of the brain.

Pearce et al. (2013) concluded that Neanderthals had a larger visual cortex and therefore had less development in social areas of the brain. However, Holloway (2015) has argued that this difference has been exaggerated as differences in face size and individual variation wasn't accounted for when predicting visual cortex size from orbital size. Further, the fact that the occipital regions of the brain are larger in Neanderthals may suggest they were better at creating virtual models of objects and the spatial world around them when they are not in current view (Langbroek, 2014). I would argue this is explicitly seen in the production of Levallois stone tools, where the flake to be removed is not as explicitly visible as when producing a blade through reduction. As stated above this is a more efficient method of production. Therefore, this is an example of divergent technical evolution.

The parietal lobe is considerably different in Neanderthals. Bruner (2010) conducted a study into the differences of *Homo erectus*, Neanderthal and AMH parietal cortices. He concluded that relative to *Homo erectus*, Neanderthals had experienced enlargement of the inferior parietal lobe. In contrast, AMH had experienced enlargement of the superior parietal lobe. As stated above, an increase in inferior parietal lobe would enhance shape recognition, the ability to visualize and plan an operation to produce a wanted shape, and possibly ToM. These aspects are all related to creating virtual models of an object in the absence of current explicit stimuli. Whereas, the superior parietal lobe is related to coding the spatial environment, attentional flexibility, working memory and integrating spatial information with past experience to create intentions and goals (Bruner, 2010). From this evidence we may further Langbroek’s (2014) interpretation that Neanderthals evolved to focus on the virtual and invisible whereas humans evolved to focus on the visible and actively produced explicit forms (such as art) to understand aspects that may be virtual. However, the connectivity of the Neanderthal brain suggests some differences which may have hindered some of these abilities and promoted other unique abilities.

Neanderthals are argued to lack a globularization phase during early postnatal brain development (Gunz et al., 2010). Although there is new evidence suggesting that morphological development and growth rates were similar to humans (Ponce de León et al., 2016; Rosas et al., 2017), genetic evidence suggests that human specific divergent nucleotides related to neural development caused significant differences in behaviour, with mutations in these areas causing psychological conditions today (Green et al., 2010). Thus, although there are debates surrounding the nature of developmental differences of Neanderthals and humans, it is reasonable to conclude that there were differences. I believe these were primarily prenatal, with further differences following birth during the globularization phase, and an extended growth period overall (Gunz et al., 2010; Ponce de León et al., 2016; Rosas et al., 2017). These differences would have had a significant impact on connectivity, thus leading to pronounced functional differences. This may have hindered social functions which rely on long ranging complex connections, such as ToM, but also created novel connections leading to unknown Neanderthal specific skills.

As noted by Hodgson (2013) the cognitive processes investigated above are primarily social. The fact that different functions are manifest in Neanderthals may suggest that they engaged in a more strictly technical and functional evolution to reduce resource expenditure. While there are clear social developments in the form of care for the infirm, it must be noted that empathy for pain and personal distress may be heightened in individuals with Autism (Rogers et al., 2007). Therefore, the empathetic mechanism leading to care for the injured and unwell may develop independent of a neurotypical ToM. Neanderthals likely lived a more functionally based life with less of an emphasis on outward sociality, as is suggested by the material evidence. In contrast, the extensive social networks of AMH led to increases in population inventiveness and collective technological knowledge, and provided mitigation during stressful environmental events. Through this, AMH became more adaptable and more technologically proficient utilizing an alternate means to Neanderthals. The Neanderthal lifestyle was a challenging one, with frequent food shortage and high energy budgets. Without a social buffer they likely could not provide the vast energy needed for both body and brain growth, leading to an extended period of brain development with differences in growth pattern (Gunz et al., 2010; Rosas et al., 2017). They therefore didn't develop the same connections in the brain, which produce the social mechanisms of humans. As will be seen in Chapter 4, a slight change in development causes differences in modern populations. Therefore, it is possible that the more dramatic differences between Neanderthal and human ontogeny would be responsible for cognitive differences outside of modern human variability, and perhaps a more domain specific mind in Neanderthals. Contrary to theories of sociality, Neanderthals likely evolved for strict near-sighted technological efficiency to mitigate the difficulties of the climate, through unique technical enhancements. In contrast, AMH evolved social buffers which are less efficient but have long term benefits.

3.5 Conclusion

As we can see from the information presented above, areas of the brain specialized for sociality developed gradually through time. These likely accentuated methods used for behaviour reading, which led to ToM, and enabled more complex social structures and relationships. The temporal, parietal, and frontal lobes of Early Homo all expanded thus increasing social and lingual capacities. This trend continued in *Homo erectus* and *heidelbergensis* with the widening of the frontal and temporal lobe as well as a likely increase in connection between the frontal, temporal, and parietal lobes all of which increase social and ToM abilities. However, following this the human lineage continued to develop for large scale socially, whereas the Neanderthal brain developed more for other technical functions, such as 3D visualization, to increase efficiency. This shows that not all cognitive developments in the hominin lineage have been social.

On the contrary, through the hominin lineage there have been many changes linked to technical proficiency. The constant increases in size of the parietal lobe have been connected to object manipulation and the ability to impose shape. Increases in lateralization of the brain and the size of the Broca's area are connected to precision with tools. Therefore, we may argue that encephalization was also impacted by technical pressures.

Lingual abilities have many overlaps with technological abilities. For example, the development of the Broca's area was both for language and action. It is thought that this is a general module for processing hierarchical information (Fadiga et al., 2009). Developments like this may be seen as both technical and social. Similarly, two other areas of the brain activated when producing Oldowan tools are the parietal cortex and the medial prefrontal cortex. Both areas involved in ToM. Therefore, areas of the brain specialized for technical and social abilities are closely linked. While this may stress coevolution, it is important to note that the social functions of the brain are largely determined by long range connections, which were likely different in Neanderthals. These differences can lead to less socially driven minds. If these differences are present in Neanderthals, then the shorter ontogeny and less white matter of earlier hominins would support even more accentuated differences. This suggests even lower levels of sociality than is previously suggested from morphological analysis.

Further, due to the disparity between the SBH estimates of Neanderthal group size based upon brain size and the estimates based upon archaeological evidence, it can be concluded that these estimates are not reliable for both Neanderthals and earlier hominins. I believe this shows that there are complicating factors to these estimates, this may be the impact of technical pressures on the evolution of the brain. Based upon the presented evidence, I conclude that the brain developed to its current form and size for multiple reasons. Both social and technical ability were strong pressures for encephalization. Thus, contrary to the current focus of research archaeologists must broaden their research to explore other pressures of cognitive evolution and not limit themselves to defining one cause where there were likely multiple.

Commonly, when a species is under significant conflicting evolutionary pressures, individuals vary in how they adapt, and some individuals specialize more for one pressure than another (Wilson, 1994). Individuals with Autism Spectrum Condition (ASC) are less socially oriented, however they commonly have significant accentuations in technical abilities. Therefore, in order to assess the impact of conflicting social and technical evolutionary pressures on our species we will use ASC as an example of an alternate, more technical, adaptive strategy and investigate what impact autistic traits may have had on our AMH ancestors.

Chapter 4: An Evaluation of Conflicting Evolutionary Pressures Within Species: A Case Study of Autism Spectrum Condition

This section will explore an alternate, more technical, adaptive strategy within our species for coping with the conflicting social and technical pressures - Autism Spectrum Condition (ASC). We will explore the social and technical behavioural differences associated with the condition, existing archaeological theories of ASC in prehistory (4.1), the neurological causes (4.2), and the heritability and genetic causes of the condition (4.3). This will enable us to determine whether ASC and its associated technical traits may have had an impact on prehistoric groups.

4.1 Behaviour

Autism Spectrum Condition (ASC) is a collective term used to describe individuals with Autism, and individuals who either show only some of the symptoms of Autism or milder symptoms. Individuals with ASC are predominantly characterized in the literature as having differences in three cognitive functions, Theory of Mind (ToM), central coherence - termed Weak Central Coherence (WCC), and executive functions. The character of these differences will be explored below. However, individuals with autism also have associated technical skills. Individuals may show sensory hypersensitivity, high attention to detail, enhanced memory, strict focus on particular subjects, and a better understanding of complex systems (Baron-Cohen et al., 2009). These differences may lead to many diverse talents, leading Baron-Cohen (2000) to conclude that when put in a different, less social environment individuals with high functioning Autism or Asperger Syndrome may not be termed ‘disabled’ but may have much success. In more extreme cases individuals may show spectacular spontaneous talents in drawing, music, and other detail oriented activities.

The behaviour of individuals with Autism will be explored in this section as an example of difference. This will focus on differences in the three cognitive functions listed above, and will explore enhancements associated with the condition.

Theory of Mind

As stated in Chapter 2, ToM is the ability to infer the thoughts and beliefs (mental states) of other individuals, measured in levels of intentionality. Individuals with Autism have delays in the development of ToM. This was initially shown by Baron-Cohen et al. (1985). They conducted a Sally-Anne false belief test assessing level 2 intentionality on 20 children with Autism between the ages of 6 and 16 using dolls. This showed that 80% of the children with Autism failed to recognise that Sally held a view alternate to reality of where the marble was. In Contrast 85 and 86% of neurotypical and Down-syndrome individuals passed the test. Although this study was heavily critiqued due to the need for imaginative play, the linguistic format of questioning, and whether it was strictly tailored to assess the ability to assign false beliefs (de Gelder, 1987), subsequent studies accounting for these criticisms have yielded similar results. Leslie and Frith (1988) showed that while using real people to act the Sally-Anne test, children with Autism were still less successful than controls. However, this study also showed that older children with Autism performed better than younger children. This suggests a developmental delay in ToM abilities.

The hypothesis of a developmental delay has been challenged due to conflicting results (Perner et al., 1989), however this was further confounded by the large variance per study of individuals with ASC being able to pass first order (inferring one other person's mind) ToM tests, which ranged between 15-60% (Happé, 1995). This suggests that differences per study were due to small sample sizes. Happé (1995) conducted a meta-analysis of 27 different studies to gain a larger sample (N=70). This showed that individuals with ASC required a Verbal Mental Age (VMA) above 11-7 to pass both the Sally-Anne test and the Smarties test, whereas neurotypical individuals could consistently pass both tests with a VMA of 6-9. The conclusion that VMA is related to ToM performance is also supported by Philpott et al. (2013) and Yirmiya et al. (1996). Sparrevohn and Howie (1995) found a progression in the difficulty of the tasks which shows the developmental trajectory of the skill (Table 1). Nevertheless, even when the second order false belief test is passed this only represents the ability of a neurotypical 6-year-old. Therefore, individuals with ASC may be unable to reach an adult level of ToM (Baron-Cohen et al., 1997). Further, correct responses may be due to individuals using 'hacking strategies', where learned associations to specific problems are used to work around the problem, rather than inferring an individual's thoughts (Frith et al., 1991; Happé, 1994; Tager-Flusberg & Sullivan, 1994). Tager-Flusberg and Joseph (2005) have also shown that an individual's understanding of sentential complements (e.g. asked, said, thought, knew) correlates with success on ToM tests. They suggest that sentential complements may be used by individuals with ASC to create explicit representations of the issue that allow them to solve the problem. Frith et al. (1994) tested this 'hacking' hypothesis using the Vineland Adaptive Behaviour Scales to assess the use of ToM in real life. If individuals were 'hacking' then they would not be able to use this method in the more fluid and unpredictable everyday life. It was found that only 3 out of 8 autistic individuals who passed first order belief tasks showed signs of mentalizing in everyday life. The other 5 individuals showed very low use of ToM in an everyday setting and didn't differ from those who failed the tasks. Even those individuals who used ToM in everyday life showed differences when compared to other children of their age. This suggests that while individuals with ASC may develop to a certain level of ToM there are still difficulties in everyday life. This is supported by the research of Baron-Cohen et al. (1997) and Happé (1994). By using more adult ToM tests, the Reading the Mind in the Eyes Test (RMET) and the Strange Stories Test, they showed that individuals with ASC who passed previous easier ToM tests made more mistakes than neurotypical individuals in these more difficult tests. This shows that although ToM is delayed at reaching the neurotypical 6-year-old level, there may still be difficulties on more adult tests and in real life.

Differences in ToM may cause difficulties in everyday sociality. For example it may be difficult to identify and respond appropriately to other's emotions, alter conversation when in a certain group (e.g. peers) to respond in a way that is 'cool' or most accepted, understand metaphor and engage in subjective conversation, which leads to a preference for objective topics (Ochs & Solomon, 2010). However, it must be emphasised that these differences do not lead to an absence of sociality in individuals with autism, but rather differences in how that sociality is expressed.

Task	***Percentage of ASC participants successfully passing the test***
Inferred belief - assessing someone's belief based upon what they see.	100%
Not own belief - understanding an individual’s belief when it conflicts with your own and false belief is not present.	83%
Explicit False Belief - understanding false beliefs when explicitly told about them.	67%
Smarties task - understanding first order false beliefs.	53%
Ice cream van test - understanding second order false beliefs.	30%

Table 1. Theory of Mind tasks suggesting a developmental progression (Sparrevohn & Howie 1995).

Weak Central Coherence

WCC entails a difficulty to process information in context. Rather than processing information globally, individuals with Autism prefer local, detail based processing. Contrary to the name ascribed to this theory no value is attributed to the term ‘weak’. Rather it is a term used to suggest *reduced* central coherence which is affiliated with technical advantages and social difficulties (Frith, 2012). Central coherence is measured through the use of tests like the homographs test (Frith & Snowling, 1983), embedded figures tests (figure 6), and block design tests (figure 7). Through this research it has been shown that individuals with ASC are better at identifying embedded ‘hidden’ figures within an image (Jolliffe & Baron-Cohen, 1997; Shah & Frith, 1983), and completing block design tests, which require the reassembly of a whole image from components (Shah & Frith, 1993). Although, a recent meta-analysis has found that these differences are less extreme than has previously been suggested, with less extreme advantages in local processing and disadvantages in global processing (Muth et al., 2014). This study also found a high amount of variability in individuals’ scores for each test, suggesting high variability in visuo-spatial ability within diagnosed individuals.

Research using homograph tests have shown that individuals with ASC have difficulties contextualizing the words for meaning (Frith & Snowling, 1983; Happé, 1997). In everyday conversation WCC may also make it difficult to alter conversation based upon the social context (e.g. with peers or adults), understand metaphors in the context of the conversation, ensure that replies are directly related to the current topic, engage in large complex conversation where previous points must be related to the whole (Ochs & Solomon, 2010). Further, WCC has been argued to contribute to individual’s difficulties in using ToM in everyday life. This is due to a need to process social information in context to be able to attribute mental states, even when only focusing on one detail of a person like in the RMET (Baron-Cohen & Hammer, 1997; Frith & Happé, 1994; Jarrold et al., 2000; Skorich et al., 2016). However, this hypothesis is contentious with much evidence pointing to the contrary (Happé, 1997). For example, it has been found that WCC may be present in the parents and siblings of those with ASC, yet these individuals show no social difficulties in their lives (Briskman et al., 2001; Happé et al., 2001). This shows two things, firstly that WCC may be present without ToM difficulties, and secondly that WCC is a highly heritable trait. Due to the conflicting findings on how WCC relates to ToM it is perhaps better to conclude that while WCC can cause further difficulties in inferring another's mind it is not necessarily a determinant (Happé, 1999).

As stated above WCC can lead to many technical assets. Local processing bias has been associated with enhanced musical talent and talent in art. The former is due to the ability of individuals with ASC to learn the labels of musical notes and acquire perfect pitch (Heaton et al., 1998). The latter is due to the construction of drawings by reproducing particular details rather than whole forms. This is seen in the artwork of Nadia and Jamie, who will be further explored below, and also individuals such as Stephen Wiltshire and Peter Myers who have received acclaim for their work. Baron-Cohen (2002) suggests that local detail processing may be used to understand complex systems. He states that individuals with ASC start by processing information locally to see whether independent features may fit together into a system. By understanding the particularities of the system in relation to how finite parts interact, the entire system may be understood more fully. This may account for restricted and repetitive interests, but it also explains the increased aptitude for maths, science, and engineering. Further, a focus on producing systems may be a causal factor for decreased global processing as contextual information is harder to systemize (Baron-Cohen, 2006).

Grandin (2006) has revealed that she thinks in pictures. She has used this visualization of detail to become a very successful livestock equipment designer. She states that she is able to visualize the point of view of the cattle to help define details that might frighten them. Further, she can test-run her designs using her imagination as if it were a videotape piecing together the details to create the 'new whole'. This is a skill which utilized local detail processing and a systematic mind in an effective way. Clearly this cognitive style may produce exceptional, functional, and culturally valued talent.

These cognitive styles of local processing and systemizing are prevalent in the wider population as well as in those with ASC and represents a normal distribution (Happé, 1999). The relations this cognitive style has with exceptional talent will be explored further below with reference to the archaeological implications.

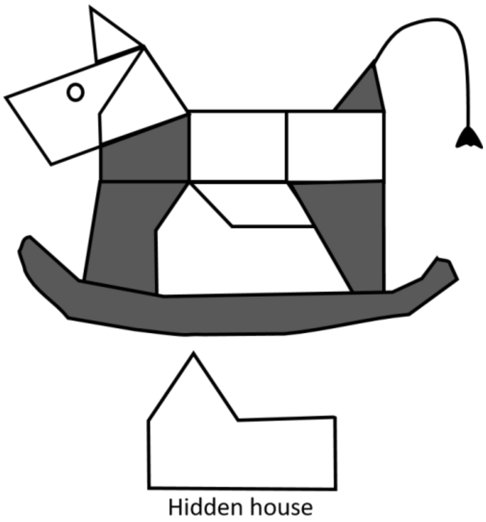


Figure 6. Example of an Embedded Figure, where the image of the ‘hidden house’ must be found within the horse.

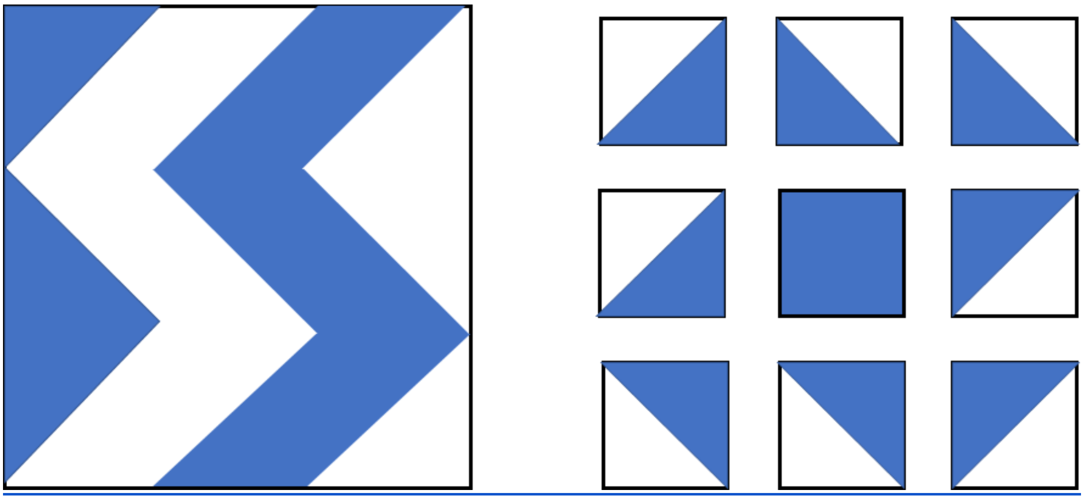


Figure 7. An example of a block design test, where the blocks on the right must be arranged to produce the image on the left.

Executive Functions

Executive functions are abilities for problem solving used to achieve a future goal or intention. These include planning, impulse control, inhibition, working memory, task switching and monitoring of action, and require the individual to detach themselves from the world around them.

