Article:

Spikins, Penny orcid.org/0000-0002-9174-5168, Wright, Barry John Debenham orcid.org/0000-0002-8692-6001 and Hodgson, Derek (2016) Are there alternative adaptive strategies to human pro-sociality? The role of collaborative morality in the emergence of personality variation and autistic traits. Time and Mind. pp. 289-313.

https://doi.org/10.1080/1751696X.2016.1244949

Time and Mind

The Journal of Archaeology, Consciousness and Culture

ISSN: 1751-696X (Print) 1751-6978 (Online) Journal homepage: http://www.tandfonline.com/loi/rtam20

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To cite this article: Penny Spikins, Barry Wright & Derek Hodgson (2016) Are there alternative adaptive strategies to human pro-sociality? The role of collaborative morality in the emergence of personality variation and autistic traits, Time and Mind, 9:4, 289-313, DOI: 10.1080/1751696X.2016.1244949

To link to this article: http://dx.doi.org/10.1080/1751696X.2016.1244949

Published online: 15 Nov 2016.

TIME & MIND, 2016
VOL. 9, NO. 4, 289–313
http://dx.doi.org/10.1080/1751696X.2016.1244949

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Taylor & Francis Group

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Are there alternative adaptive strategies to human pro-sociality? The role of collaborative morality in the emergence of personality variation and autistic traits

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ABSTRACT
Selection pressures to better understand others' thoughts and feelings are seen as a primary driving force in human cognitive evolution. Yet might the evolution of social cognition be more complex than we assume, with more than one strategy towards social understanding and developing a positive pro-social reputation? Here we argue that social buffering of vulnerabilities through the emergence of *collaborative morality* will have opened new niches for adaptive cognitive strategies and widened personality variation. Such strategies include those that that do not depend on astute social perception or abilities to think recursively about others' thoughts and feelings. We particularly consider how a perceptual style based on logic and detail, bringing certain enhanced technical and social abilities which compensate for deficits in complex social understanding could be advantageous at low levels in certain ecological and cultural contexts. 'Traits of autism' may have promoted innovation in archaeological material culture during the late Palaeolithic in the context of the mutual interdependence of different social strategies, which in turn contributed to the rise of innovation and large scale social networks.

ARTICLE HISTORY
Received 20 July 2016
Accepted 26 September 2016

KEYWORDS
Cognitive evolution; collaborative morality; Palaeolithic archaeology; personality variation; autistic traits

Introduction

Over the last decade attention has focused on the role of complex social understanding in human evolutionary success. There is little doubt that being highly tuned to understanding other minds is a capacity that has been selected for, and is a major component of hominin brain expansion (Dunbar 2002; Gamble, Gowlett, and Dunbar 2011). Humans have become far better than any other primate in being able to cogitate about the thoughts and motivations of others. Whilst first order theory of mind allows a mind to consider the thoughts of another in a linear way, most humans have higher levels of cognitive theory of mind (i.e. ability to guess what x might

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understand what y understands about what z is thinking) (Dunbar 2002). Developments in society, social behaviour and social understanding have been seen as reflecting a progressive increase in the complexity of theory of mind through time (Dunbar 2002; Gamble, Gowlett, and Dunbar 2011).

The evolution of social cognition may be more complex than increasing complexity of theory of mind abilities however. High levels of 'recursive' theory of mind (thinking though several levels of others' thoughts) do not carry the advantages we might at first assume. Recursive theory of mind is cognitively costly. Moreover on an individual level, recursive mentalising can lead to anxiety as to what others think or feel, and is associated with psychosis (Brosnan et al. 2010). Recursive mentalising in response to social situations can also carry negative judgements from others as we trust and respect those who cooperate without counting the costs, i.e. those motivated by another's wellbeing adhere to moral principles *without attempting to think through the intentions of others*. We collaborate and go to great lengths to support such individuals as they can be trusted in important situations (Hoffman, Yoeli, and Nowak 2015). Advanced levels of perspective-taking can even increase competitiveness between individuals (adding 'fuel to the fire'), where it becomes 'do unto others as you think they will try to do unto you' (Pierce et al. 2013). Whilst *low* theory of mind abilities carry a reduced understanding of complex social relationships they also bring advantages which enable their persistence in collaborative contexts (Devaine, Hollard, and Daunizeau 2014).

Whilst we generalise evolutionary pressures as proceeding towards greater cogitation of other's thoughts and feelings and increasingly complex intuitive models of other minds, the reality is likely to have been more complex. We argue that social buffering of vulnerabilities in increasingly complex human societies may have encouraged a range of different strategies to pro-sociality that go beyond increasingly recursive theory of mind, and lead to a wider range of pro-social human *personalities*.

The emergence of collaborative morality and the potential for new adaptive strategies

The evolutionary emergence of collaborative morality

Extensive evidence for support for individuals with disabilities in the distant archaeological record (Hublin 2009; Spikins, Rutherford, and Needham 2010; Spikins 2015a; Tilley 2015) argues that selection pressures within human societies were not simply orientated around immediate responses or short-term social value, and that social buffering of vulnerabilities was common.

Social selection in humans is clearly distinctive. Social relationships in other primates revolve around personal alliances. This is likely also to have been the case in an early stage of the evolution of human collaborative social relationships. Social relationships and selection will have been orientated around personal alliances, such that here individuals were sympathetic or fair to *particular others* (Tomasello and Vaish 2013a) and selection pressures principally came to bear on abilities to persuade others to become allies and be able to detect cheats. However as human *collaborative morality* emerged the following of and enforcement of *group norms* became primary, and reputation, influence and selection were structured through these norms (Figure 1). This transition is significant in opening up a niche for alternative adaptive strategies to sociality for several reasons. First, collaborative morality brings with it the punishment of free-riders, bullies and cheats and third-party retaliation for anti-social behaviour (Boehm 2011) creating an environment in which those with less complex theory of mind abilities would be protected from exploitation. Second, as relationships shift focus from individual alliances seen in other primates (where monitoring of potential personal exploitation is of prime importance) to a larger-scale group, judgements and contributions to group wellbeing become important (Tomasello and Vaish 2013b). Rather than social astuteness, signals of pro-social motivations and behaviours that positively affect the group thus become a major factor in reputation and selective success (Tomasello et al. 2012; Silk and House 2016). Third, the food sharing, collaborative parenting and maintenance of egalitarian dynamics which form the basis of human evolutionary success (Whiten and Erdal 2012) buffer individual shortfalls not only in resources (the basis for economic success) but also in abilities. An expert hunter need not also be an attuned and sensitive parent to be reproductively successful, and the converse is equally the case.

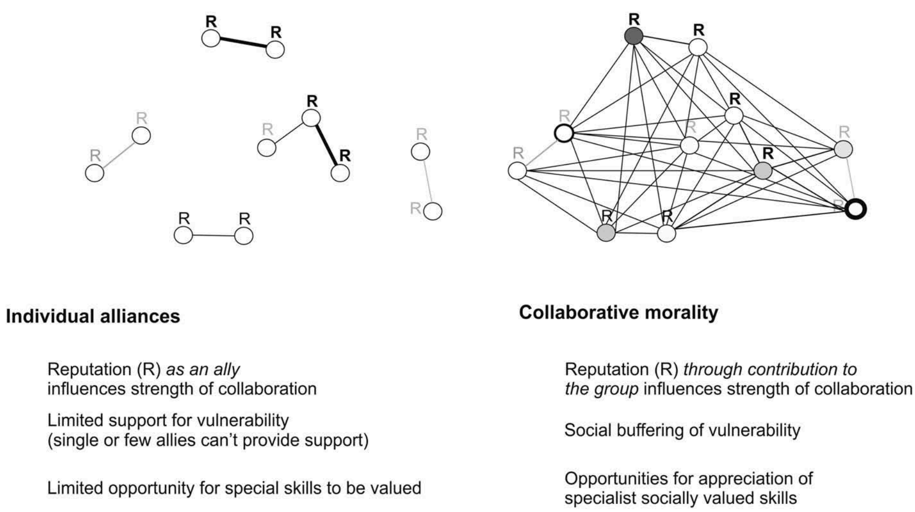

Figure 1. Selection pressures on reputation and support for vulnerability in groups structured by individual alliances (left) and collaborative morality (right). (Authors).