Individuals with ASC have shown difficulty with harder versions of the Tower of Hanoi and Trail Making B test, tests which requires high levels of planning (Kleinhans et al., 2005). This is likely in part due to difficulties with mental flexibility, as shown by results on the Wisconsin Card Sorting Task, where participants with ASC often struggle to adapt to a new rule. Further differences are that individuals with ASC are less likely to suppress prepotent responses, less likely to spontaneously generate pretence and may have difficulty monitoring their own actions and thoughts, although evidence for this is tenuous (Hill, 2004, 2004). These differences may lead to more rigid behaviour, narrow interests, and perseverations (Ozonoff et al., 1991). As seen there are difficulties associated with this trait. However, having a narrow interest may be an asset in particular contexts. For example, Baron-Cohen (2008) states that individuals with ASC may use their narrow focus to check and recheck systems and gain pleasure from doing so, this would be interpreted as a perseveration. These ‘obsessions’ focus on folk physics and thus cause an enhancement in folk physics. Within settings such as scientific higher education, or careers such as engineering, this would be an asset (Baron-Cohen & Wheelwright, 1999).

Further, similar to the findings of WCC, parents of those with ASC are also liable to have similar executive differences (Piven & Palmer, 1997). It is likely that abilities in executive functions are also normally distributed through the population. ASC is merely an extreme, which leads to some difficulties but also advantages, and similar to WCC can lead to success.

Spikins, Wright and I have also explored how individuals with ASC relate to objects (Spikins et al., 2017). This involved asking several questions about disaster scenarios, such as what they would take if there was a fire at work, home or they were stranded on a desert island. We found that rather than taking sentimental objects that remind them of relationships and past events, they were more likely to take functional objects. Therefore, during these theoretical disasters those with an AQ score above the threshold which suggests an ASC are more practical and have more selectively advantageous responses. In a past where how a disaster is managed could mean life or death the selection of functional objects rather than a predilection towards sentimental objects was likely a highly advantageous asset.

Archaeological Interpretations

The differences outlined above have begun to be integrated into theories of prehistoric groups, as discussed by Spikins, Scott and Wright (in press). The extensive observations of Nadia, a child with Autism who possessed extraordinary drawing abilities early in life, by Selfe (1977), were reinterpreted by Humphrey (1998) to explore the similarities between the child’s art and ice age cave art (figure 8). Humphrey suggests that there is an intense naturalism in both Nadia’s and the cave artists’ works, which doesn’t adhere to stereotypes of an image, but rather are depictions of the singular animal. The outline of the animals are depicted by Nadia as single linear lines with similar methods of producing perspective as the cave artists. Further similarities are a preference for a side on view, need for exceptional memory, emphasis on the faces and feet of the animals, overlapping of figures and the creation of composite animals. These similarities are striking, however Humphrey focused on Nadia’s lack of language suggesting that the creators of cave art may not have had language to categorize or name animals therefore paintings were based on the actual forms rather than stereotyped mental images of the named category (e.g. horse). Humphrey argues that this is what has led to the highly detailed images in the caves. Mithen comments within the paper that the idea that language is not necessary for the production of these images is interesting as it breaks an assumption that underlies much work on Palaeolithic art. However, he states that due to the universality of language, and the continuity of the archaeological record, language must have evolved at least 100 ka. This is a recurring argument in many of the comments.

Kellman (1998) took a different perspective to Humphrey, suggesting that aspects of visual processing rather than a lack of categorization of images through language was the key connection. She suggests that the ability to think in pictures, as Grandin is able to do, may be responsible for the high attention to detail and other commonalities seen in both cave art and the art of individuals with ASC. According to this theory the meaning of the artwork is to order the world around them, their own thoughts, and interests in a visual way, or to put that another way - to systemize them.

Spikins (2009) takes a different stance on this debate. Rather than there being similarities between the minds of those who created cave art and individuals with ASC, she states that individuals with autistic traits may have influenced the way that individuals around them thought. Spikins also extended the theory to suggest that the high attention to detail needed to produce microliths would favour an autistic mindset and that the transition to a modern mind may in fact be the transition to the inclusion of different minds. This theory of integration was recently extended by Spikins et al. (2016). They suggest that the emergence of collaborative morality led to conditions where an individual’s vulnerabilities could be buffered, and specialized talents could be recognized and utilized more effectively. Asperger syndrome is suggested as a condition with assets which may have been integrated, valued, and had a significant impact on the success of a group. Spikins and Wright (2016) further explored this subject suggesting that beyond art the recording of natural systems would favour an autistic mindset. For example, at Abauntz Cave (13,660 ka) Maps were produced which depict rivers, flooded areas, mountains, entrance to a cave and the location to ford the river. These depictions are haphazardly organized with overlying and underlying animal depictions (Utrilla et al., 2009). A second example used by Spikins and Wright (2016) is the Abri Blanchard plaquette, which depicts the position and phase of the moon using a coordinate system. They argue that these forms of recordings are characteristic of many individuals with ASC. However, rather than suggesting that it is individuals with ASC producing these items, they suggest that it is the autistic vision, or traits of Autism which are responsible for these products. This is an important differentiation because ASC would have been uncommon and, as shown above, the traits of Autism may be distributed through the population. Therefore, the technical traits of Autism, and the influence of individuals with these traits on those around them, may have had a profound impact on human technological and cultural evolution.

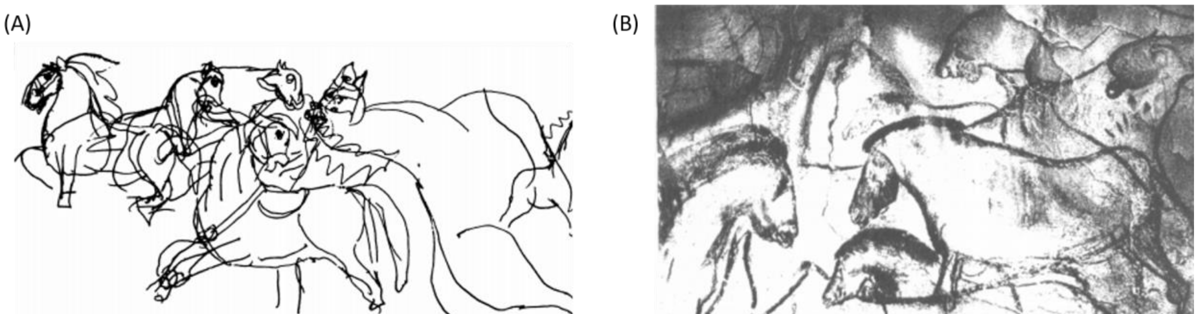


Figure 8. Comparison of horses by Nadia 3 years 5 months (Selfe 1977), and the horses at Chauvet Cave (Humphrey 1998).

This theory is not without opposition. Pickard et al. (2011) and Bednarik (2013, 2016) have each presented counter arguments. Pickard et al. (2011) regard ASC as a deleterious pathological by-product of human variation, and believe that even if individuals with the condition were integrated they would not have significantly influenced groups to produce advantages. Further he suggests that it takes considerable therapy to encourage the creativity of individuals with Autism, which is unlikely to have occurred during the Palaeolithic. Therefore, they are unlikely to be the producers of Palaeolithic art. They suggest psychotropic drugs as an alternative. Pickard et al. also refute Spikins' (2009) assertion that individuals with ASC may have provided the mindset for an insight into the natural systems of animals and the weather. They state that WCC would inhibit the processing of these systems which would require global processing. There are several issues with Pickard et al.'s arguments. Firstly, new genetic evidence which will be explored below (3.3) directly refute the idea of ASC as a deleterious phenomenon. Secondly, the use of psychedelic drugs changes sensory experience, but it does not lead to accurate and realistic artistic ability (Spikins, Scott and Wright in press). Thirdly, the suggestion that individuals with ASC would not be able to provide an insight into the natural systems of the landscape directly contrasts with the psychological literature (see above). Bednarik (2013, 2016) shares Pickard et al.'s view that ASC is a deleterious by-product. He suggests that the social difficulties of individuals with ASC would lead to negative selection and that the recent prevalence is due to a suspension of natural selection. Bednarik also suggests that the rigidity of the mind of individuals with ASC would prevent innovative thought. However, as shown above the mindset of individuals with ASC may actually lead to success in innovative professions, as shown by Grandin (2006). Bednarik suggests that trance states may be an alternative. However, as stated above, while an altered state of consciousness may lead to decreased inhibitions and an increase in the production of art, it does not lead to spontaneous talent (Spikins, Scott and Wright in press).

The behaviour and cognition of individuals with ASC produce many technical advantages to compensate for social difficulties. These advantages range from increased detail processing, systemizing, and having an intense focus upon narrow interests, to selecting more functional items during a crisis.

We will now briefly explore the neurological causes of these differences and then assess whether the genetic literature supports the assertions of Bednarik and Pickard. Following this we will test whether traits of Autism may have had an impact on Palaeolithic artwork.

4.2 Neurology

The Neurological causes of ASC are currently unclear. However, there are a significant number of differences suggested as causal. Primarily it is accepted that atypical neural connections are responsible for at least some of the behavioural differences of individuals with ASC. Long range underconnectivity has been found across the brain, with local overconnectivity in particular areas. Both areas of over and under connectivity are correlated with the strength of behavioural differences (Kana et al., 2014; Maximo et al., 2014). However, due to the wide range of connective differences seen, it is difficult to identify patterns in these difference (Maximo et al., 2014). Conflicting results further confuse this.

Aberrant connectivity in individuals with ASC is most likely caused by developmental differences. Individuals with Autism on average have a larger brain size than controls at the age of 2-4. Estimates of the difference vary widely most probably due to individual variation within samples which effect averages between samples. One estimate is that individuals with Autism have a brain size 18% larger than controls. This is suggested to be due to greater neuronal growth or less pruning, which is likely responsible for differences in connectivity (Penn, 2006). However, when put into a developmental frame, individuals with Autism show increased connectivity during childhood, followed by reduced connectivity in adolescence and adulthood, therefore these studies need to be contextualized with age (Uddin et al., 2013). This may help to reduce conflicting results and elucidate a pattern. The current view held by neurologists is that there is an increase in local connectivity and a decrease in global connectivity in the brain. Therefore, there are areas of hyper-connectivity, such as the frontal lobe, yet these areas are not as connected to other components which are highly intra-connected (Courchesne & Pierce, 2005). Connective differences are also apparent in individuals with milder forms of ASC. However, connective differences may vary depending on the phenotype of the condition. This is shown by connective differences in the left hemisphere of individuals with Asperger Syndrome relative to individuals with Autism, which facilitate the acquisition of language (Duffy et al., 2013). Thus, we can conclude that there are connective differences in individuals with ASC, but must acknowledge that there is also high individual variability.

Penn (2006) provided an extensive review of the likely neurological causes of Autism (table 2). This highlights how widespread the differences are. However, it must also be noted that conflicting results are rife within this research. What is clear is that there are morphological as well as connective difference, which may be correlated to the degree of symptoms and phenotype of the condition (Schumann et al., 2009). Due to the discrepancies between research teams it may be possible that individual variation within groups with ASC has more of an impact than is currently accepted. Nevertheless, it is clear from this that the developmental differences of individuals with ASC has an impact on the morphology of components of the brain. The microstructure of the brain also appears to have differences. Minicolumns, the smallest level of organisation in the brain (Buxhoeveden & Casanova, 2002), are more numerous, but smaller with less compact cells (Casanova et al., 2002). This is argued to be a factor contributing to the differences in connectivity.

Cortical difference	***Likely Effects***
Cerebellum - difference in volume and activation.	Differences in shifting and orienting attention.
Temporal lobe - overconnectivity in medial temporal lobe, atypical activation of the temporal poles, increased activation of Wernick’s area during sentence comprehension, larger size of the	Differences in lingual abilities, facial processing, ToM, cross modal association, and central coherence.

amygdala, little or no activation in the amygdala and fusiform gyrus when inferring emotion.	
Frontal lobe - Abnormal activation during ToM tasks, less activation of the right dorsolateral prefrontal cortex, posterior cingulate cortex, parietal cortex and increased occipitotemporal activation during embedded figures tests, WCC suggests decreased connection with other cortices.	Highly connected with the triad of Autism symptoms, difficulty with ToM, executive functions, and central coherence.

Table 2. The differences in the brain identified by Penn's (2006) review.

There are two further neurological difference in ASC. Differences in von Economo Neurons (VENs) and Mirror Neurons. VENs are argued to be more numerous, have morphological differences, and be absent within a dimple in the right fronto insular cortex (rFIC) in individuals with Autism (Santos et al., 2011). VENs rapidly relay simple information processed in the FIC and the Anterior Cingulate Cortex (ACC) to the frontal and temporal cortices where slower judgements are made (Allman et al., 2005). The impact of these differences was shown by Baron-Cohen et al. (1999), who showed that the rFIC was significantly less active when inferring mental states from pictures. The developmental history of VENs also supports their importance for social interaction, with their completion of growth coinciding with the development of first order ToM at the age of 4 (Allman et al., 2005). These neurons seem imperative for the fast, intuitive decision making needed for ToM. It is also suggested by Butti et al. (2013) that different variations of VENs may be responsible for different subgroups of ASC. Allman and Mareschal (2016) recently proposed that mental time travel is the mechanism leading to ToM development and that VENs may be the mechanism allowing this disassociation with the present. However, more research is needed to firmly determine the impact of VENs on ToM due to the small sample sizes and the inability to directly study these neurons in vivo. Sridharan et al. (2008) have also displayed that the rFIC and ACC may be imperative for executive functions, as they play a causal role in switching from the default mode networks to the central executive networks. This is supported by the work of Hodgson et al. (2007) which showed that individuals with lesions on the rFIC had difficulties with rule switching and antisaccade tasks. Therefore, VENs may be significant for executive functions. Disorganisation or reduced connectivity in the right side of the brain has long been implicated in disrupting global processing (Happé, 1999; Melillo & Leisman, 2009). The FIC has also been found to be sensitive to sublexical pronunciation, which is reliant on the dorsal (global processing) stream (Borowsky et al., 2006). Therefore, it may be posited for future research that the different organization of VENs may impact central coherence. Thus, VENs may be an example of long ranging, fast acting connections that have been impacted by the developmental differences of individuals with ASC, and likely are partially culpable for the triad of symptoms.

The Mirror Neuron System (MNS) has also been implicated in difficulties with ToM (Ramachandran & Oberman, 2006). Mirror neurons have been predominantly located in the premotor cortex, posterior parietal cortex and inferior frontal gyrus, although they have also been found in areas such as the insular cortex and ACC (Caruana et al., 2017; Iacoboni & Dapretto, 2006; Ramachandran & Oberman, 2006). The MNS is related to imitation, goal understanding and empathy (Rizzolatti et al., 2001). In Neurotypical individuals mirror neurons activate when performing an action, however they also activate when observing another person perform an action, this elicits similar motor evoked potentials to the person performing the action (Di Pellegrino et al., 1992; Gallese et al., 1996). This is thought to be essential for representing other's minds (Gallese & Goldman, 1998). However, mirror neuron activation during observation tasks and the cortical thickness of MNS associated areas are negatively correlated with AQ (Dapretto et al., 2006; Hadjikhani et al., 2006; Martineau et al., 2010; Oberman et al., 2005; Puzzo et al., 2010; Ramachandran & Oberman, 2006). It is suggested that this contributes to the social differences of individuals with ASC. However, this is debated (Gallese et al., 2011). A brief meta-analysis of studies between 2008 and 2013 shows that 76% support the impact of mirror neurons on social cognition in Autism (Neta & Varanda, 2016). While it is not currently understood whether this is causative or derivative, statements of how this may aid treatment imply that it is a cause (Ramachandran & Oberman, 2006). Functionally, it has been argued that this causes difficulties in the social understanding of intentions, emotional empathy, and imitation. It must be noted that this mirror neuron response is automatic to another's actions or emotions, which is unconscious and simulatory; therefore, it doesn't represent or prevent conscious appraisal of another individual's actions or emotions (Gallese et al., 2007). This division has been demonstrated by McIntosh et al. (2006) who showed that while individuals with ASC do not have automatic imitation responses they may have voluntary conscious responses when prompted. This may be consistent with the 'hacking strategies' outlined above and suggests that individuals with ASC are reliant on a conscious 'theory theory' (constructed through causal laws) rather than an unconscious 'simulation theory' (where another person's mindset is adopted) utilizing the MNS (Gallese & Goldman, 1998). This may also account for studies such as Hamilton et al. (2007) where individuals are overtly prompted to imitate, which negate the MNS hypothesis. Further it has recently been shown that motor imitation is intact despite difficulties with empathetic emotional simulation (Schulte-Rüther et al., 2017).

I am aware that this section largely has focused on the difficulties of individuals with ASC. This is due to the current focus of the literature on identifying methods of treatment for these difficulties. Nevertheless, many of the differences referenced in this section may be equally viewed in the manner of the previous section, as producing assets as well as the commonly cited difficulties. For example, the increased local connectivity of the brain may be responsible for certain talents associated with ASC due to accentuation of domains rather than general integration. One example of this may be the increased intra-connectivity of the frontal lobe. While the different connection may be responsible for some executive difficulties it may enhance other, such as memory. Additionally, the differences in connectivity of the right hemisphere increase the use of the ventral stream (for local processing). Hence, the connective differences may also be responsible for increased attention to detail and analytical ability. This has also been shown to account for acoustic hypersensitivity, with early left temporal and frontal lobe activation in individuals with Autism. This increases the likelihood of developing perfect pitch and extraordinary musical ability and may account for the high rates of enhanced perceptual abilities (58%) and domain specific skills (62.5%) seen in individuals with Autism (Meilleur et al., 2015). Further, due to the fact that imitation of motor action is not inhibited it can be concluded that, in a prehistoric as well as modern context, individuals with ASC would have been able to utilize the larger social group sizes to learn complex tool production skills.

It is interesting to observe that this is a condition which leads to social differences and often difficulties, but enhances technical abilities. If the genetics that cause this condition are positively selected for, and there is significant heritability, then I believe this is an alternative cognitive style responding to the conflicting social and technical pressures active upon our species, which focuses on technical ability. Additionally, this is a condition which causes significant behavioural differences which would be invisible when assessing archaeological cranial remains. This highlights just how fragmented the record presented in Chapter 3 may be. Autism causes minimal morphological difference in the brain which would not be observable in the archaeological record. However, it leads to a considerably different social life, with much more emphasis on objects and systems. Therefore, a key question which should be considered in future research is how much of an impact changes in connectivity could have had during human evolution? A further question to be posed is, could the changes in morphology of the brain have occurred for different functional reasons and then their ultimate nature was changed as connections developed between areas, leading to more social or different functioning? If so then there is a considerable gap in our ability to assess the evolution of the human mind.

4.3 Genetics

Heritability

The genetic mechanisms causing autism are poorly understood. However, it is considered a highly heritable condition. This was initially shown by Folstein and Rutter (1977), who found a concordance of 36% between monozygotic (MZ: N=11) twins compared to 0% between dizygotic (DZ: N=10) twins for strict Autism. They also showed high concordance rates for other social differences, 82% and 10% for MZ and DZ twins. This led them to conclude that Autism is highly heritable, through the transmission of a broad range of hereditary social and lingual abnormalities which may interact with other genetic and environmental factors to cause Autism. As a consequence, a broader autism phenotype (BAP) was defined, where individuals show similarities to those with Autism. Concordance estimates for BAP were as high as 92% for MZ twins, however, for DZ twins concordance remained as low as 10%. Based upon these results the heritability of the condition was estimated between 91-93% (Bailey et al., 1995).

More recent estimates of concordance range between 39-94.7% and 15-31% for MZ and DZ twins (Huguet et al., 2016; Lichtenstein et al., 2010; Ronald & Hoekstra, 2011; Rosenberg et al., 2009; Taniai et al., 2008). Modern heritability estimates also have a broad range, between 38-80% for ASC (Hallmayer et al., 2011; Huguet et al., 2016; Lichtenstein et al., 2010; Sandin et al., 2014). This is likely due to the small sample sizes used in these studies, which may be composed of different types of twins. Hallmayer et al. (2011) have shown that there are differences in concordance between different types of twins (table 3). They argue that this may be the impact of non-shared environmental factors. Hence, if a study is composed of a high proportion of sex discordant twins with male probands heritability estimates will be lower. Differences such as this may be responsible for the high variation seen in estimates based upon twin studies.