We argue that as a transition to *collaborative morality*(Tomasello and Vaish 2013b) occurred within human groups, new opportunities arose for alternative strategies to sociality, including those which do not depend on complex social understanding and theory of mind.

Collaborative morality in ethnographic and archaeological contexts

In ethnographically documented small-scale modern hunting and gathering contexts the effects of collaborative morality on selection pressures are evident. Constraints on cheating, bullying and dominance are universal, and strong selective pressure is placed on displaying pro-social morality (Boehm 2012; Van Schaik et al. 2014). Amongst the Martu of Australia for example those showing the greatest spontaneous generosity are favoured as hunting collaborators (Bliege Bird and Power 2015), whilst amongst the Ache of Paraguay a similar history of past generosity leads to greater support towards an ill or elderly person (Gurven et al. 2000). Within the hunting and gathering societies of modern humans it becomes more important to be *valued* and *pro-socially motivated* than to be socially clever.

Archaeological evidence supports the emergence of *moral reputation* as a key driver of selection from early in human evolutionary history. Selection for pro-social intentions and behaviours occurs from at least 1.5 million years ago, with increasing material evidence for care of the vulnerable (Hublin 2009; Spikins, Rutherford, and Needham 2010; Spikins 2015a) as well as displays of positive reputation in material culture (Spikins 2012). Complex social dynamics similar to those of modern hunter-gatherers and associated with collaborative morality become identifiable by at least 100,000 years ago (Spikins 2015b), which is commensurate with an expansion of the brain at this time (Shultz, Nelson, and Dunbar 2012). Widespread support for those who were physically vulnerable generated physically and cognitively diverse societies. Remarkably debilitating conditions were supported (such as the 60,000 year old Neanderthal from Shanidar with a withered arm, withered leg and blind in one eye who was looked after for around 15 years: Spikins 2015a) and opportunities are found to exploit what strengths exist. In a modern context amongst the Baka severely disabled individuals form a social nexus, being those who bring different groups together (Toda. 2013). In archaeological contexts individuals with disabilities are frequently given elaborate burial (Wengrow and Graeber 2015), which may reflect a recognition of their unique status and strength in adversity.

Collaborative morality opens up opportunities to be respected and appreciated through the emergence of distinct abilities, virtues or spheres of elevated influence and respect even when these are associated with deficits. Egalitarian hunter-gatherers place well documented constraints on any attempts to gain power over others (Boehm 2015), although temporary inequalities (Wengrow and Graeber 2015) or social differentiation on the basis of knowledge (Artemova 2016) are common. Distinctive sets of valued skills (e.g. technical skills) also lead to specific social roles. Amongst the Baka for example adolescents and young men, hoping to become more attractive to potential mates, travel hundreds of miles to learn skills from craft specialists (such as basket makers) who are acknowledged innovators (Hewlett 2013). Amongst the Hadza, certain men are acknowledged as particularly skilled hunters, with one of the main features that women look for in a potential mate being to be a 'good hunter' (Marlowe 2004). Good hunters are more reproductively successful even though the food they hunt is widely shared as good hunters attain a social-moral value through their effort, and it is this value, rather than any direct economic benefit which is seen as attractive.

The attitudes and skills which are most valued are not necessarily static and can be influenced by environments and subsistence methods. Cross-cultural studies demonstrate that subsistence practices affect a cultural emphasis on altruism for example (Heinrich et al. 2004). Moreover specific skills can be valued in certain environments. Amongst the Inuit, for whom life in extreme cold depends on well designed and well functioning technology particular social values are placed on boldness, perseverance and exactitude, with these values expressed both in storytelling and through innovative designs, patience and attention to detail in soapstone carving (Graburn 1976). Similar attitudes and skills are expressed where we see similar environments at the time of glacial maximum in Europe, with finely made Solutrean points for example taking up to 11 hours to produce, and displaying patience, precision, and a commitment to many hours of practice (Sinclair 1995). The extent of craft specialisation in lithic manufacture at the last glacial maximum suggests that specialised craft roles developed and were supported by others (Sinclair 2015).