Type of twin	***Concordance for strict autism***	***Concordance for ASC***
Monozygotic males	58% (N=40)	77% (N=45)
Monozygotic females	60% (N=7)	50% (N=9)
Dizygotic males	21% (N=31)	31% (N=45)
Dizygotic females	27% (N=10)	36% (N=13)
Dizygotic female co-twin of male proband	3.7% (N=54)	5.3% (N=76)
Dizygotic male co-twin of female proband	50% (N=2)	50% (N=6)

Table 3. Differences in concurrence between types of twins (Hallmayer et al. 2011).

The rates of recurrence in siblings also suggest high heritability. If a family has a single child with an ASC, then there is a 25% chance that a second child will also have an ASC. If a family has two or more children with ASC, then the third sibling is 50% likely to have an ASC (Ozonoff et al., 2011). Sandin et al. (2014) produced a study of 2,049,973 children, which showed that a person's risk of having ASC or Autism increased with relatedness to an affected proband. Heritability was estimated at 50%, with the largest causes being additive genetics and non-shared environmental factors. This is the largest study of familial risk to date, therefore making it less susceptible to sampling issues than small scale twin studies.

The heritability of autistic traits has also been assessed in the wider population. Heritability estimates range between 36-87%. However, there is a clear reporter bias, with these estimates being more modest when self-reported (36-57%) and more extreme when reported by a teacher or parent (60-90%). Heritability estimates are lower when younger children are rated by teachers or parents (40-44%). This contrasts with the reporter bias and suggests that heritability increases with age (Ronald & Hoekstra, 2011).

It can be seen that ASC and autistic traits are highly heritable. Therefore, it must have an evolutionary history and an evolutionary impact. To fully understand this evolutionary impact the genetic architecture of ASC must be explored.

Genetic Causes

Genetically, three different mechanisms may cause Autism: single nucleotide polymorphisms (SNPs), copy number variants (CNVs), and de novo mutations.

SNPs are a difference in a single nucleotide in the DNA sequence which is common across 1% of the population. This causes common variation. It is estimated that common variation such as this contributed to at least 25% of liability for ASC (Cross-Disorder Group of the Psychiatric Genomics Consortium et al., 2013; Gaugler et al., 2014; Klei et al., 2012; Robinson et al., 2016). Klei et al. (2012) have suggested that this contribution may vary between simplex (40%) and multiplex (60%) families. However, it has been argued that even the most associated SNPs have a small effect (El-Fishawy & State, 2010). Consequently, individually SNPs have low penetrance, but additively they may have a high impact and be responsible for up to 95% of the heritability of ASC (Gaugler et al., 2014; Huguet et al., 2016). This supports the assortative mating hypothesis and the spectral view of Autism (Baron-Cohen, 2006; Ronald & Hoekstra, 2011). Nevertheless, due to the low penetrance and how numerous (>1000) SNPs are, no causative polymorphism has been found; even the most significant (CNTNAP2) only has a modest effect (Anney et al., 2012; Arking et al., 2008; Huguet et al., 2016; Warrier et al., 2015).

Evolutionarily, these findings support the Common Disease Common Variant (CDCV) hypothesis. CDCV predicts that common genetic diseases (affect >1% of the population) must stem from common SNPs. Due to our species expanding to our current population in just 100,000 years from an original populace of 10,000, it is thought that the original population couldn’t have supported a large amount of disease alleles. Rapid expansion meant that new mutations and rare mutations didn’t have time to become prolific. Therefore, common diseases are caused by the same common variants as 100,000 years ago. This suggests that these risk alleles aren’t selected out by evolution. In the case of polygenic conditions such as autism, this may be the case as each individual polymorphism carries low risk and has associated advantages (El-Fishawy & State, 2010; Pickard et al., 2011). For example, Polimanti and Gelernter (2017) have shown that SNPs associated with Autism are under positive selection due to their functional relationship with neurogenesis and cognition. Therefore, a highly heritable phenotype of ASC may have been present in prehistory prior to 100 ka with at least milder traits and phenotypes under positive selection.

CNVs are microdeletions and microduplications within the genome. They are significantly associated with ASC, seen in 5-11.6% of cases in contrast to 1% of controls. De novo CNVs are more prevalent in probands of simplex (7-10%) than multiplex (2-3%) families (Christian et al., 2008; Colosimo, 2010; Cook & Scherer, 2008; Devlin & Scherer, 2012; Marshall et al., 2008; Pinto et al., 2010; Sebat et al., 2007; Zhao et al., 2007). This difference is due to de novo CNVs becoming inherited variants. Transmission is estimated at 50%, with 40% coming from non-ASC parents, most likely females (Cook & Scherer, 2008; Devlin & Scherer, 2012; Zhao et al., 2007). However, even when siblings are concordant for ASC they may be discordant for a specific inherited CNV. This suggests that CNVs interact with other genetic and environmental factors and may not be causative on their own. Further, CNVs are complicit in causing more severe phenotypes of ASC. De novo CNVs target networks related to synapse development, axon targeting and neuronal motility, often causing lower IQ and even intellectual disability (Gilman et al., 2011; Leppa et al., 2016; Pinto et al., 2010). I believe this suggests that different genetic causes underlie high and low functioning ASC. This echoes de la Torre-Ubieta et al.’s (2016) interpretation that the genetic evidence suggests that ASC is not only comprised of one condition, but a number of genetically distinct conditions which cause similar behaviour.

A number of CNVs implicated in ASCs have a recent evolutionary history, developing following the divergence from Neanderthals approximately 588 ka (Mendez et al., 2016). CNVs at 16p11.2 account for 1% of autism. These are caused by a duplication that occurred at BOLA2 specifically in humans 282ka which was strongly selected for due to its function in iron regulation during embryonic development. However, this duplication caused instability within chromosome 16p11.2 and led to an increased susceptibility to CNVs (Nuttle et al., 2016). AUTs2 is the genomic region that most differentiates humans and Neanderthals. CNVs and deletions in this region are significantly associated with Autism and a number of other neurological conditions (Oksenberg & Ahituv, 2013; Oksenberg et al., 2013). Dosage of DUF1220 has been shown to correlate with 3 major symptoms of autism: social differences, communicative difficulties, and repetitive behaviour (Davis et al., 2014). CNVs within or near DUF1220 domains have also been related to brain size and the number of domains have been shown to increase linearly with relation to humans (e.g. Number of domains: Human=212, Chimpanzee=34, Macaque=30, Mouse=1). Suggesting it has been under recent positive selection. However, by allowing such a rapid increase in the copy number of DUF1220, it has led to instability in 1q21.1 (where most DUF1220 sequences map), and created an increased susceptibility to autism (Dumas & Sikela, 2009). Therefore, DUF1220 has two affects: (1) it increases instability in 1q21.1 leading to more disadvantageous CNVs, (2) dosage of DUF1220 itself directly influences autistic traits. Similarly, chromosome 15q13.3 has become unstable due to large expansion between 500-900ka (Antonacci et al., 2014).

Rare de novo point mutations occur in two ways, through causing loss of function (LOF) or missense (which causes it to function differently, for example coding for a different amino acid). Iossifov et al. (2014) have shown that missense mutations have little effect on autism, only occurring marginally more often in ASC patients (rate: ASC=0.94; control = 0.82), this means that when observed they are only 12% likely to influence ASC diagnosis. Similarly, they have very little impact on heritability, 0.04%. Whereas, LOF mutations have a much higher impact with 43% of LOF mutations contributing to 9% of diagnosis and 1.11% of heritability (Gaugler et al., 2014; Iossifov et al., 2014). Due to their higher impact, functional analysis will focus on LOF mutations.

LOF mutations associated with ASC have been significantly associated with intellectual disability (ID) and lower IQ as they are often in areas linked to synaptic transmission, neuronal development, axon guidance, and fragile X mental retardation protein (De Rubeis et al., 2014; Iossifov et al., 2014; Robinson et al., 2016; Ronald & Hoekstra, 2011; Ronemus et al., 2014). Ronald and Hoekstra (2011) argue that this may be a key difference between individuals with comorbid ID and those without ID. Similarly, Warrier et al. (2016) have shown an increase in de novo missense and LOF mutations in areas also enriched for genes associated with educational attainment, with larger mutations causing more severe phenotypes and smaller mutations leading to talents.

These findings suggest that while 31% of individuals with ASC have comorbid ID, it is largely due to de novo LOF, missense, and CNV mutations with low prevalence and (excluding CNVs) heritability (Leppa et al., 2016). Thus, similar to de la Torre-Ubieta et al. (2016), I suggest that there are at least two genetically distinct phenotypes of ASC. One associated with ID caused by de novo mutation, the other caused by common variants under positive selection. It must be recognised that de novo mutations are not human specific. For example, a Japanese macaque was found to exhibit autistic traits and had 2 CNVs and 32 LOFs (Yoshida et al., 2016). However, the increased susceptibility to these mutations has been shown to be evolutionarily recent (Tennessen et al., 2012).

4.4 Conclusions

In this section we have assessed the behaviour, neurology, and genetics of individuals with ASC. From this we can make a series of conclusions.

Firstly, ASC is a condition which is associated with many technical assets as well as social difficulties, many of which would have been highly advantageous in prehistoric hunter-gatherer societies. Further, many of the behavioural traits of individuals with ASC are normally distributed through the population (4.1).

Secondly, the neurological differences of individuals with ASC, although unclear, are largely connective with only minor differences in cerebral morphology. These differences would be invisible in the archaeological record, yet they cause considerable behavioural and cognitive differences. This raises the question of how much of an impact differences in connectivity would have had in human evolution and whether changes in the morphology of the brain through time could have occurred for different reasons, with their modern social nature forming later through changes in connectivity. This would leave a considerable gap in our ability to assess the evolution of the human mind (4.2).

Thirdly, ASC and autistic traits are highly heritable, with the majority of heritability being due to SNPs which are under positive selection. Conversely, CNVs have been shown to be a rarer cause of ASC despite being highly heritable. De novo causes of ASC are consistent with ID. Due to their lower prevalence in multiplex families and (excluding CNVs) lower heritability it is suggested that this represents a different genetic mechanism. This de novo mechanism is largely recent, with a different evolutionary history to causative SNPs. This suggests that phenotypes comorbid with ID are largely unrelated to ASC without ID and are under different evolutionary selection. Therefore, while ASC with ID is likely to have become prevalent specifically in modern humans following 200ka, due to increased genetic instability, ASC without ID was present prior to 200ka and under positive selection (4.3).

This suggests that ASC without ID is an alternate adaptive strategy which significantly enhances technical ability, at the expense of social abilities, and was present prior to 200ka.

As explored above Autism is made up of multiple traits that are normally distributed through the population. To assess the impact of an autistic way of thinking on the past we will now focus on one trait - detail focus - and assess how this trait may have impacted Palaeolithic art.

Chapter 5: Detail Focus - An Archaeological Application

This section presents an experimental case study which tests the hypothesis that ***characteristics and components of autism would influence individuals' engagement with material culture, in particular art****. With the assistance of Penny Spikins and Barry Wright, I created the Visual Perception and Cognition Survey, which was completed by 1027 participants. This showed that individuals with the technical autistic trait 'high attention to detail' were more susceptible to pareidolic illusions. Pareidolic illusions have been suggested as a stimulant for the production of Palaeolithic art. Thus, the hypothesis was supported.*

5.1 Introduction

As we have previously explored in section 4.1 detail focus or WCC is a key characteristic of ASC. This leads to many technical assets such as a more systematic mind, more realistic depictions from memory, and an enhanced ability to identify embedded figures. This investigation focuses on the final two abilities.

There has been extensive debate about the similarities between Palaeolithic art and the art of individuals with Autism, which has led researchers to suggest that individuals with autistic traits may have produced Palaeolithic art (4.1). This hypothesis has been criticized for several reasons. Firstly, it has been argued that ASC is a deleterious by-product of rapid neural evolution and that this is unlikely to have significantly influenced groups. Secondly, a large criticism is the difficulty to gain empirical evidence for this theory (Bednarik, 2013, 2016; Pickard et al., 2011). The first criticism is rectified in the previous section, as it has been shown that, while ASC with ID has increased in prevalence due to greater genetic instability following rapid encephalization, ASC without ID is a product of common variation caused by SNPs. This suggests that ASC without ID has a different genetic cause and a longer evolutionary history. Further, it is supported by the distribution of autistic traits through the population - therefore, they must have had an impact on prehistoric groups.

This study is an attempt to explore whether there are any characteristics associated with autism, or one of its key elements, which might influence material culture, specifically engagement with art. By exploring the association of different autistic traits with Palaeolithic art, a feature of the archaeological record which is considered to be social, I hope to highlight the complex pattern of selective pressures, and the impact of both technical and social abilities on this cultural development.

Past studies have found that individuals with Autism are able to identify images faster and more accurately than controls during an embedded figures test (Baron-Cohen, 1998; Jolliffe & Baron-Cohen, 1997; Muth et al., 2014; Shah & Frith, 1983). The images of Palaeolithic art chosen for this study have hidden images in them. Identifying these images may be similar to identifying embedded figures. Therefore, it is expected that individuals with a high Autism Quotient (AQ) would be more successful at identifying them. Anecdotal evidence supports this theory. Individuals with Autism at an exhibition of Palaeolithic plaquettes from Montrastruc Cave, France, could easily identify overlapping difficult to decipher images of animals (Spikins & Wright, 2016, p. 25). Thus, it is expected that individuals with a high AQ would perform better in this survey.

5.2 Methods

This study aimed to test the hypothesis that characteristics and components of autism would influence individuals' engagement with material culture, in particular art. If individuals with high AQ were better able to perceive hidden figures in Palaeolithic artwork, this would support the hypothesis.

To assess this, I collected evidence from a large population sample through an online survey. With advice and assistance from Penny Spikins and Barry Wright I developed an online survey, the 'Visual Perception and Cognition Survey' (VPCS; see Appendix A). This survey was divided into four sections. Firstly, participants provided information regarding employment, hobbies, experience of art, and Palaeolithic art. This allowed us to determine factors which might confound the results. Participants then completed the Autism Quotient (AQ) test. The AQ is a well-established self-report test used to quantify individuals' traits and estimate their placement on the autism-spectrum (Baron-Cohen et al., 2001). This test assesses 5 different traits of Autism: social interaction, communication, attention switching, imagination, and attention to detail. Thus, allowing the assessment of individual traits and their effect on perception. The test has been shown to have high validity for identifying individuals with high functioning Autism and Asperger syndrome and also for identifying broader phenotypes of ASC (Wheelwright et al., 2010; Woodbury-Smith et al., 2005). This makes it a useful substitute to diagnosis which allows a more in-depth analysis of individual traits. Participants were then asked to identify 3 images of animals, to prime them to search for embedded images of animals in the subsequent test images. 10 images were shown, where participants were asked to 'tell us what you [they] see in the image'. Participants were asked to spend no more than 1 minute on each image to establish some control on how much the images were scrutinized, as the longer an individual spends searching an image the more features they are likely to identify. The 10 images were composed of 7 images of Palaeolithic artwork, 2 control images and 1 image produced by Peter Myers, an artist with Autism. The control images were interspersed within the test images to identify whether participants were seeing animals and other features where there were none. The modern image created by Peter Myers was used to investigate whether a modern example was more easily identifiable.

This survey used self-selection sampling and was publicized in a press release connected to two publications (Spikins & Wright, 2016; Spikins et al., 2016), by departments at the University of York, the Autism Research Centre, and by multiple Autism support groups across the country including members of the National Autistic Society. Publicising in these areas enabled us to gain a large enough sample of individuals with high and low levels of autistic traits. The participants in this study are therefore not representative of the wider population as they will be composed of a larger proportion of individuals with high AQ. The Arts and Humanities Ethics Committee at the University of York approved the survey.

1027 participants took part in the survey. Participants were separated differently for each test, based upon their experience of art, Palaeolithic art and their scores for different categories of the AQ test (social skills, communication, attention switching, imagination and attention to detail). Scores for categories of the AQ test were determined in the same way as the overall AQ score is determined, by adding one point for each answer which was related to an autistic trait whether the participant answered ‘definitely’ or ‘slightly’. Participants could score a maximum of 10 on each category. They were then divided into 2 groups for each category based upon their score. All participants were grouped in two different ways. Firstly, above 5 (high) or below and equal to 5 (low) due to 5 being the halfway point of possible scores. Secondly, they were grouped according to the average scores of each category, above average and below and equal to average. Due to the sampling method of this data being specifically designed to achieve a high proportion of autistic traits, it was necessary to utilize data from a previous study to avoid bias when determining the normal mean of each factor of the AQ test. The study by Hurst et al. (2007) was selected as an unbiased large (N=1005) sample which provided an alternative means to analyse our current dataset (table 4). These groups were then tested against their ability to correctly identify depictions in the images of Palaeolithic art. Due to the difficulty of the images, a correct identification was defined as identifying a single figure regardless of incorrect additions or whether there were more animal figures to be identified. Correct identifications scored 1 point. These scores were then collated into an overall score for all 8 test images, hereafter referred to as the ‘Correct Identification Score’. Participants were also scored on the number of imagined images they saw. One point per image was scored for imagined images, regardless of whether a correct identification was also made. Scores were collated for the 8 test images and the 2 control images. This score is hereafter termed the ‘Imagined Figure Score’. The participants were tested on each category and their Correct Identification and Imagined Figure scores were used to determine whether individuals’ scores on particular categories of the AQ test, or experience of art and Palaeolithic art were significantly correlated with scores on the images. Groups were also tested for difference in the number of imagined figures seen on the control images, as the identification of real figures in the test images may have reduced the number of imagined figures identified.

Unless specifically stated statistical significance was determined using the chi square test to a threshold of 0.05. All statistical analysis was completed using SPSS.

5.3 Results

The results will be divided into several sections to investigate the results of the AQ test, Correct Identification Scores, and the Imagined Figure Score.

AQ Test

Figure 9 shows the distribution of participants scores on the AQ test. This shows that 66% of participants (N=679) scored under the threshold suggestive of an ASC (here termed NT participants), whereas 33% (N=339) scored above the threshold suggestive of an ASC (here termed AU participants). This sample is not representative of the wider population (Baird et al., 2006; Baron-Cohen, Scott, et al., 2009). However, it allows us to test the hypothesis of this study with greater confidence than a typical population might, due to the larger sample size of individuals with high AQ.

Figure 10 shows the distribution of the participants across the different categories of the AQ test. This shows three things, the traits are distributed through our population, this sample has high rates of autistic traits (see table 4), and the extremes of the traits are represented in this sample. As expected, the distribution of scores was skewed towards larger scores for AU participants on all categories of the AQ test (figure 11). These results also show that Autism is composed of several different components, which may have been subject to different selection pressures. Further, it was found that AU participants were more likely to have above average experience of art outside of the classroom (P=0.002, figure 12A). However, they didn't have more experience of Palaeolithic art (figure 12B).

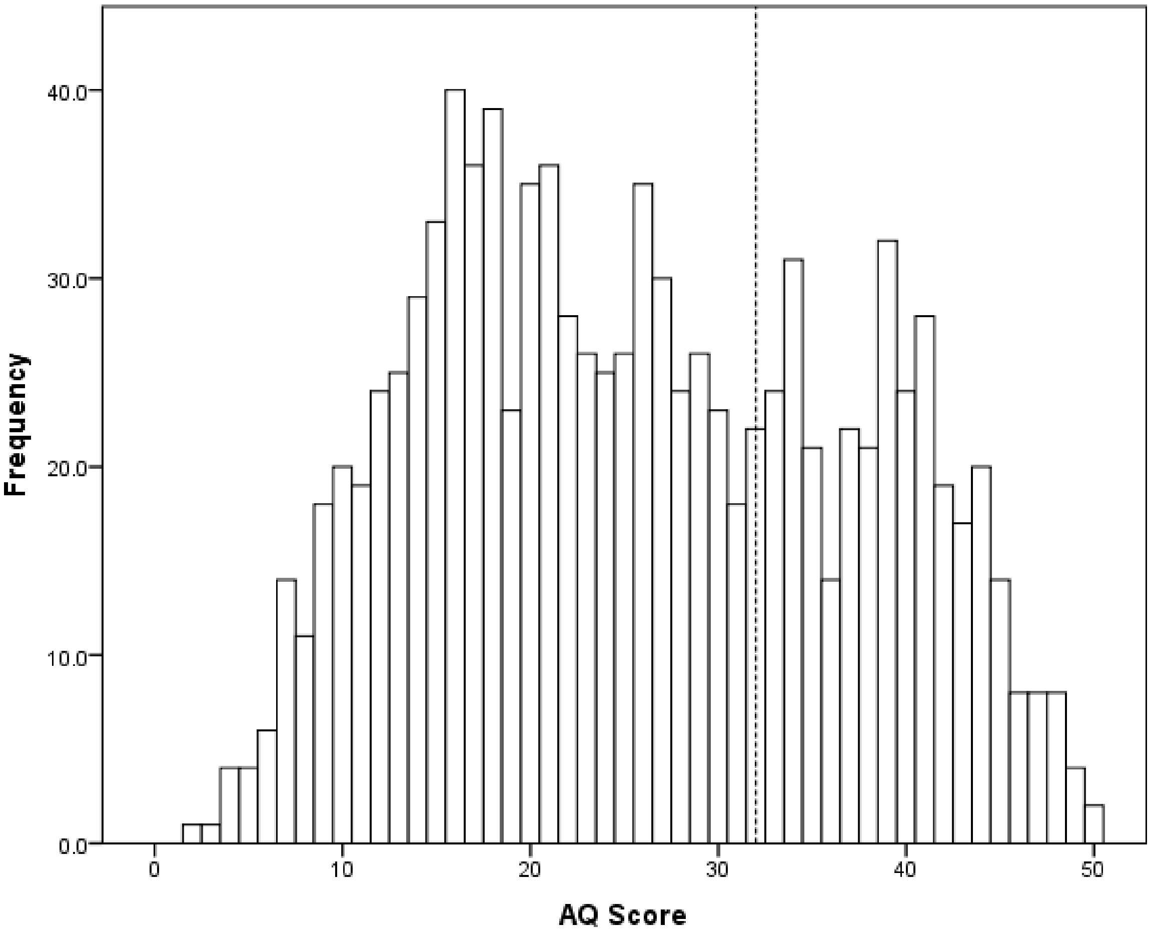


Figure 9. Participants distribution of AQ scores with the threshold of 32 marked (dotted line) which suggests a high risk of an ASC.

AQ Category	**Mean Current Study**	**Mean Hurst et al. (2007)**
Social	4.62	2.14
Communication	5.20	2.26
Attention Switching	6.02	4.72
Attention to Detail	6.03	5.27
Imagination	3.52	2.34

Table 4. Showing the differences in means for each category of the AQ test between the current study and the study by Hurst et al. (2007).

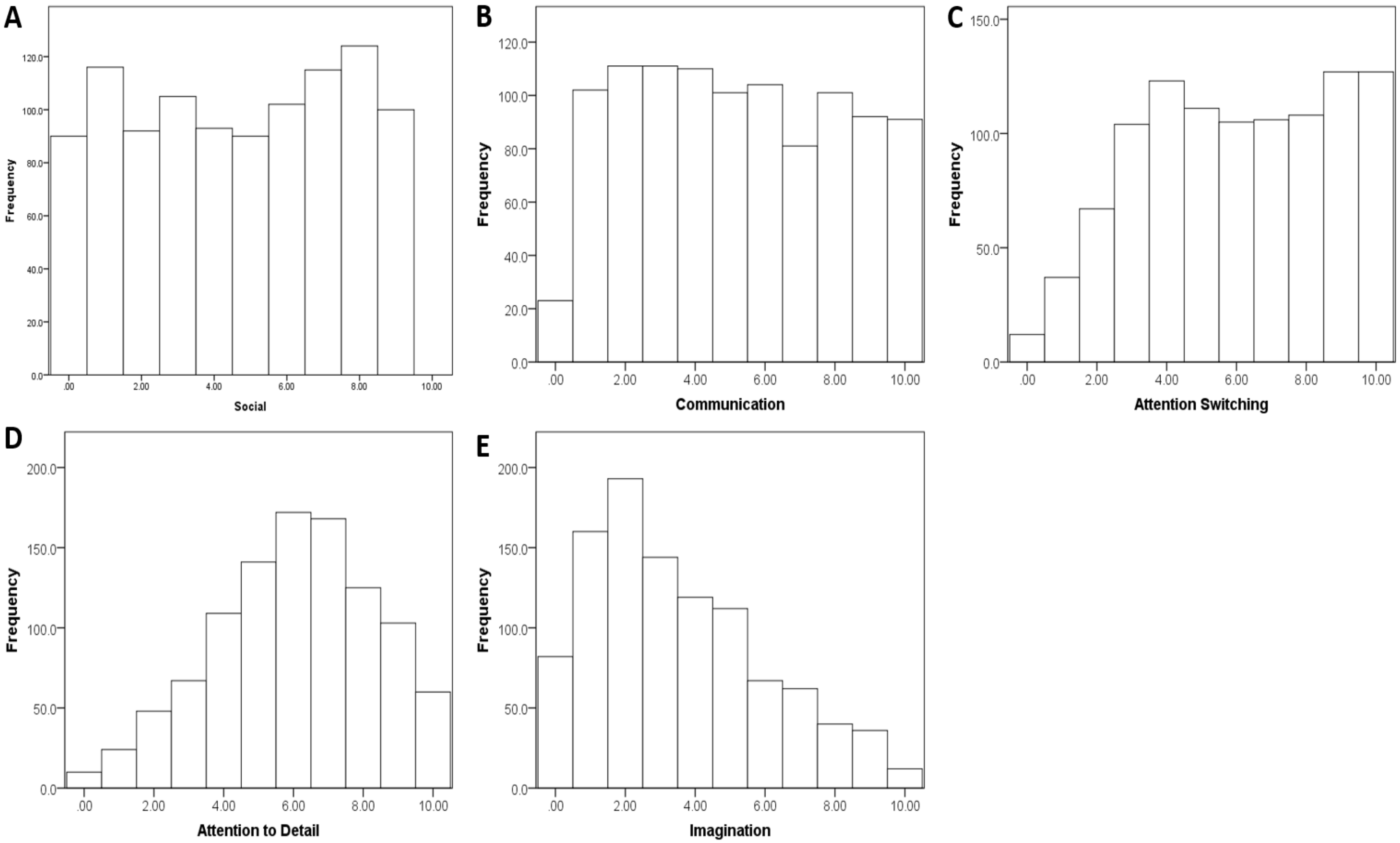


Figure 10. Participants distribution of scores on individual categories of the AQ test.

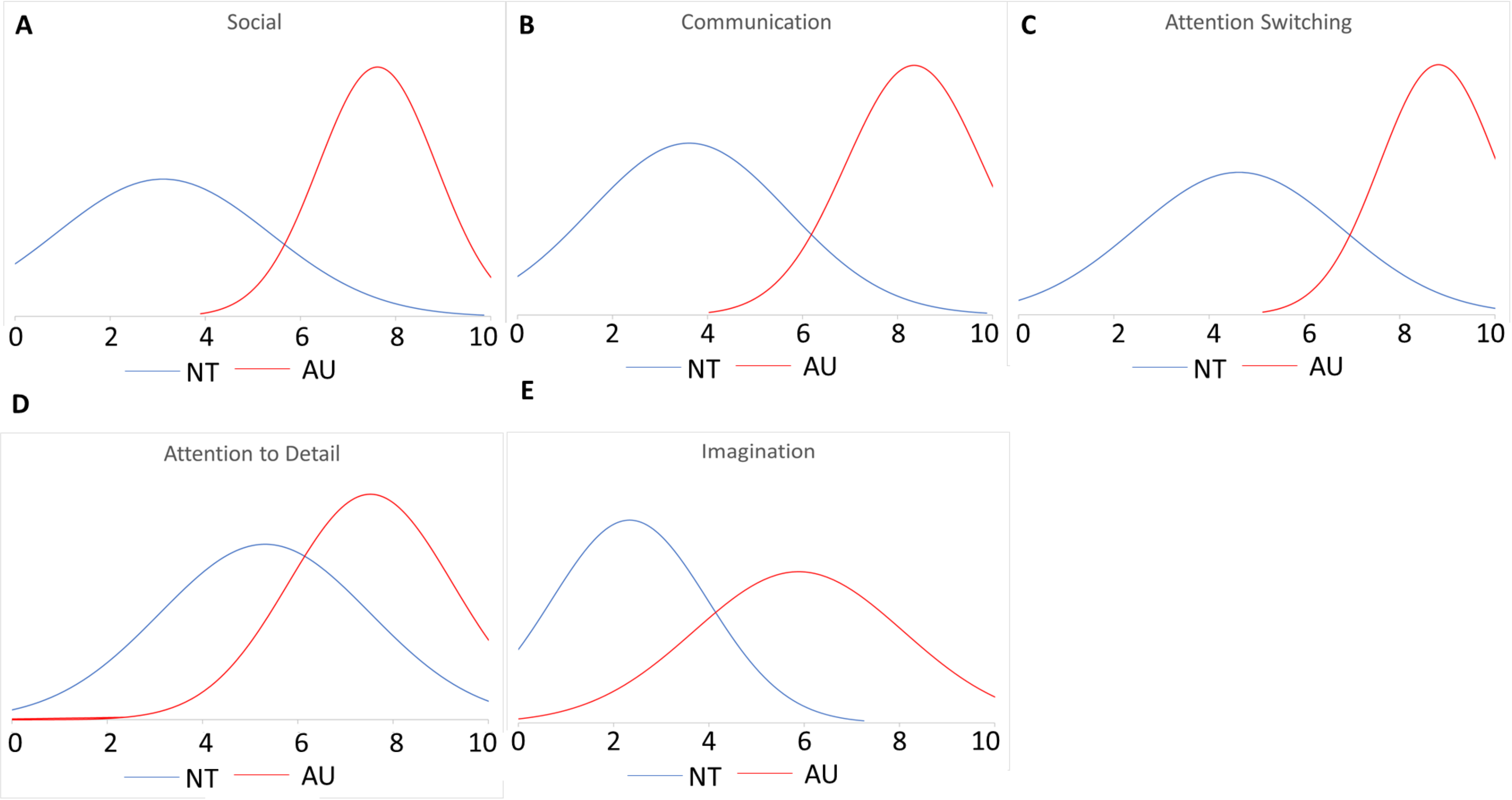


Figure 11. Distribution of participants scores on different categories of the AQ test, grouped according to those who scored below the threshold 32 (NT) and those above (AU).

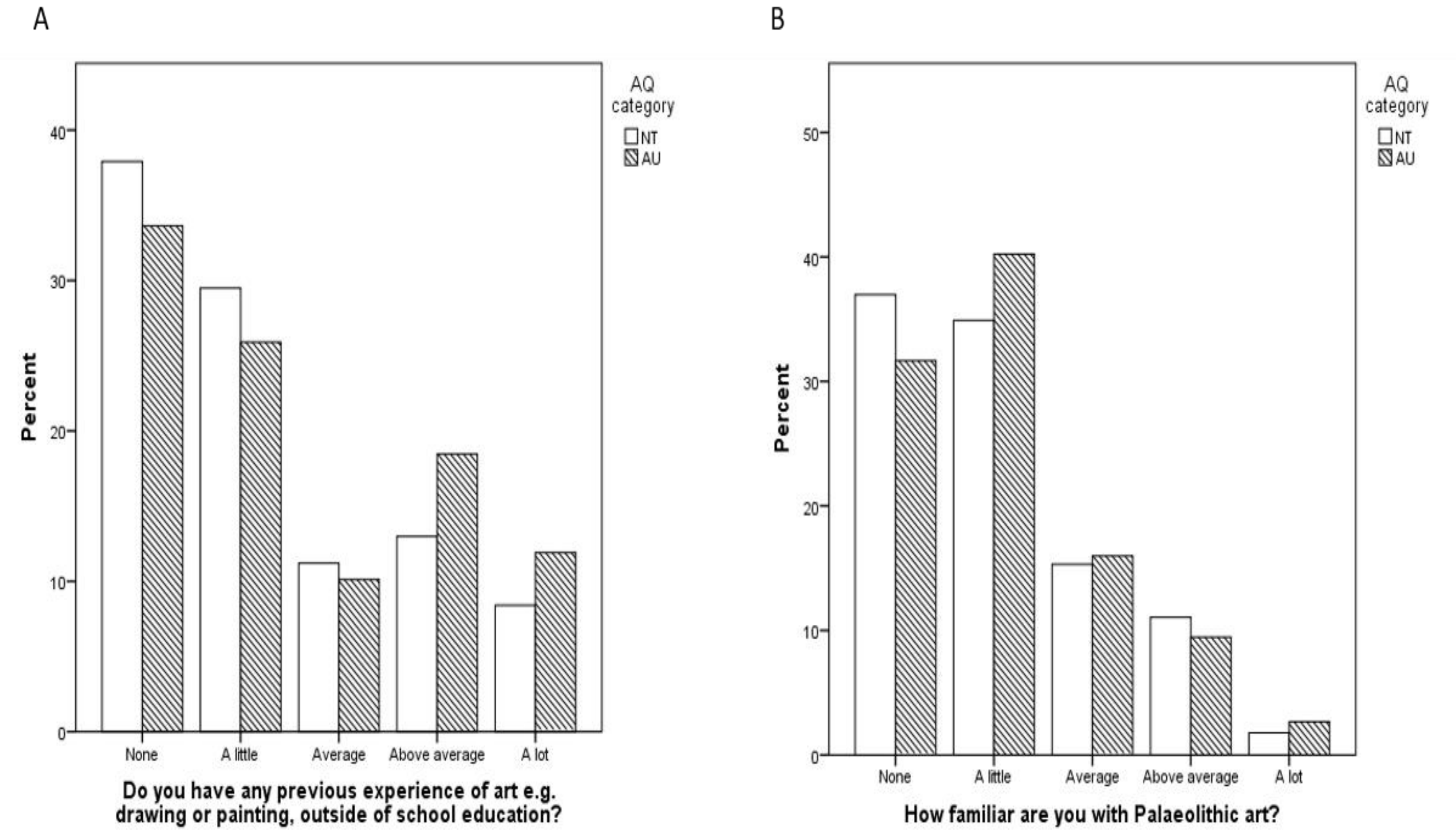


Figure 12. Experience of art (A) and Palaeolithic art (B) grouped by AQ group. Showing that individuals with high AQ are more likely to have experience of art but not Palaeolithic art.

Correct Identification Scores

Figure 13 shows the distribution of correct identification scores of the participants, this is split by category of the AQ and whether the participant scored low (below or equal to 5) or high (>5). As can be seen the score groups on all categories do not significantly differ. This point is further highlighted by figure 14, which shows that when using the mean score of each category according to Hurst et al. (2007), there is still no significant difference. Additionally, when the images are assessed individually there are very few cases of statistical significance (Appendix B). The lack of difference between the groups overall and the inconsistency of statistical significance on individual test images suggests that the ability of participants to identify the hidden figures in the images was not affected by their autistic traits. This is interesting as it contradicts the extensive work by psychologists on the WCC theory (4.1), and may suggest that identifying these images required different perceptive skills. However, this finding may be due to several limitations of the study which will be explored below (5.5). Therefore, we cannot reject the hypothesis.

Imagined Figure Scores

Participants imagined figure scores did show a significant difference. While all other categories of the AQ test do not show significant differences between high and low scorers in both methods of testing, individuals with a high attention to detail saw more imagined figures through the test than those with lower attention to detail (Figure 15 and 16). Moreover, this is also seen consistently when assessing the images individually, with 6 out of 10 of the images showing this trend with statistical significance (Appendix C). Further, when the control images are assessed they each show strong statistical significance individually and when assessed together (P= <0.002, Figure 17). Therefore, individuals with high attention to detail were more likely to see imagined images.

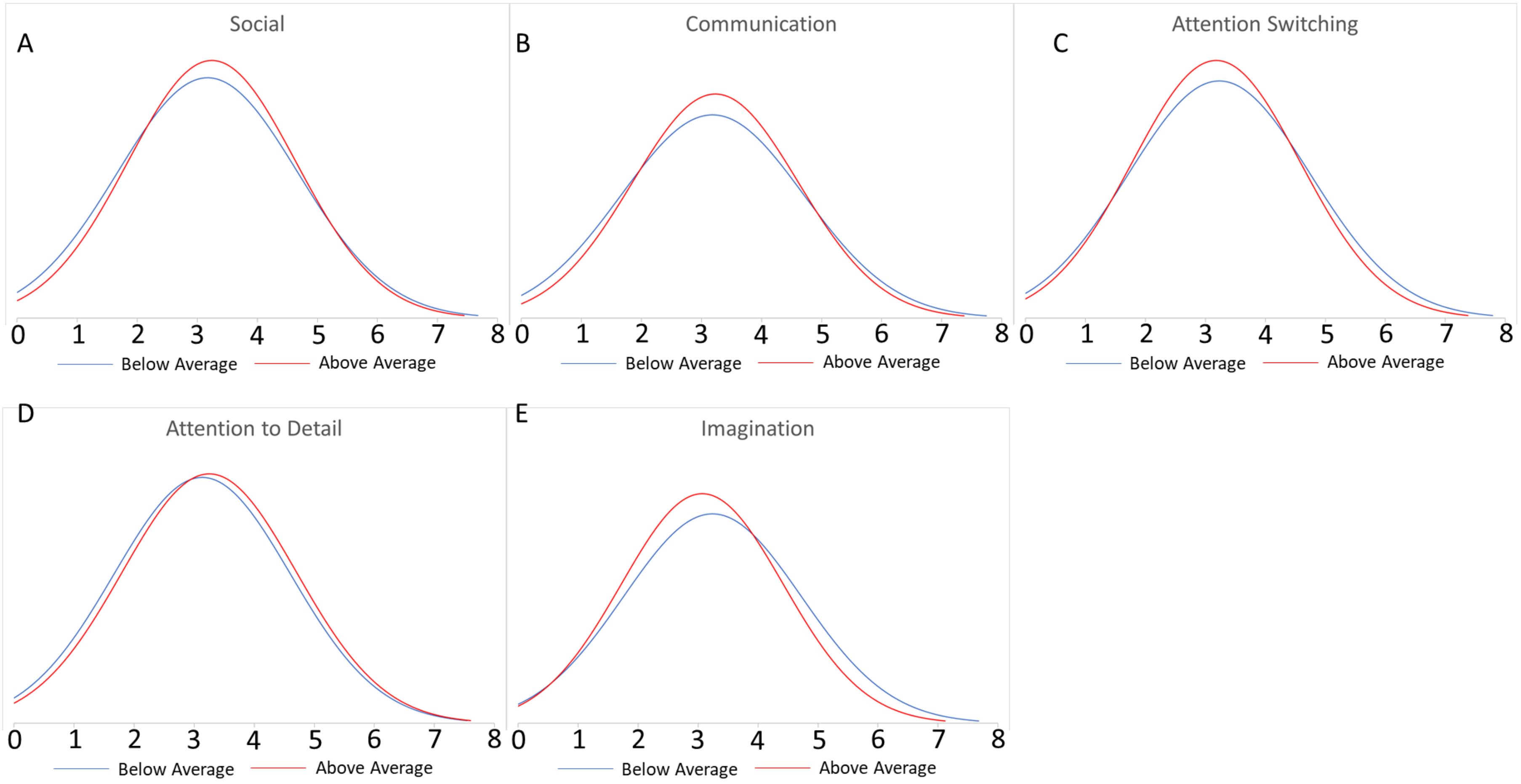


Figure 13. Participants Correct Identification Scores separated by their score groups, below average (≤5) or above average (>5), for each category of the AQ test.