Collaborative morality provides a catalyst therefore for different adaptive strategies to pro-sociality, and a widening of human personality variation. Nettle (2006) for example argues that selection for creativity drove a widening of personality variation to include schizotypy. Whitley (2009) argues for the significance of bipolar disorder in producing traits valued in shamans in hunter-gatherer societies. It seems likely that many of the mental syndromes that have been identified over the recent past for example as set out in DSM-5, have a genetic component and before these were identified as such they were often regarded in other ways by particular communities based on ongoing belief systems (for example descriptions of obsessive compulsive disorder in Babylon: Reynolds and Kinnier Wilson 2012). Here, however, our argument focuses on the traits of autism. We consider psychological research into the advantages, disadvantages and potential contribution of associated skills and talents seen in *autism without intellectual impairment* (i.e. Asperger Syndrome, hereafter referred to as AS) within populations, and as well as genetic and archaeological evidence which supports the argument that AS, and traits of autism, can be regarded as an alternative pro-social adaptive strategy.

Autism without intellectual impairment as an alternative pro-social adaptive strategy

Autism without intellectual impairment is not necessarily a disadvantage

Autism spectrum conditions are often conceived of as disorders requiring intensive social support, and thus reproductively disadvantageous. However *autism associated with intellectual impairment* (which usually requires organised social support and derives from traumatic brain damage, tuberose sclerosis, fragile x syndrome or de novo genetic mutations) only comprises about 30% of the cases of diagnosed autism today (Iossifov et al. 2014). The earliest identified cases of autism were of this type; however, the later identified *autism without intellectual impairment* (AS and high functioning autism) is notably distinct, with different genetic causes (Ronemus et al. 2014) and much lower levels of wider neurological damage.

Autism without intellectual impairment, AS, is widely prevalent in modern society. Research into population-wide variability of the Autism Quotient (which measures the extent of rule-based, analytical thinking and matches diagnostic criteria for Autism and Asperger Syndrome: Baron-Cohen et al. 2001) suggests around 2% of individuals within populations would be diagnosed with AS. Most however remain *undiagnosed*, despite their notable cognitive difference. In a study of 557 students at the University of York as part of the 'Lost in Translation: Autism and Material Culture' Project, 2% scored in the AQ range suggestive of AS for example, and in a similar study of 840 Cambridge University students, Baron-Cohen et al. (2001) found the same percentage, which also match the distribution of a control sample of the general (i.e. non-student) population (Baron-Cohen et al. 2001). As Baron-Cohen comments:

> None of those meeting criteria complained of any current unhappiness. Indeed, many of them reported that within a University setting their desire not to be sociable, together with their desire to pursue their narrow or repetitive interests (typically mathematics and computing) was not considered odd, and was even valued. (Baron-Cohen et al. 2001, 12)

Rather than see individuals with AS as outside society, anthropological perspectives argue that we should recognise a *different* sociality (Grinker 2010; Ochs and Solomon 2010). Individuals with AS certainly develop a theory of mind which is *different* in being based on the use of rules and logic, but nonetheless works. Theory of mind develops late in children and is constrained (with individuals with AS being more likely to fail at the level of second order theory of mind, i.e. 'Y believes that X believes this': Baron-Cohen 1989).

However rather than being asocial, a rule-based theory of mind is sufficient to 'get along' socially (Baron-Cohen 2009), including facilitating long-term collaborative planning (W. Yoshida et al. 2010). One is often unaware from casual acquaintance that someone has autism and individuals with AS often have high levels of role and function in society (Howlin 2000) particularly in spheres such as engineering, mathematics, physics, information technology and law (Rodman 2003; Fitzgerald 2004) and have partners and children (Baron-Cohen et al. 1998; Lau and Peterson 2011).

A social understanding based on logic may bring disadvantages to understanding emotionally and socially complex situations, but it frees up cognitive potential for enhanced abilities in other realms, both technical and social, which can contribute to a *positive social reputation*.