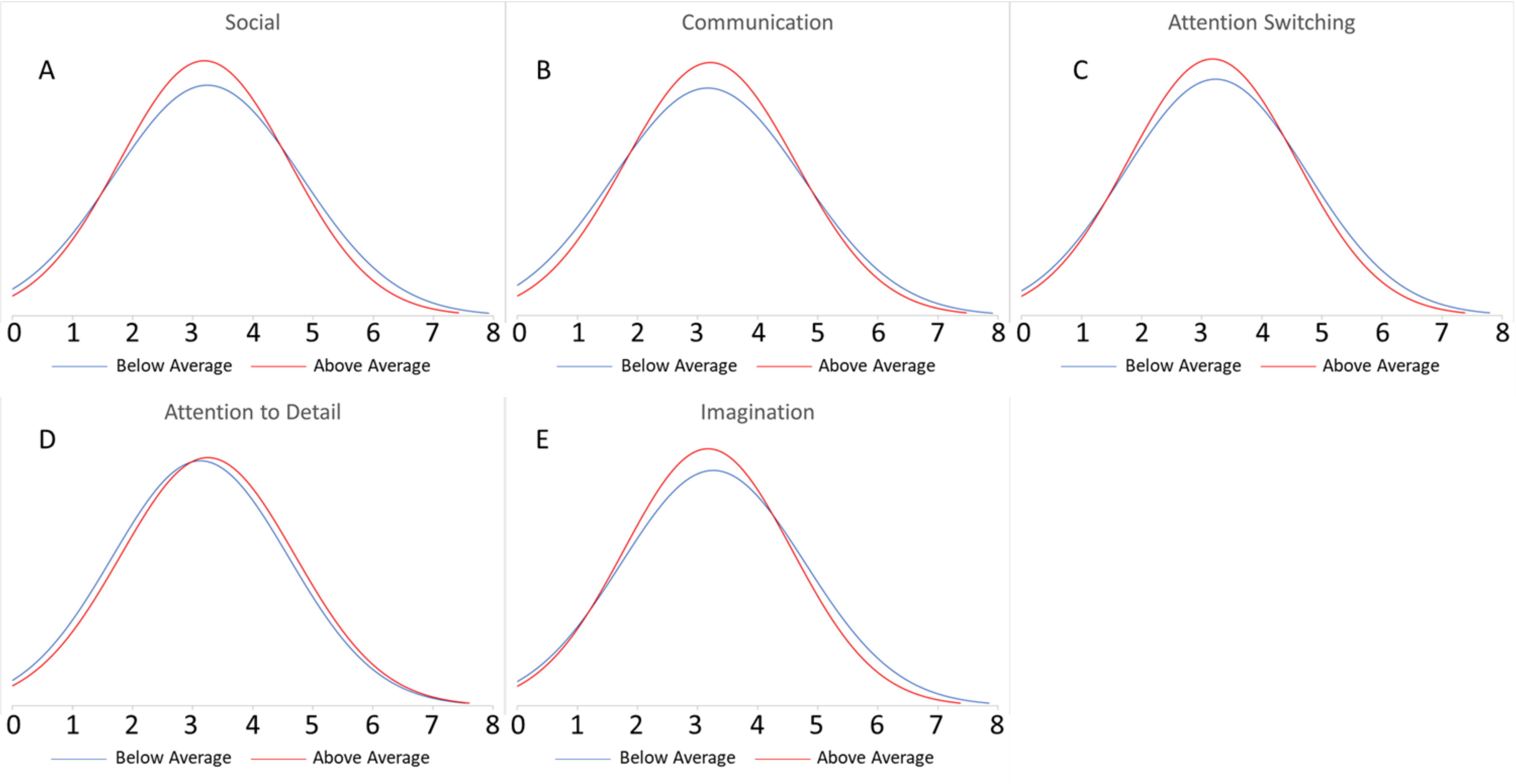


Figure 14. Participants Correct Identification Scores separated by their score groups, below or equal to average or above average, for each category of the AQ test. The averages were determined using Hurst et al. (2007: see table 4).

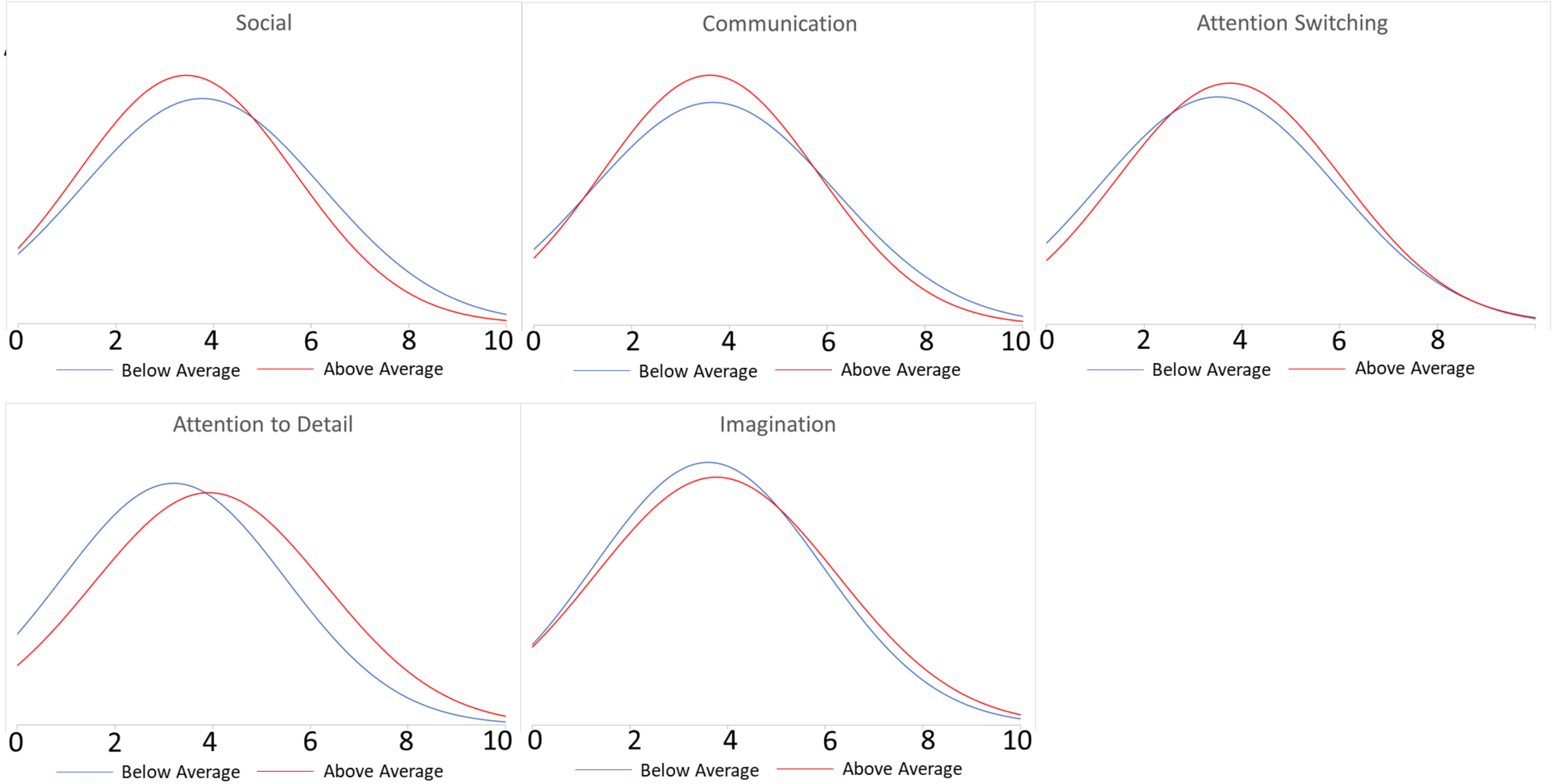


Figure 15. Participants Imagined Figure Scores separated by their score group, low (≤5) or high (>5) for each category of the AQ test.

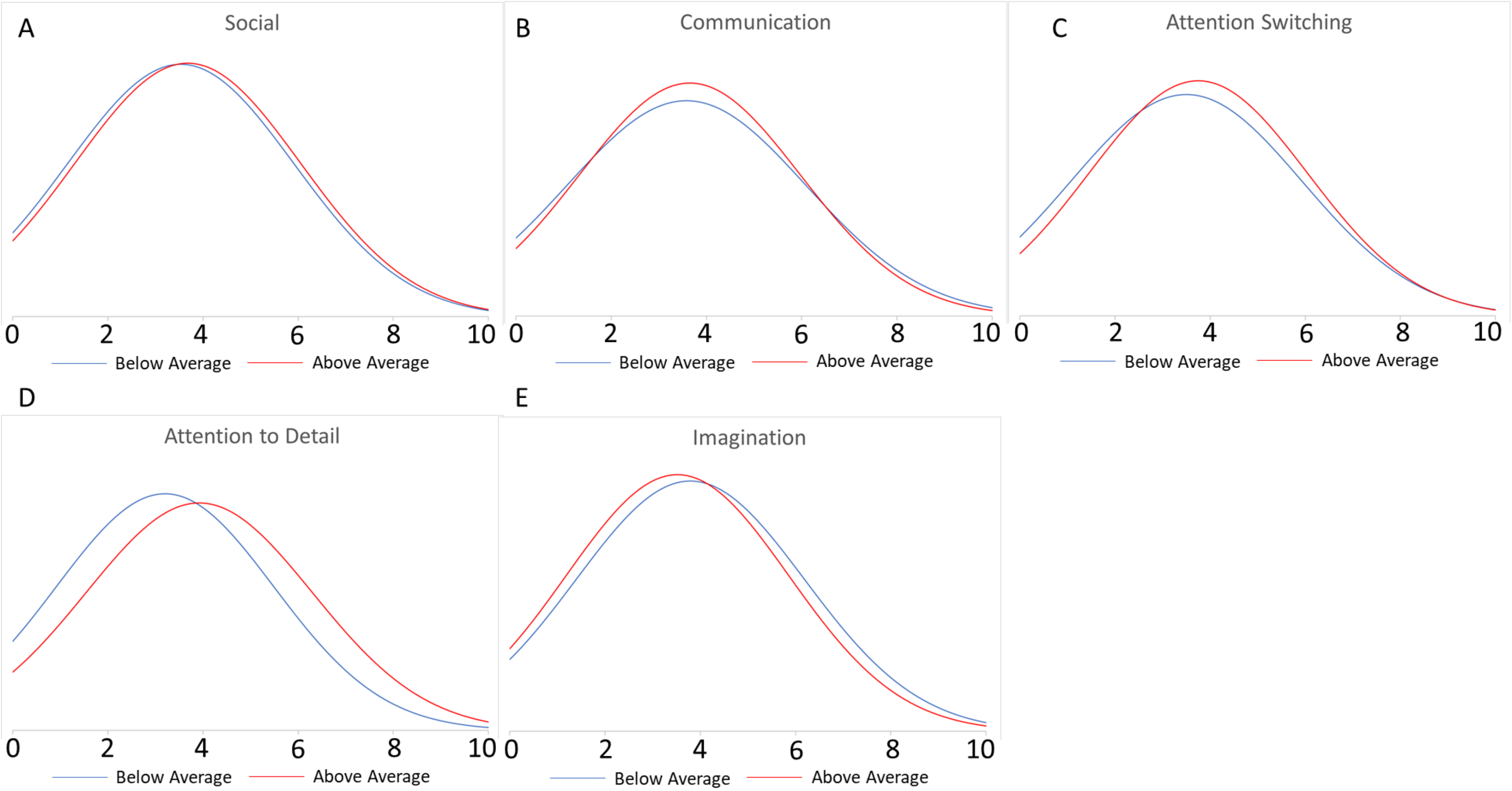


Figure 16. Participants Imagined Figure Scores separated by their score groups, below or equal to average or above average, for each category of the AQ test. The averages were determined using Hurst et al. (2007: see table 4).

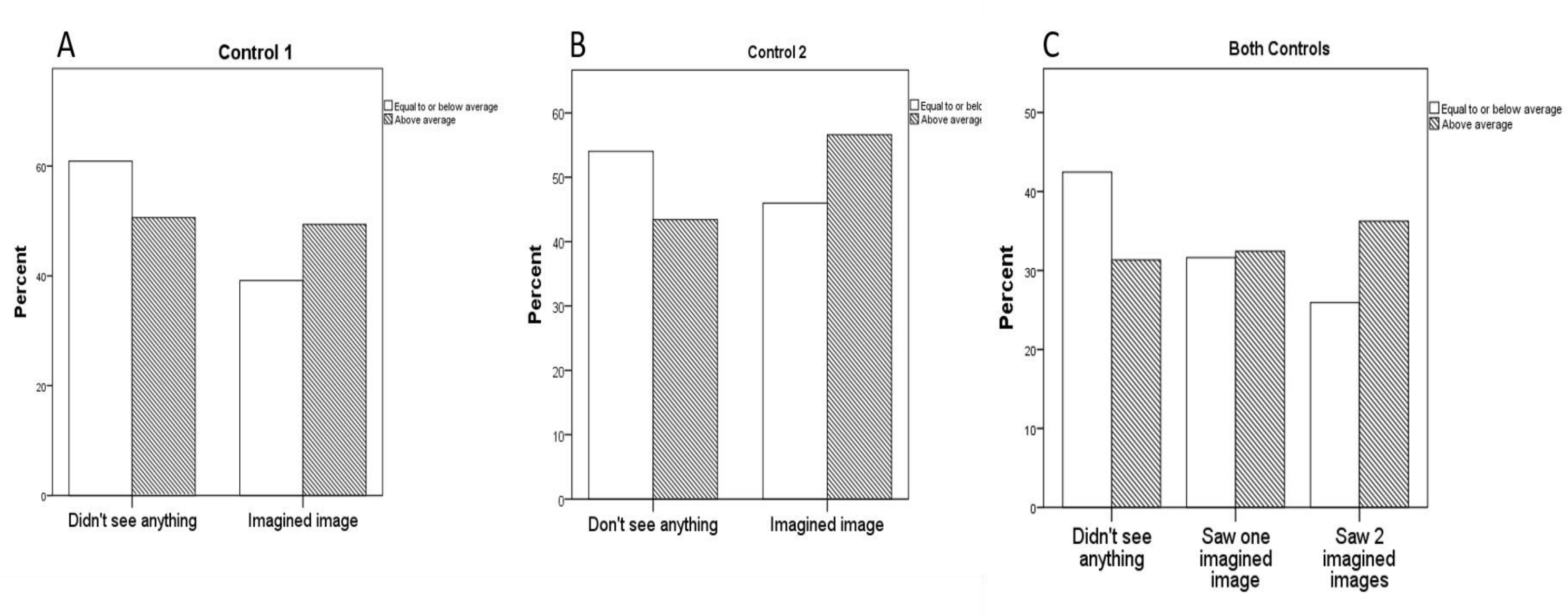


Figure 17. The percentage of participants that saw imagined images on each of the control images and whether they saw images on both controls. Participants are divided by whether they scored average or below or above average on the attention to detail category.

5.4 Discussion

Spikins and Wright (2016, p. 25) put forward anecdotal evidence to suggest that individuals with Autism were better able to identify hidden figures in Palaeolithic plaquettes from Montrastruc Cave, France. The results of this study cannot verify this observation. However, it cannot be rejected either due to several limitations which will be outlined below (5.5). Nevertheless, this study has produced an interesting and unexpected result. Individuals with increased attention to detail were more likely to see imagined figures in both the test images and control images.

These imagined images are a form of pareidolia. Pareidolia is where the mind creates a familiar pattern within an image where there is none. This has become popularized in recent years on social media due to people's reactions to inanimate objects which resemble faces (figure 18). However, it has had a wider impact on Archaeology and in particular Paleoart interpretation.

The Makapansgat pebble is the earliest case of a hominin taking interest in an item due to a pareidolic experience (figure 19). This pebble closely resembles a face in two orientations. It has not been artificially altered with all markings being natural. This pebble was transported between 2.5 and 3Ma to Makapansgat from an unknown and indeterminable distance, most likely by an australopithecine (Bednarik, 1998). This form of experience in our ancestors is also supported by artefacts such as the Berekhat Ram figurine, a piece of volcanic material with natural features reminiscent of the female form which were accentuated artificially 250-280,000 BP (d'Errico & Nowell, 2000). A further example is the mask of La Roche Cotard, which was moderately worked and had a bone splinter pushed through a natural perforation to accentuate the face like characteristics of the stone 32,100 BP (Marquet & Lorblanchet, 2003). These examples highlight that the origins of art were highly influenced by experiences of pareidolic illusions, where the features eliciting this response were then accentuated.

Hodgson (2008) argued that illusions such as this may be implicated in later art production. He argues that hyperimages, a form of pseudohallucination which may not be perceived as real, may be fragmentary, and are connected to a particular space or object from which it may appear to radiate, may be a principal cause or inspiration for much Franco-Cantabrian Palaeolithic cave art. Hyperimages occur due to a decrease in external stimuli, an increase in activity within the sensory modalities, an increase in drive states due to suppression of instinctual needs (such as food and sleep), a decrease in inhibition and a change in the dynamic between internal and external input (Beck & Rector, 2003). Hodgson suggests that all of these conditions were likely to occur in the Palaeolithic. Extended concentration on animals during the hunt would cause their images to become imprinted upon the neural circuits which would cause a mental system already sensitive to animal detection to become further primed. Individuals would have been mentally and physically exhausted, and possibly have suffered from starvation due to failed hunts which would increase the sensitivity of the visual system to perceiving items which may be construed as food. The darkness of the caves they were entering would also have had two effects. Firstly, it would have substantially decreased external stimuli, and secondly it would have provoked fear of predators. Thus, further increasing the sensitivity of prehistoric people to detect animals falsely from suggestive natural features. Hodgson cites the fact that 10-15% of

Palaeolithic art is situated in close proximity to or incorporates natural features, and highlights that hyperimagery may explain many of the features found in Franco-Cantabrian cave art (White, 2003, pp. 112–116).

Pareidolic illusions similar to these hyperimages, caused by intense concentration on one stimuli for an extended period of time, have also been shown to have a significant impact on how archaeologists may misinterpret prehistoric art. The most extraordinary example of this being the falsely interpreted 350 boulders of the Xiaojinggou salvage yard, Mongolia. These boulders were thought to have extraordinary depictions which represented the earliest religion in the world. The patron who collected these boulders sought the advice of rock art specialists before applying for the site to become a UNESCO World Heritage Site. However, upon inspection the specialists found that the art was in fact non-existent and nothing more than a pareidolic illusion shared among the students and patron at the site. The workers at the site were nevertheless convinced of what they were seeing and after several days of intense searching even the specialists began to perceive these illusions of art (Bednarik, 2017). This shows how this phenomenon may have an extraordinary influence over individuals' perception, particularly when there is a shared belief.

Participants of the current study, particularly those with high attention to detail (a technical trait), similarly perceived illusions of art. Individuals were primed to search for animals. Thus, their visual system was sensitive to the detection of animals in a similar way to Hodgson's (2008) cave artists and the archaeologists at Xiaojinggou. Although the participants were not subject to the extreme circumstances and urgency that the cave artists would have been subject to, this priming was enough to elicit a series of illusory false positives.

Bednarik (2017) states that individuals see what they expect to see because it is more time-consuming to see what isn't expected. The visual system uses approximations such as this to rapidly relay information to produce an appropriate response. In dangerous situations Bednarik argues that false positives are less costly than negatives, therefore false positives such as pareidolia are not selected against. Interestingly, he suggests pareidolia is an effect of people's tendency to attempt to see patterns in meaningless information. It may be interesting to posit for future research that individuals with more systemizing cognition may be more prone to doing this and that this is the cause of our results.

Figure 18. An image of pareidolia on an inanimate object which resembles a smiling face (Annunziata 2009).

Figure 19. The Makapansgat Pebble, in two orientations showing two different face-like patterns caused by natural processes (Bednarik 1998).

Pareidolia has been extensively studied in psychological research through the use of Rorschach inkblot tests. These ink blots use an amorphous shape, symmetry, differences in colour and hue, and blank spaces to evoke the perception of non-existent figures. Most commonly, the figures perceived are of animals (25-50%) and are very rarely of human faces (Schott, 2014). This is significant as depictions of humans are rare in Palaeolithic artwork, which may suggest that the artists were having a similar experience to participants viewing an inkblot test. As notable artists such as Leonardo da Vinci and Alexander Cozens have expressed that they were influenced by this phenomenon, and in particular that da Vinci had this reaction when staring at stains upon a wall (Schott, 2014), the notion that Palaeolithic artists and the participants of this study may have been inspired in the same way is not unrealistic. Therefore, we will investigate whether individuals with ASC have shown differences on the inkblot test and tests of pareidolia in previous research, and what neurological differences may cause individuals with high attention to detail to experience these illusions more often.

The areas of the brain activated by inkblot tests in neurotypical individuals are the amygdala, right temporal pole, anterior prefrontal cortex and bilateral occipitotemporal regions (Asari et al., 2010b). Asari et al. (2010a) found that the size of the amygdala related to the rate of unique responses on the test. Further, in a later paper they presented that the amygdala modulated the responses of the other areas listed above. It positively modulates the connection between the anterior prefrontal cortex and the temporal pole, but negatively modulates the connection between the temporal pole and occipitotemporal regions. This creates a system where increased activity in the amygdala reduces the accuracy of spontaneous recognition of ambiguous stimuli in the occipitotemporal region due to an increase in emotional input on perception. This leads to the anterior prefrontal regions testing internal representations against the stimuli in an attempt to rectify this issue. Hence, increased activation of the amygdala leads to a more emotion driven, top-down perceptual processing based upon previous experiences, which in turn may lead to unusual responses (Asari et al., 2010b). Unusual responses on this test have been correlated with artistic creativity (Schott, 2014).

Interestingly, the amygdala of individuals with ASC has been characterized in contrasting research as being hypoactive and hyperactive, as well as having atypical connectivity with other regions (in particular with the MPFC), and decreased volume (Zalla & Sperduti, 2013). Limited research has been conducted using the Rorschach inkblot test on participants with ASC. This research has shown that individuals with ASC were less organized in the way they scanned the images, created fantastical combinations, gave unusual summaries of the appearance of the stimuli, and perceived discordant combinations (Dykens et al., 1991; Ghaziuddin et al., 1995; Minassian et al., 2005). Further, their answers were largely spurred by details of the images rather than their overall form, with an exceptionally high focus on animals (41±31%) and a low rate of human figures identified (9±7%: Manuela et al., 2015).

Dykens et al. (1991) suggest that the unique responses of individuals with ASC were a product of poor reality testing. Atypical functioning of the amygdala likely causes this. If the amygdala is hyperactive then this would cause an increased emotional response and a decreased accuracy of spontaneous recognition. Additionally, atypical connectivity with the MPFC would lead to a reduction in reality testing of these emotionally driven internal perceptions, leading to unusual responses. Atypicalities in connectivity with the MPFC have also been hypothesised to inhibit the production of hierarchical relevance maps of stimuli thus causing intense reactions. The startle response to sudden fearful stimuli has been shown to be intact with limited or no latency in reaction times (Bernier et al., 2005; South et al., 2008). However, there is contradictory evidence as to whether the response is accentuated or not (Gaigg & Bowler, 2007; Markram et al., 2008). Currently, conclusions cannot assume that individuals with ASC or high attention to detail have a more intense experience of apprehension as they enter a cave and therefore see more imagined images through fear.

Withdrawn from a state of fear, individuals with high attention to detail saw more imagined images in the current study. It is noteworthy that Manuela et al. (2015) also found that individuals with ASC gave a higher number of answers on the inkblot test. However, they ascribed this to a difficulty in forming representations. In light of the current results, I would argue that this is more likely a product of seeing more representations as a result of high attention to detail, rather than not being able to project imagined images onto the stimuli. Currently, we may state that individuals with ASC present unusual responses to the Rorschach test, identify more images, and largely focus on details of the inkblot as the stimuli for imagined images. Further, we may suggest that neurological differences in the size of and atypical activation and connection of the amygdala may account for these differences.

Significantly, individuals who are artistic are more likely to express unique responses in a similar way to individuals with ASC. This may suggest a direct link between the perception of pareidolia and an artistic character. The current study shows a significant relationship between having an above average experience of art and high attention to detail (P=0.012). Thus, in the current study we have shown a relationship between attention to detail, susceptibility to pareidolic illusions, and artistic experience. However, figure 20 shows that while high attention to detail may increase susceptibility to pareidolia, experience of art does not. Hence, we must conclude that high attention to detail singularly predicts susceptibility to pareidolic illusions. Meanwhile, high attention to detail increases the likelihood of engaging in art, but is by no means a determining factor. I would posit for future research that individuals with high attention to detail may have differences in the connectivity and activation of the amygdala, similar to individuals with ASC, which cause this increased susceptibility to pareidolic illusions. Practical functional analysis of these differences requires future investigation. To the best of my knowledge this is the largest investigation of autistic traits and pareidolia to date.

Individuals with ASC are characterized as having reduced imagination. Children with Autism have been shown to have difficulty with social pretence (Leslie, 1987). Further, they were shown to have difficulty with general creativity, when asked to create multiple drawings from minimalist stimuli, and ‘imaginative creativity’ (creating impossible scenarios and drawing impossible pictures). Also, when asked what a shape could be, responses of individuals with ASC were more determined by the shape than controls (Craig & Baron-Cohen, 1999; Craig et al., 2001). This evidence suggests that individuals with a high AQ should have lower imagined figure scores in our survey. We may however speculate for further research, that the illusions experienced by our participants stem from ‘reality-based creativity’ (creativity not reliant on abstraction). As shown by Craig and Baron-Cohen (1999), individuals with ASC are more reliant on this form of creativity, based upon features of the stimuli. As stated above, pareidolia and hyperimages are stimulated by suggestive features of an object. Thus, they don’t rely on imaginative creativity. This likely explains, and is supported by, the lack of association between imagination scores on the AQ test and imagined figure scores.

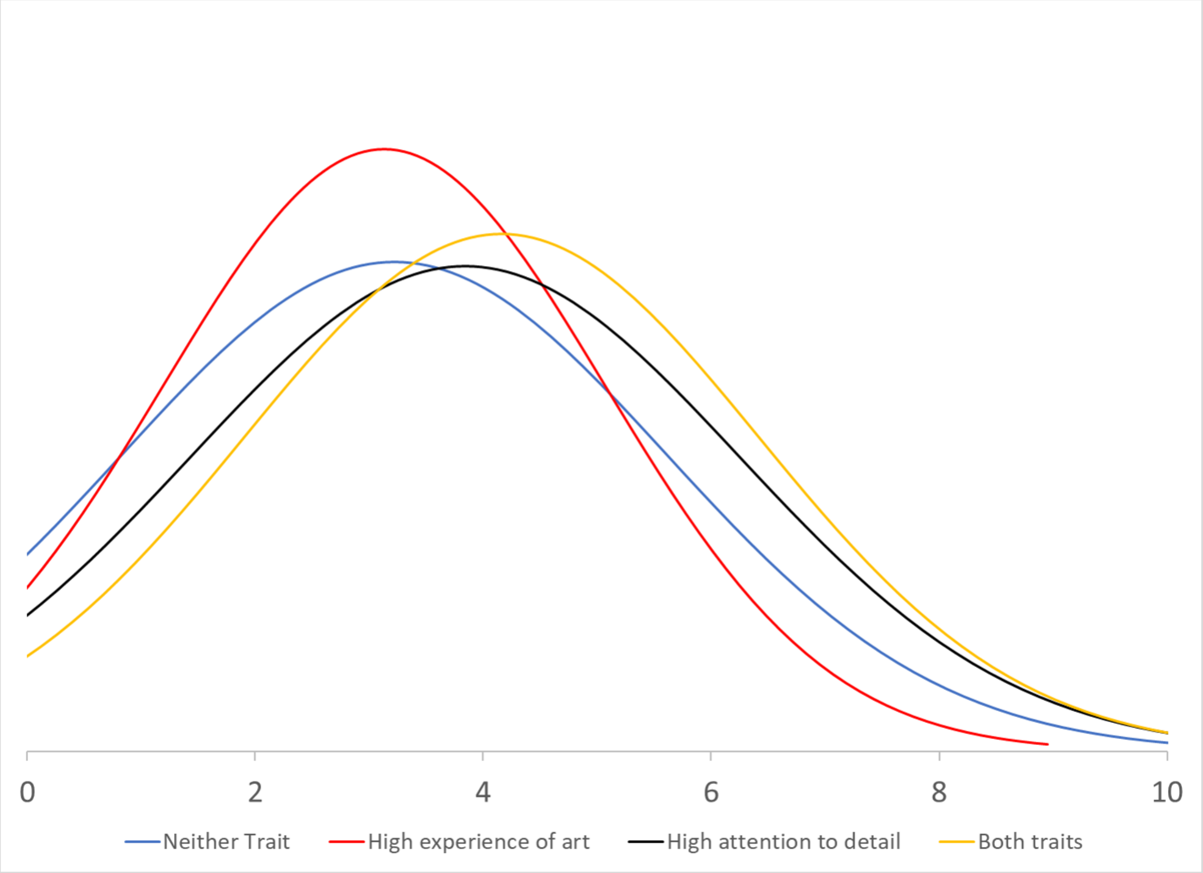


Figure 20. Showing that participants with high attention to detail were more likely to have a higher imagined figure score, while those with a high experience of art were not.

From an archaeological perspective these results are interesting for several reasons. Firstly, it further contributes to and expands Hodgson's (2008) hyperimagery theory by showing that individuals with high attention to detail would be more susceptible to these events and therefore more likely to produce artwork. It is possible that through top-down processing individuals with high attention to detail perceive specific features which mimic details of animals, for example the ventral line and face of a horse (figure 21), and through the hyperemotive effect outlined above experience illusions more often which form the inspiration for the art. This is also connected to another interpretation proposed by Hodgson (2003), that the cave art was practice and priming for implicit memory and perceptual abilities. By using fractured lines in Palaeolithic artwork to create ambiguity as to what the form represents, it provided practice for the identification of wild occluded fauna while hunting, training individuals to identify animals based upon particular details. Hence, Upper Palaeolithic groups were actively training themselves to have high attention to detail and implicitly recognize animals based upon ambiguous and suggestive shapes.

This suggestion relates to the second significant archaeological point. High attention to detail is a technical trait which has been positively selected for through time, as can be seen by the progressive development of intricate lithics. The results of this survey posit it as a highly significant factor for not only the perception of art, but its production and origins. Further, it is an example of how individuals with autistic traits may have positively influenced those around them, by training their perception. This may suggest that art, a highly social activity, was significantly impacted and perhaps a product of the technical trait, high attention to detail.

Figure 21. A possible example of natural features from Cresswell Crags on the right (highlighted blue) which resemble the ventral line, legs, and face of a horse; with a carving of a horse (left) positioned above the ventral line.

5.5 Limitations

As noted above limitations of the study did not allow us to test the theory that individuals with high AQ would be better able to identify hidden images in Palaeolithic art. Individuals with a high experience of art and Palaeolithic art were much more likely to correctly see the hidden figures (figure 22). Therefore, these were significant confounding factors. However, even when a large subsample of 704 individuals with low experience of art and Palaeolithic art was selected there was no significant difference in ability to see the hidden figures in the art (figure 23). Further issues highlighted by the participants were the quality of the images, which was determined by the quality available online, and the visibility of the survey on different devices, for example some participants using their phones struggled to see the survey. Therefore, it should be specified in the future that a computer must be used. However, even then settings of the monitor such as brightness and contrast which are beyond our control may impact participants ability to identify embedded figures. Hence the only reliable way to assess the ability of individuals to perceive embedded figures in Palaeolithic art is through a lab based study. These limitations did not confound results based upon imagined figure scores. Although a relationship was found with participants experience of art and Palaeolithic art, when the subsample of 704 participants was used the differences between those with high and low attention to detail were still maintained (figure 24). Further, although differences in the ability to clearly see the images would make it more difficult to perceive the faint lines of the Palaeolithic artwork it would not hinder or help participants project imagined figures onto the stimuli.

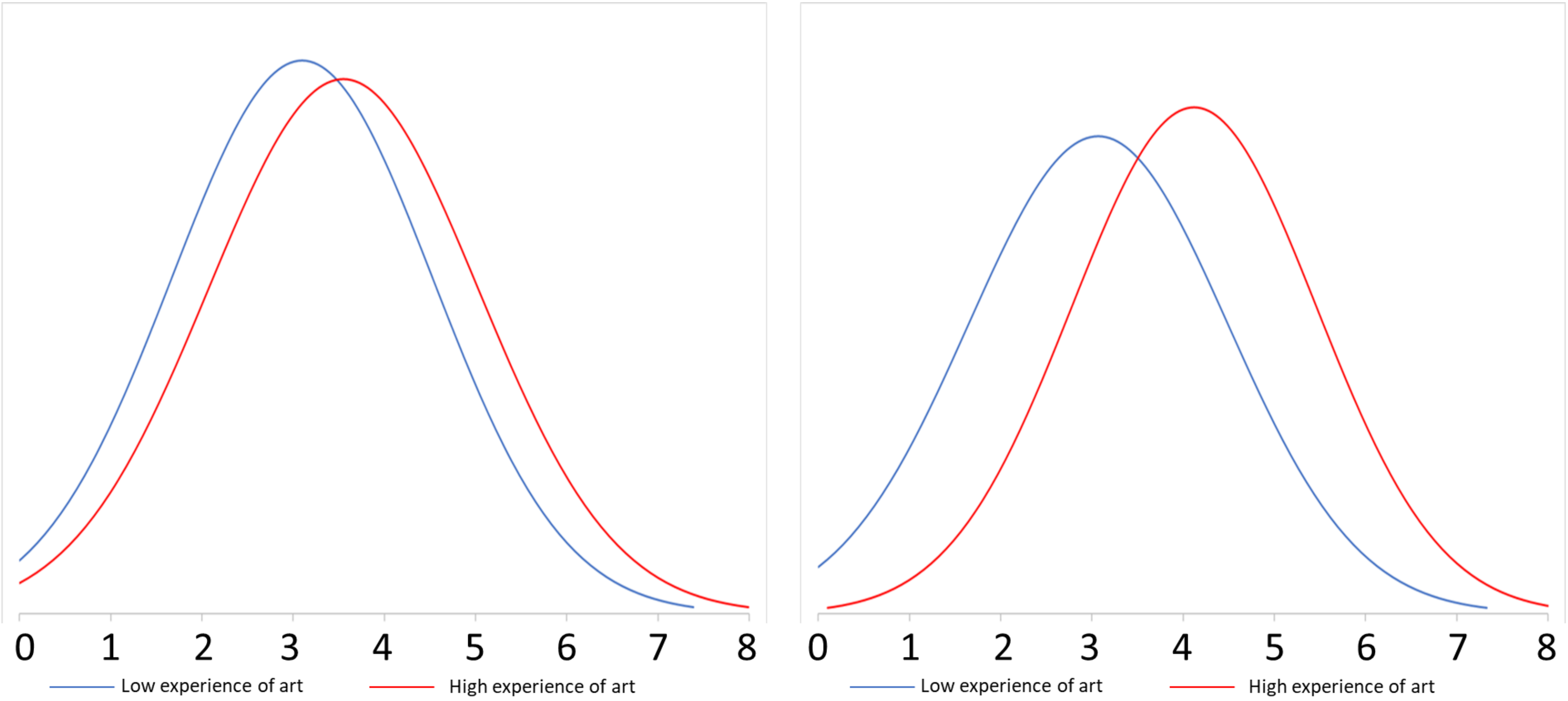


Figure 22. Showing that individuals experience of art and Palaeolithic art significantly affected their ability to see the embedded images.

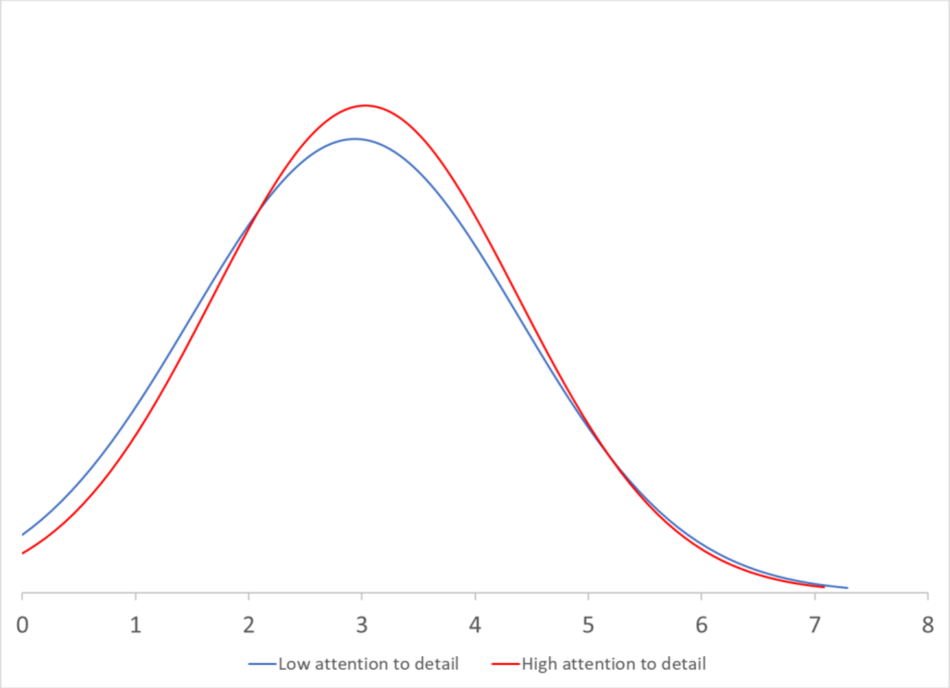


Figure 23. Subgroup of 704 participants with low experience of art and Palaeolithic art showing no difference in correctly identifying the embedded images.

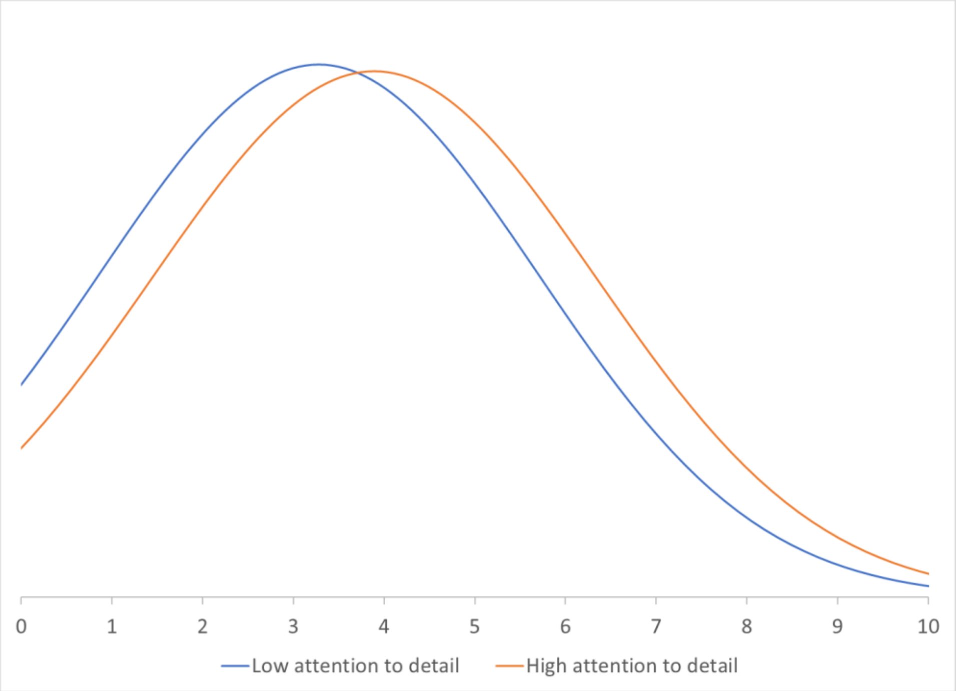


Figure 24. Subgroup of 704 participants with low experience of art and Palaeolithic art showing that the difference in quantity of pareidolic illusion between participants with high and low attention to detail is maintained.

5.6 Conclusions

This study has attempted to test the hypothesis that characteristics and components of Autism would influence individuals' engagement with material culture, in particular art. Initially, it was thought that if participants with a high overall AQ, or score on a specific trait, were able to perceive hidden figures in the art more easily and accurately, this would provide support for the hypothesis. Unfortunately, due to limitations of the survey, we were unable to test this theory. However, we did find that individuals with high attention to detail were more likely to see non-existent figures on the stimuli. This reaction is a form of pareidolia, where the mind attempts to create a familiar pattern from random visual data.