Autism without intellectual impairment is associated with valuable technical and social skills

Technical skills

Elevated (heightened beyond the norm) skills in various perceptual and analytical domains associated with AS are well researched (Figure 2).

Various perceptual skills are enhanced in those with AS. For example, superior abilities in identifying embedded figures (Figure 3) and block design (three-dimensional design) were identified as early as the 1980s (Shah and Frith 1983). In recent years, however, the understanding of superior abilities has improved significantly with enhanced skills identified in music – due to a better memory for pitch with absolute pitch being common (Heaton 2009); visual perception, including not being influenced by optical illusions and enhanced abilities to perceive visual details (Smith and Milne 2009); heightened touch sensitivity (Baron-Cohen et al. 2009) and olfactory sensitivity (Lane et al. 2010).

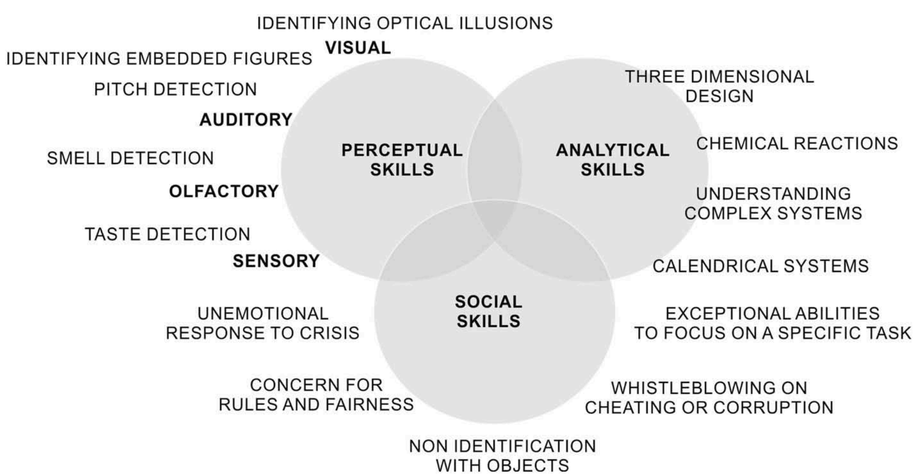

Figure 2. Skills in perceptual and analytical domains associated with AS. (Authors).

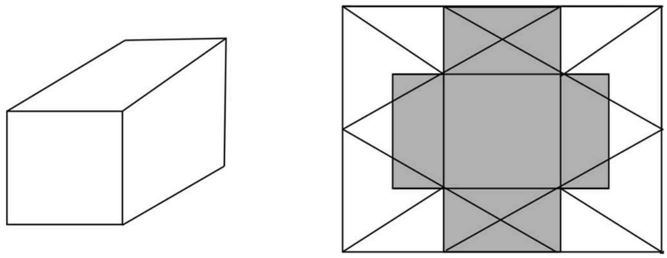

Figure 3. Example of an embedded figure test. Individuals with AS have superior abilities at identifying the shape on the left within that on the right. (Authors).

Heightened perception influences and reinforces an amplified understanding of particular skills, which facilitates a remarkable ability to focus (Figure 4) with enhanced skills in mathematics (Iuculano et al. 2014), as well as chemistry and engineering (Baron-Cohen et al. 2009).

Recently, the number of individuals with autism spectrum disorders (ASD) considered to be exceptionally talented at the 'savant' level has also been increasingly recognised (Treffert 2009). For example, Meilleur, Jelenic, and Mottron (2015) found, in detailed studies of over 250 autistic individuals, that over 60% have some special skills. In addition to those skills facilitated by enhanced perception and understanding, other individuals with AS may also possess an unacknowledged talent of some kind. So called 'savant talents' are found in several contrasting areas, as was demonstrated in Howlin et al. (2009) study of 137 randomly selected individuals with autism, where such skills include computational (listed as 'easily able to multiply two numbers in the millions together in head; can tell the elevation of both the Sun and the Moon at any time on any date without reference to any book'), calendrical