From studies of Rorschach inkblot tests, we know that the perception of ambiguous stimuli relies on a network involving the PFC, occipital cortex, and the temporal poles, which is modulated by the amygdala (Asari et al., 2010b). Autism has been related to hypo and hyperactivity of the amygdala as well as atypical connectivity (Zalla & Sperduti, 2013). This may be a cause for the differences seen in this study, as it would lead to more emotionally driven, top-down processing with depreciated reality testing, due to lower connectivity between the amygdala and the PFC. This would make individuals with autism more susceptible to pareidolic illusions. While the current study does not reveal a significant difference in the AU sample, this may be due to the fact that our participants were not formally diagnosed, and individuals could score above the 32 threshold without scoring highly for attention to detail. It should be posited for future research that individuals with high attention to detail may have similar differences in the amygdala modulated network to individuals with ASC.

These results support the hypothesis of this study, by displaying that attention to detail is connected with both frequency of pareidolic illusions and likelihood of engaging in art. These findings are also supported by past research which found that detail focus is associated with artistic ability (Drake, 2014; Drake et al., 2010). This has then been connected to Hodgson’s theories on the origins of art. Firstly, individuals using the art as priming cues to recognize details of animals are teaching themselves to enhance a technical trait connected to Autism (Hodgson, 2003). Secondly, individuals with high attention to detail would be more susceptible to hyperimages and thus more likely to produce artwork in caves (Hodgson, 2008). The perception of pareidolic illusions and hyperimages, due to their being determined by features of the object, are suggested to rely on reality-based creativity - a form not impaired in individuals with ASC. This study is significant for two reasons: it is the largest study of autistic traits and pareidolia to date; and it has provided quantifiable evidence for the impact of technical autistic traits on Palaeolithic artwork.

Chapter 6: Summary and Final Conclusions

This dissertation has assessed whether the cognitive evolution of our species can be fully explained through pressures for sociality, or a more complex mechanism of both technical and social pressures took place.

Currently, social theories are the most popular and accepted explanations for our evolutionary success (2.2). By assessing the evidence for cognitive evolution in depth we have confirmed that there has been substantial gradual change in areas of the brain specialized for sociality through time (3). However, many changes were linked to technical ability. These developments mostly occurred in tandem with social changes. However, it is important to note that long range connections govern social functions. When these connections are changed, they are likely to cause behavioural differences, as is seen in Autism (4.1). Thus, connectivity is a large factor that governs social and technical ability, which is only slightly explored.

Due to differences in ontogeny it is thought that Neanderthals had a different neural connectivity. This likely led to lower levels of social functioning than has previously been suggested. However, Neanderthals may have possessed unique technical functions, such as the ability to create virtual mental models of objects which allowed a more efficient method of tool production. The decreased white matter and shorter ontogeny of earlier hominins would suggest even more accentuated differences. Further, the disparity between estimates of Neanderthal group size using the SBH and estimates based upon archaeological evidence, suggests that complicating non-social evolutionary pressures may have affected the relationship. This supports the idea that multiple evolutionary pressures, including social and technical, were driving our cognitive evolution.

Individuals with ASC commonly exhibit social difficulties; however, they commonly have significant accentuations in technical abilities. ASC was assessed as an alternate, more technical, adaptive strategy and the impact autistic traits may have had on our ancestors determined.

The behavioural analysis of individuals with ASC explored the social difficulties often experienced, and the technical advantages thought to compensate for them (4.1). This theory has led to multiple studies of how autistic traits may have influenced prehistoric societies, with archaeologists such as Humphrey (1998), Kellman (1998), and Spikins and Wright (2016) investigating artefacts which may have been influenced by autistic traits. This has been met with resistance from Bednarik (2013, 2016) and Pickard et al. (2011). They state that Autism is a deleterious by-product of human variation with difficulties that would have inhibited contribution and led to negative selection. They counter argue that trance states and psychedelic drugs would have induced a mindset conducive to the creation of Palaeolithic artwork. This claim is not substantiated by psychological research, as neither produces spontaneous talent (Spikins, Scott and Wright in press). Further, the genetics of the condition show that there are two genetically different variants. One of which is caused by common variants under positive selection, and isn’t associated with intellectual disability (4.3). One final criticism remains, however. Currently, there is limited empirical evidence for the theory.

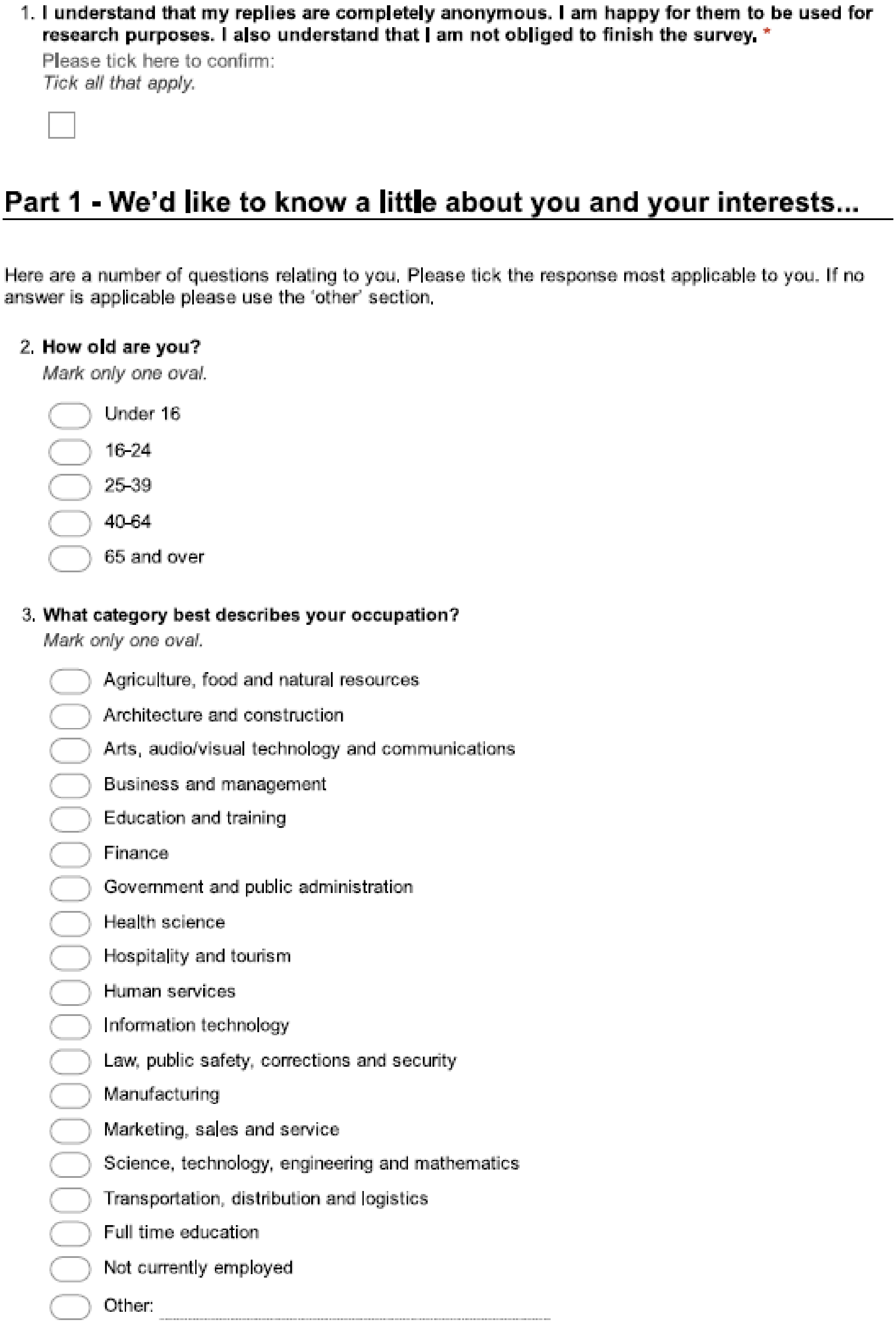
Chapter 5 provides a study designed to test the hypothesis that characteristics and components of autism would influence individual’s engagement with material culture, in particular art. This study utilized a large self-selection sample (N=1027) with high rates of autistic traits. Participants completed the Visual Perception and Cognition Survey, which required them to search for hidden figures in Palaeolithic art. The survey found that individuals with the technical trait high attention to detail were significantly more susceptible to seeing imagined pareidolic illusions in the images. This is likely due to atypical amygdala activation and connectivity causing an increase in top-down emotion based processing. However, other explanations, which are not incompatible with the amygdala theory, are that individuals with high attention to detail have a more systemizing cognition and therefore are more likely to patternize random stimuli into figures, or they are more likely to see natural features which mimic specific details of animals. Further, the basis of these illusions is argued not to be strict abstract imagination, but rather reality-based creativity centred upon features of the observed object, which is not impaired in individuals with ASC.

The cause requires further analysis. Nevertheless, this study has also shown a direct connection between high attention to detail and the likelihood of engaging in art. The finding that high attention to detail promotes pareidolic illusions, and is also related to artistic experience, supports, and adds to Hodgson’s (2008) theory of hyperimagery. Thus, this study has provided empirical evidence which suggests individuals with the technical autistic trait, high attention to detail, would be more likely to produce Palaeolithic art. Although, this doesn’t suggest that they produced it exclusively, as our study has shown that a large proportion of participants with high experience of art did not have high attention to detail. Additionally, Hodgson’s (2003) theory of using fragmented images to train individuals to recognize animals from minimal details suggests that Palaeolithic people were actively training to use this trait. Therefore, high attention to detail is a technical trait which may be in part responsible for this major change in human culture.

Thus, we have shown that the evolutionary pressures acting on the hominin mind were more complex than the social theories allow. Technical pressures have had a large impact on hominin cognition both between species, and as shown by our case study of ASC, within species. Technical pressures are significant enough to cause alternate cognitive strategies and traits which conflict with social functions. One technical ability, high attention to detail, has been associated with the origin of a significant cultural development, art, and was likely a desirable trait in Palaeolithic groups. Thus, the role of technical pressures in our evolution and how they relate to social pressures requires more attention.

Appendix

Appendix A – The Visual Cognition and Perception Survey



1. **I understand that my replies are completely anonymous. I am happy for them to be used for research purposes. I also understand that I am not obliged to finish the survey.** *

Please tick here to confirm:
Tick all that apply.

☐

Part 1 - We'd like to know a little about you and your interests...

Here are a number of questions relating to you. Please tick the response most applicable to you. If no answer is applicable please use the 'other' section.

2. **How old are you?**

Mark only one oval.

○ Under 16
○ 16-24
○ 25-39
○ 40-64
○ 65 and over

3. **What category best describes your occupation?**

Mark only one oval.

○ Agriculture, food and natural resources
○ Architecture and construction
○ Arts, audio/visual technology and communications
○ Business and management
○ Education and training
○ Finance
○ Government and public administration
○ Health science
○ Hospitality and tourism
○ Human services
○ Information technology
○ Law, public safety, corrections and security
○ Manufacturing
○ Marketing, sales and service
○ Science, technology, engineering and mathematics
○ Transportation, distribution and logistics
○ Full time education
○ Not currently employed
○ Other: ____________________

4. **What hobbies do you have?**
Mark only one oval.

○ Sports related (e.g. football, netball...)
○ Craft related (e.g. carpentry, knitting)
○ Art related (e.g. drawing)
○ Observation related (e.g. bird watching)
○ Collection hobbies (e.g. stamp collecting)
○ Other: ______________________

5. **Please tell us a little more about your hobbies...**

6. **Do you have any previous experience of art e.g. drawing or painting, outside of school education?**
Mark only one oval.

○ None
○ A little
○ Average
○ Above average
○ A lot

7. **How familiar are you with Palaeolithic art?**
Mark only one oval.

○ None
○ A little
○ Average
○ Above average
○ A lot

Part 2 - About how you see the world...

Here are a number of statements relating to characteristics that may or may not apply to you. For example ' I prefer to do things the same way over and over again'. Please tick to what extent you AGREE OR DISAGREE with the statements.

8. **I prefer to do things with others rather than on my own.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

9. **I prefer to do things the same way over and over.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

10. **If I try to imagine something, I find it very easy to create a picture in my mind.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

11. **I frequently get so strongly absorbed in one thing that I lose sight of other things.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

12. **I often notice small sounds when others do not.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

13. **I usually notice car number plates or similar strings of information.**
Mark only one oval.

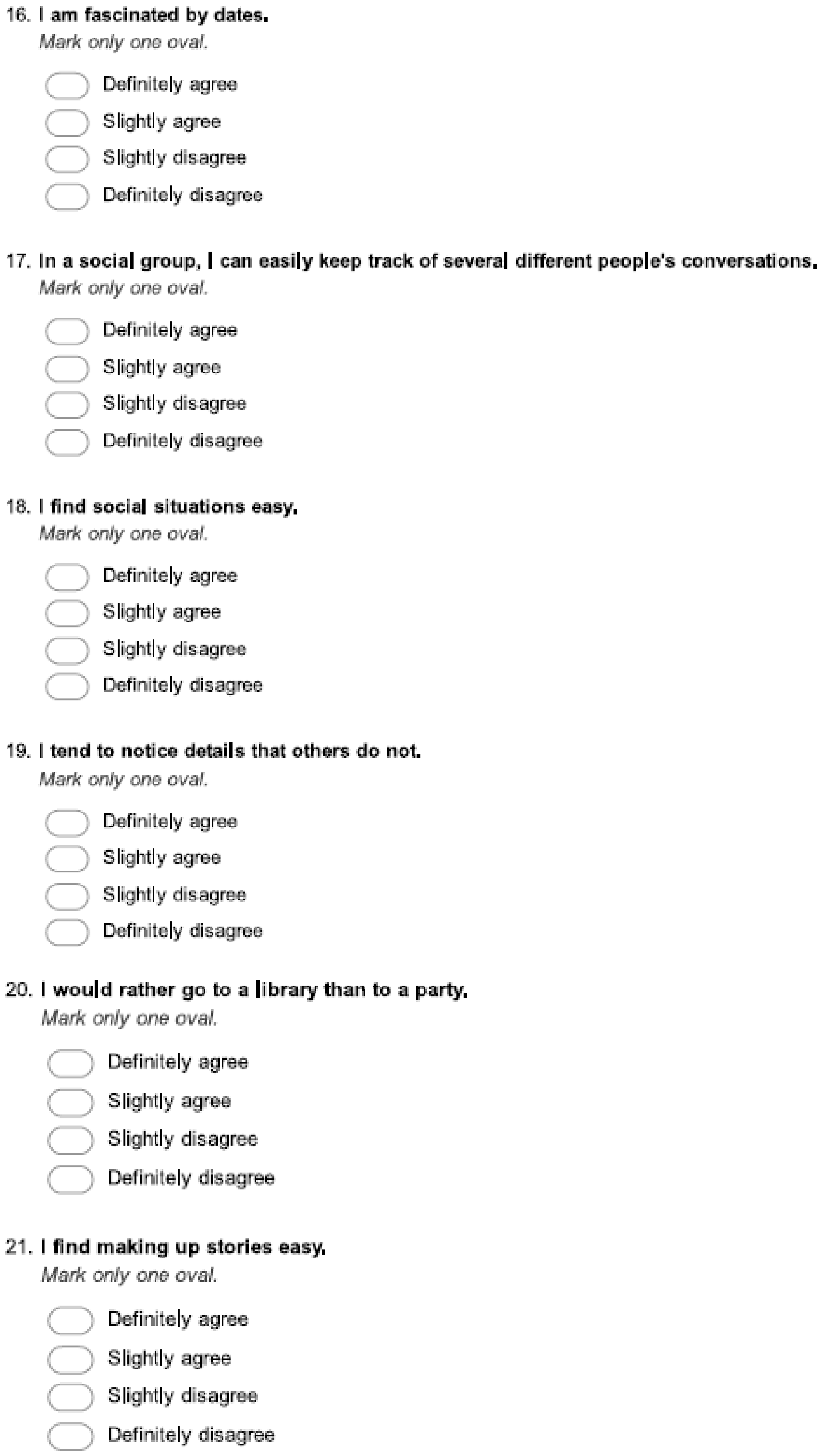
○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

14. **Other people frequently tell me that what I've said is impolite, even though I think it is polite.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

15. **When I'm reading a story, I can easily imagine what the characters might look like.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree



16. **I am fascinated by dates.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

17. **In a social group, I can easily keep track of several different people's conversations.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

18. **I find social situations easy.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

19. **I tend to notice details that others do not.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

20. **I would rather go to a library than to a party.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

21. **I find making up stories easy.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

22. **I find myself drawn more strongly to people than to things.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

23. **I tend to have very strong interests, which I get upset about if I can't pursue.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

24. **I enjoy social chitchat.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

25. **When I talk, it isn't always easy for others to get a word in edgewise.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

26. **I am fascinated by numbers.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

27. **When I'm reading a story, I find it difficult to work out the characters' intentions.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

28. **I don't particularly enjoy reading fiction.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

29. **I find it hard to make new friends.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

30. **I would rather go to the theater than to a museum.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

31. **I notice patterns in things all the time.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

32. **It does not upset me if my daily routine is disturbed.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

33. **I frequently find that I don't know how to keep a conversation going.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

34. **I find it easy to 'read between the lines' when someone is talking to me.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

35. **I usually concentrate more on the whole picture, rather than on the small details.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

36. **I am not very good at remembering phone numbers.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

37. **I don't usually notice small changes in a situation or a person's appearance.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

38. **I know how to tell if someone listening to me is getting bored.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

39. **I find it easy to do more than one thing at once.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

40. **When I talk on the phone, I'm not sure when it's my turn to speak.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

41. **I enjoy doing things spontaneously.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

42. **I enjoy doing things alone.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

43. **I find it easy to work out what someone is thinking or feeling just by looking at their face.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

44. **If there is an interruption, I can switch back to what I was doing very quickly.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

45. **I am good at social chitchat.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

46. **People often tell me that I keep going on and on about the same thing.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

47. **When I was young, I used to enjoy playing games involving pretending with other children.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

48. **I like to collect information about categories of things (e.g. types of cars, birds, trains, plants).**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

49. **I find it difficult to imagine what it would be like to be someone else.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

50. **I like to carefully plan any activities I participate in.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

51. **I enjoy social occasions.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

52. **I find it difficult to work out people's intentions.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

53. **New situations make me anxious.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

54. **I enjoy meeting new people.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

55. **I am a good diplomat.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

56. **I am not very good at remembering people's date of birth.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

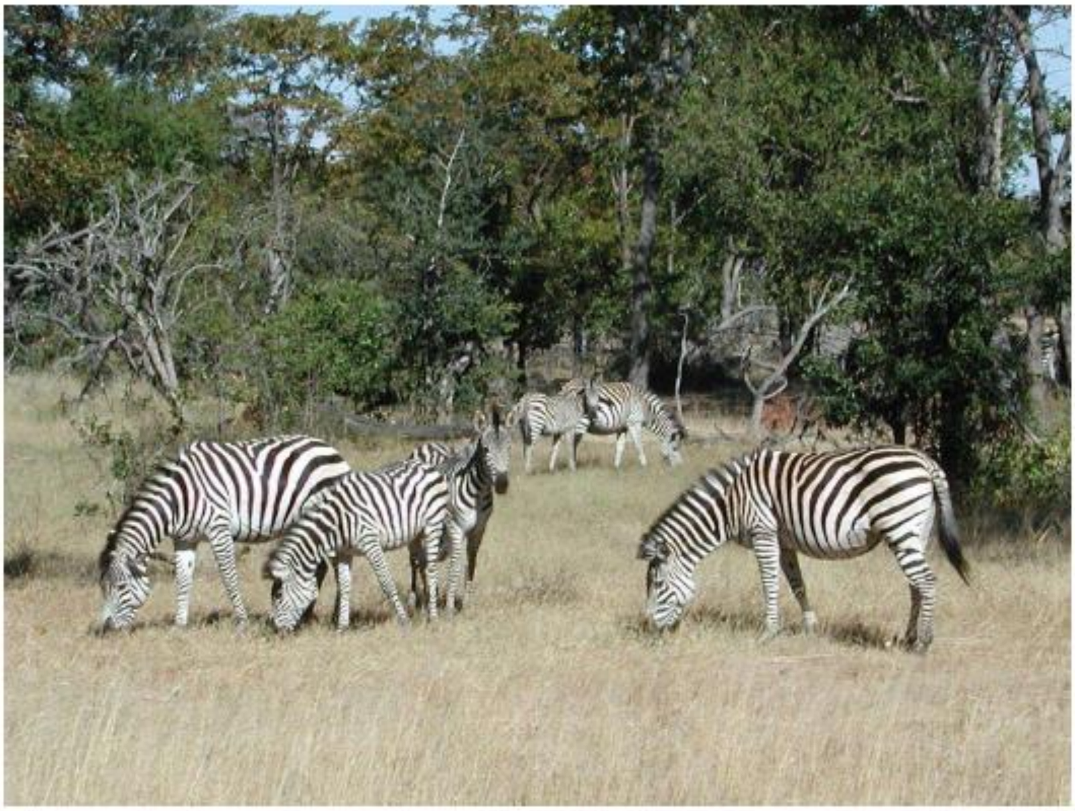
57. **I find it very easy to play games with children that involve pretending.**
Mark only one oval.

○ Definitely agree
○ Slightly agree
○ Slightly disagree
○ Definitely disagree

That is the long part over, here is the fun part!

Part 3 - Please tell us about these images

You will now be presented with 3 pictures of animals both modern and prehistoric. Please name what animal is depicted.



58. **What do you see in this image?**

59. **What do you see in this image?**

60. **What do you see in this image?**

Part 4 - We'd like you to tell us what you see in these examples of Palaeolithic art...

You will now be shown 9 pictures of Palaeolithic artwork. Tell us what you see in the pictures.

Images Part 1

Please don't spend more than a minute on each picture.

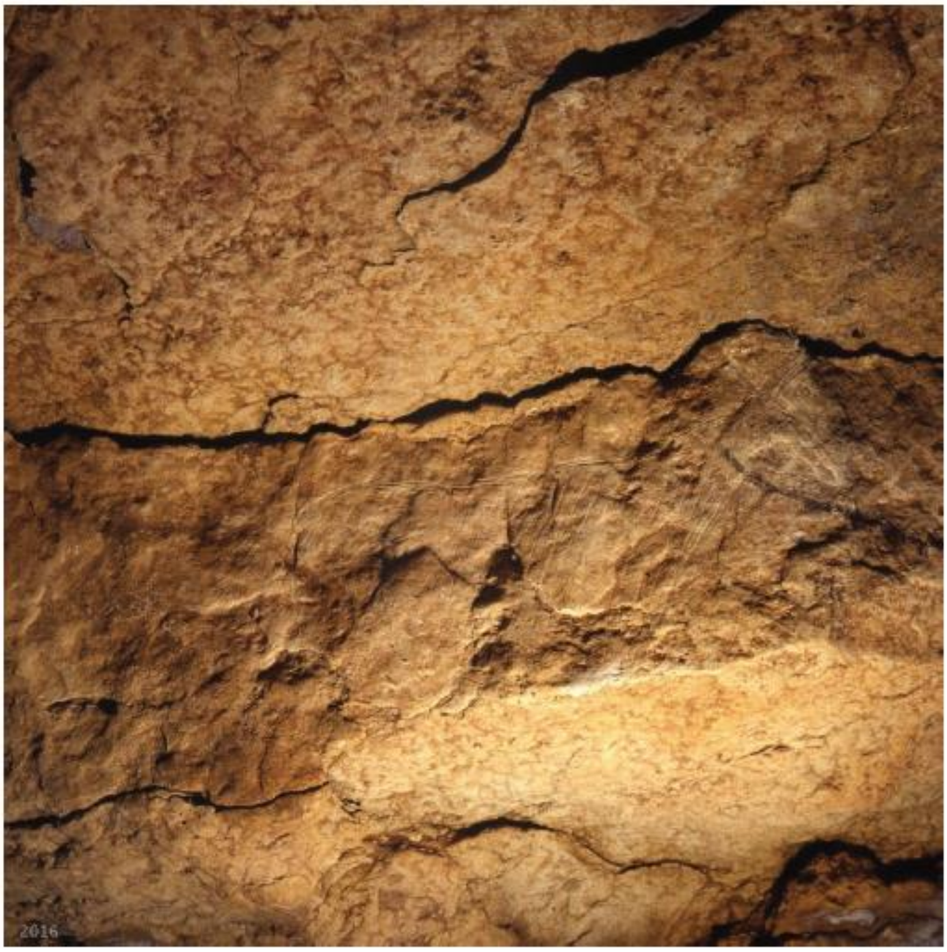
61. **What animal(s) do you think is depicted here?**

62. **What animal(s) do you think is depicted here?**

63. **What animal(s) do you think is depicted here, if any?**

64. **What animal(s) do you think is depicted here, if any?**

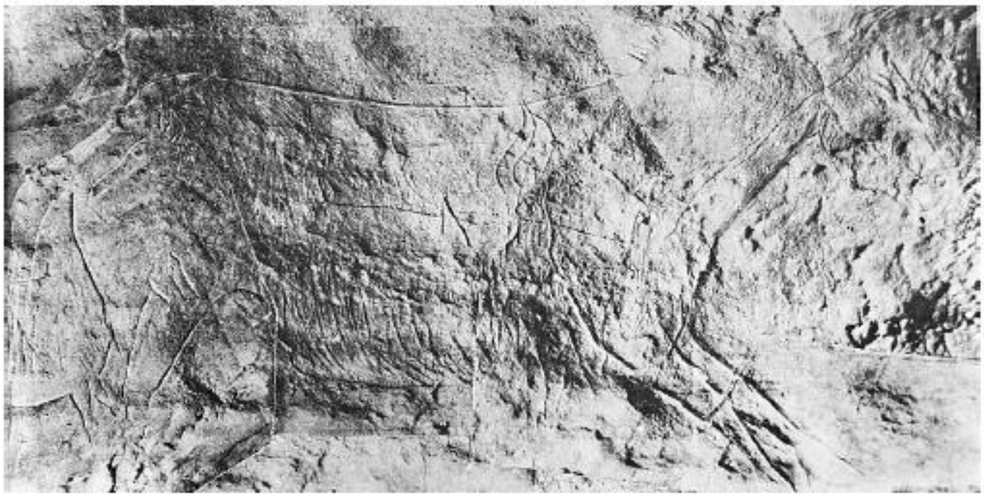
65. **What animal(s) do you think is depicted here, if any?**



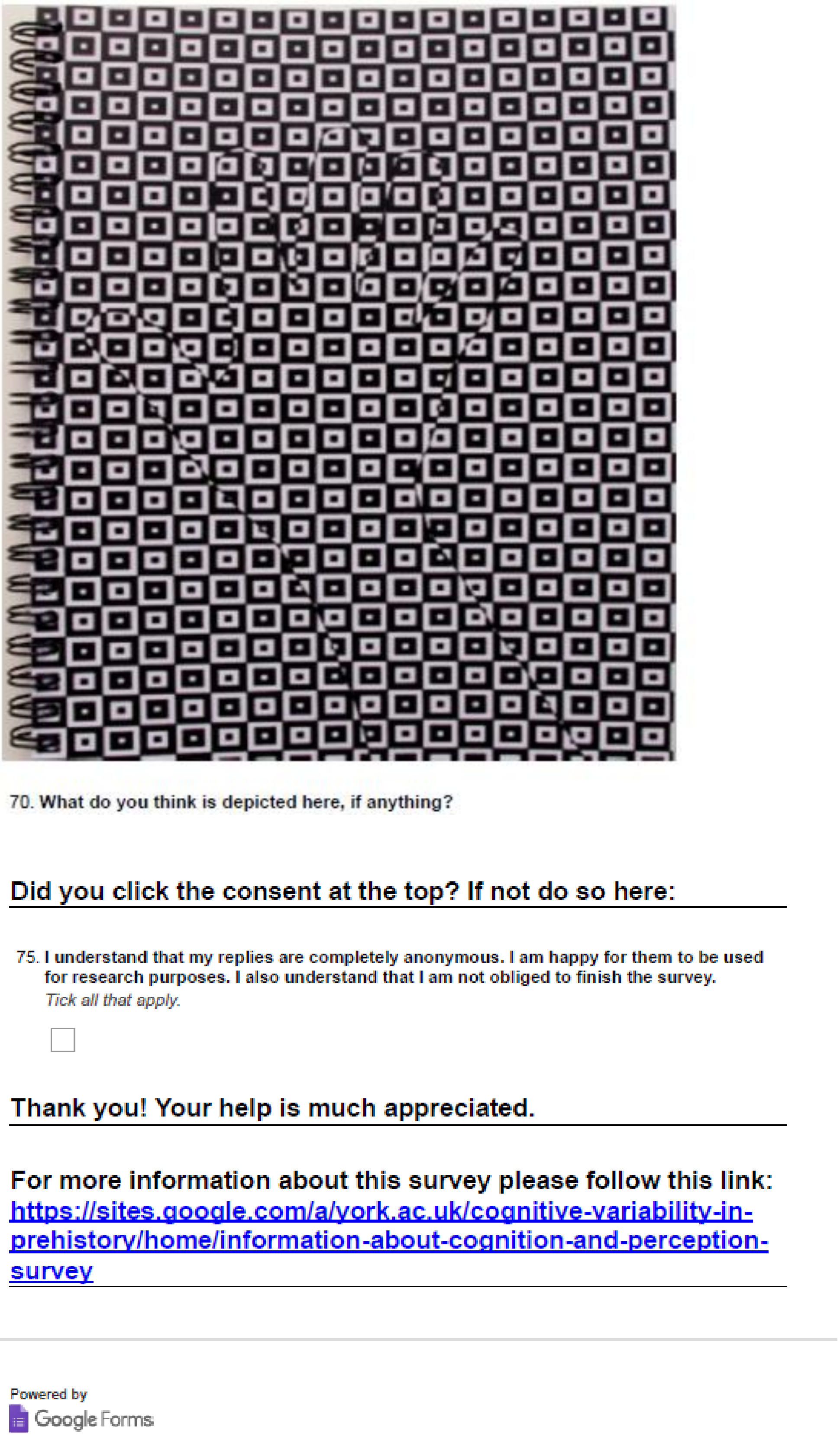
66. **What animal(s) do you think is depicted here, if any?**

67. **What animal(s) do you think is depicted here, if any?**

68. What animal(s) do you think is depicted here, if any?



69. What animal(s) do you think is depicted here, if any?



70. What do you think is depicted here, if anything?

Did you click the consent at the top? If not do so here:

75. I understand that my replies are completely anonymous. I am happy for them to be used for research purposes. I also understand that I am not obliged to finish the survey.
Tick all that apply.

☐

Thank you! Your help is much appreciated.

For more information about this survey please follow this link: https://sites.google.com/a/york.ac.uk/cognitive-variability-in-prehistory/home/information-about-cognition-and-perception-survey

Further Details Regarding the Survey

This survey was designed in cooperation with Dr Penny Spikins and Dr Barry Wright, with both Dr Spikins and myself contributing images and questions, and Dr Wright providing advice for further refinement. The survey was initially disseminated through a press release for the book ‘The Prehistory of Autism’ (Spikins and Wright 2016). The three of us further disseminated the survey to Autism support groups across the country, and the Autism Research Centre at the University of Cambridge sent it to their database of volunteers.

From the raw data collected I created a database suitable for analysis. I conducted all analysis and produced all graphics. Some of these results then formed part of a paper (Spikins, Scott and Wright in press). This paper discusses the significance of local processing bias (or high attention to detail) for talent at realistic depiction, and its implications for understanding the cause of similarities between the artwork of individuals with Autism and Upper Palaeolithic artwork. For this paper I provided a paragraph on the genetics of Autism based upon section 4.3 of this thesis, a graphic of a block design test (figure 7 in this thesis), some statistical data and a graphic of the relationship between high AQ and high attention to detail based upon the survey. The results are discussed in more detail in the present thesis, and the interpretation of the results are my original work.

Appendix B – Tables of Correct Identification Scores for individual categories of the AQ test.

(High and low determined using the averages of the VPCS dataset)

Social

Image	1	2	4	5	6	7	9	10
Low	5.7%	43.2%	17.0%	34.9%	43.3%	6.0%	79.5%	89.6%
High	6.9%	40.5%	15.3%	39.8%	43.4%	2.9%	82.1%	92.3%
Significance	0.466	0.447	0.524	0.152	0.969	0.50	0.361	0.196

Communication

Image	1	2	4	5	6	7	9	10
Low	6.1%	45.2%	16.8%	34.9%	43.4%	6.2%	79.4%	89.8%
High	6.0%	35.8%	15.9%	39.4%	43.0%	2.6%	82.1%	91.7%
Significance	0.947	0.005	0.714	0.171	0.906	0.019	0.327	0.340

Attention Switching

Image	1	2	4	5	6	7	9	10
Low	5.2%	42.5%	17.1%	34.9%	44.2%	6.7%	80.1%	90.0%
High	7.6%	42.4%	15.5%	38.6%	41.8%	2.4%	80.4%	91.0%
Significance	0.114	0.976	0.493	0.239	0.474	0.003	0.904	0.585

Attention to Detail

Image	1	2	4	5	6	7	9	10
Low	4.9%	42.9%	15.8%	36.3%	45.2%	5.3%	78.9%	89.2%
High	8.2%	41.5%	18.1%	36.2%	39.8%	4.8%	82.8%	92.7%
Significance	0.035	0.662	0.340	0.975	0.101	0.707	0.139	0.071

Imagination

Image	1	2	4	5	6	7	9	10
Low	6.4%	43.5%	17.3%	36.2%	44.2%	5.6%	80.6%	90.4%
High	3.3%	34.4%	10.7%	36.1%	36.9%	1.6%	77.9%	90.2%
Significance	0.173	0.056	0.062	0.969	0.126	0.061	0.485	0.938

(High and low determined using the averages of Hurst et al.’s (2007) data)

Social

Image	**1**	**2**	**4**	**5**	**6**	**7**	**9**	**10**
Low	6.7%	45.0%	19.5%	31.2%	44.3%	8.4%	79.9%	88.9%
High	5.8%	41.4%	15.4%	38.3%	42.9%	3.8%	80.4%	90.9%
Significance	0.562	0.298	0.109	0.033	0.690	0.003	0.850	0.319

Communication

Image	**1**	**2**	**4**	**5**	**6**	**7**	**9**	**10**
Low	5.5%	43.6%	16.9%	29.7%	41.1%	8.5%	81.4%	90.3%
High	6.2%	42.1%	16.4%	38.2%	44.0%	4.2%	79.9%	90.4%
Significance	0.698	0.673	0.852	0.017	0.431	0.009	0.622	0.950

Attention Switching

Image	**1**	**2**	**4**	**5**	**6**	**7**	**9**	**10**
Low	5.3%	43.8%	17.4%	33.7%	46.0%	7.3%	79.7%	89.9%
High	6.6%	41.4%	15.9%	38.2%	41.2%	3.5%	80.6%	90.8%
Significance	0.369	0.426	0.515	0.135	0.119	0.007	0.721	0.634

Attention to Detail

Image	**1**	**2**	**4**	**5**	**6**	**7**	**9**	**10**
Low	4.5%	40.1%	15.8%	34.3%	45.6%	5.5%	79.2%	88.0%
High	7.0%	43.9%	17.0%	37.4%	41.9%	4.9%	80.9%	91.9%
Significance	0.102	0.224	0.600	0.316	0.239	0.683	0.506	0.039

Imagination

Image	**1**	**2**	**4**	**5**	**6**	**7**	**9**	**10**
Low	6.9%	46.4%	19.1%	33.6%	44.4%	6.4%	79.5%	89.2%
High	5.4%	39.5%	14.7%	38.2%	42.6%	4.2%	80.7%	91.2%
Significance	0.321	0.027	0.062	0.129	0.565	0.113	0.632	0.278

Appendix C – Tables of Imagined Figure Scores for individual categories of the AQ test.

(High and low determined using the averages of the VPCS dataset)

Social

Image	1	2	3	4	5	6	7	8	9	10
Low	53.9%	26.3%	46.2%	50.1%	45.6%	28.9%	54.2%	51.9%	16.5%	5.5%
High	45.3%	22.5%	43.3%	44.7%	42.1%	29.0%	53.0%	54.0%	14.7%	4.1%
Significance	0.024	0.267	0.423	0.135	0.331	0.961	0.739	0.557	0.497	0.351

Communication

Image	1	2	3	4	5	6	7	8	9	10
Low	52.8%	24.6%	47.1%	50.0%	45.5%	29.2%	53.6%	52.2%	16.4%	5.6%
High	48.8%	27.3%	41.5%	45.6%	42.7%	28.3%	54.5%	52.9%	15.2%	4.0%
Significance	0.286	0.410	0.111	0.213	0.418	0.780	0.802	0.849	0.637	0.297

Attention Switching

Image	1	2	3	4	5	6	7	8	9	10
Low	52.5%	26.2%	45.6%	48.4%	45.1%	27.0%	52.4%	50.6%	15.4%	5.6%
High	50.2%	23.7%	45.1%	49.3%	43.8%	32.4%	56.6%	55.7%	17.2%	4.4%
Significance	0.512	0.416	0.872	0.790	0.691	0.077	0.221	0.134	0.459	0.425

Attention to Detail

Image	1	2	3	4	5	6	7	8	9	10
Low	52.6%	24.0%	44.1%	48.8%	44.4%	26.8%	51.9%	50.7%	15.7%	5.6%
High	49.8%	27.8%	47.9%	48.5%	45.0%	32.8%	57.6%	55.8%	16.7%	4.3%
Significance	0.438	0.228	0.265	0.927	0.858	0.050	0.094	0.140	0.687	0.358

Imagination

Image	1	2	3	4	5	6	7	8	9	10
Low	52.0%	25.0%	46.3%	48.8%	45.7%	29.0%	54.0%	52.5%	15.9%	5.3%
High	49.1%	27.8%	38.9%	47.8%	36.8%	28.2%	53.2%	52.3%	16.7%	4.2%
Significance	0.571	0.545	0.139	0.838	0.074	0.860	0.876	0.974	0.843	0.619

(High and low determined using the averages of Hurst et al.'s (2007) data)

Social

Image	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Low	54.0%	24.3%	46.8%	45.8%	46.6%	28.4%	54.8%	47.8%	14.3%	5.5%
High	50.6%	25.7%	44.9%	49.9%	43.9%	29.1%	53.5%	54.4%	16.7%	5.0%
Significance	0.358	0.660	0.595	0.262	0.439	0.833	0.724	0.069	0.340	0.762

Communication

Image	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Low	53.7%	26.3%	49.8%	49.8%	47.0%	32.1%	58.0%	50.5%	12.3%	6.0%
High	51.0%	25.0%	44.2%	48.4%	44.0%	28.0%	52.7%	53.0%	17.1%	4.9%
Significance	0.508	0.700	0.141	0.717	0.428	0.234	0.172	0.517	0.084	0.487

Attention Switching

Image	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Low	52.4%	26.0%	44.6%	46.9%	45.2%	26.4%	52.7%	49.1%	14.4%	5.4%
High	51.0%	24.8%	46.1%	50.1%	44.2%	30.8%	54.9%	55.0%	17.3%	5.0%
Significance	0.694	0.693	0.635	0.328	0.748	0.135	0.511	0.078	0.220	0.766

Attention to Detail

Image	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Low	47.3%	23.5%	39.1%	47.2%	43.8%	24.9%	46.5%	46.0%	13.1%	6.2%
High	54.5%	26.5%	49.4%	49.7%	45.2%	31.5%	58.5%	56.6%	17.9%	4.5%
Significance	0.036	0.330	0.002	0.454	0.657	0.027	<0.001	0.002	0.046	0.252

Imagination

Image	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Low	53.5%	23.4%	48.0%	49.6%	47.9%	31.1%	56.7%	56.1%	16.6%	6.3%
High	50.3%	26.8%	43.6%	48.0%	42.3%	27.3%	51.9%	49.8%	15.6%	4.3%
Significance	0.351	0.256	0.173	0.622	0.084	0.202	0.139	0.060	0.679	0.153

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