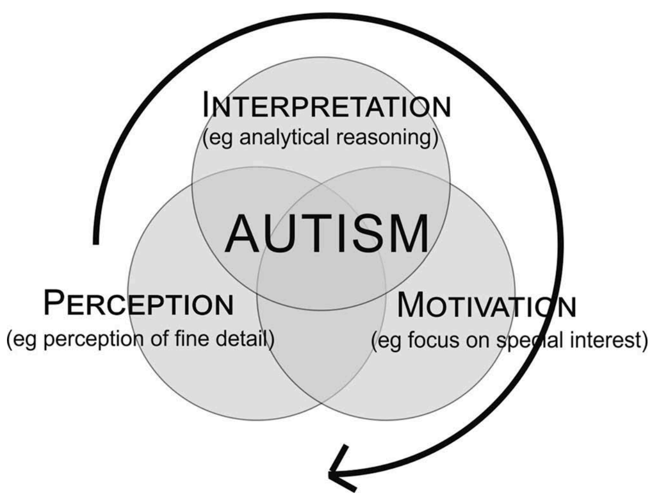

Figure 4. The relationship between perception, interpretation and motivation in AS. (Authors).

('could tell people what day of the week their birthday would occur and what day of the week they were born on'), memory ('a few years ago, he was bought a book which was read to him; this year we read it to him again after over a year – if we stopped he would finish the rest of the sentence quite accurately'), and visuospatial abilities ('successful in painting portraits of friends, friends' children and selling them'), with some showing special skills in several of these domains (Howlin et al. 2009).

It isn't difficult to see how such skills might contribute to survival and be accorded a certain respect in a Palaeolithic context. Indeed, Happé and Frith concluded that the persistence of an extreme cognitive focus on detail within the gene pool, 'is not hard to explain' (2006, 16). Enhanced perceptual abilities alongside exceptional memory for example provide advantages in domains such as identifying plant resources (from smell or fine visual details) to discrimination of animal properties (through enhanced differentiation of movement and sound) with acute perception of motion likely to be significant in hunting success. Enhanced understanding of animal behaviour, plus a unique connection with and focus on animals, is likely to be particularly significant in hunting. Several authors also argue that the technical and analytical focus of AS in past hunter-gatherer contexts can facilitate improvements in tool making and mechanical thinking (Spikins 2009; Lomelin 2011; Reser 2011), and others for their role in agricultural contexts (Del Giudice et al. 2010; Charlton and Rosenkranz 2016). The incorporation of these skills into a community would, in this way, play a role in the development of specialists, the construction of specialist niches and enhanced innovation.

Distinctive technical and social roles for the skills of individuals with AS that collaborative morality allows to be integrated can be seen in ethnographically documented contexts. In his study of Siberian reindeer herders for example Vitebsky describes 'old grandfather', an individual who had a detailed memory of the parentage, medical history and character of each one of the 2,600 reindeer in the herd, vital knowledge which made a significant contribution to their management and survival. Old grandfather was more comfortable in the company of reindeer than of humans, but was much respected and had a wife, son and grandchildren (Vitebsky 2005, 133). In archaeological contexts the elaborate specialisation on precision and extensive practice seen in lithic manufacture at the last glacial maximum (Sinclair 2015) provides another example where autistic traits would be advantageous with technical specialists also recognised amongst modern Inuit.

Social skills

AS even brings certain skills which are of particular value in a social context, and which have rarely been acknowledged given a preconception that the condition implies being *asocial*, rather than *differently social*. A distinctive AS perception and understanding feeds into particular social roles in certain types of communication, in crisis and even potentially may have been significant in the formation of large-scale networks and intergroup collaborations.

The logic-based theory of mind of AS for example confers an elevated understanding of *certain minds*. Individuals with AS understand, and can predict, *each other's* thoughts and motivations better than neurotypicals (Chown 2014), and some appear to possess a heightened understanding and sensitivity towards animals (Prothmann et al. 2009). This latter facility may have been significant not only in hunting, but in domestication, for example of wolves, which occurs from at least 30,000 years ago.

Most particularly, however, AS brings a distinctive understanding of, and responses to, others' emotions. A perception that individuals with AS do not *feel for* others, is wrongly placed. Affective empathy for example is shown to be relatively preserved compared with cognitive empathy in some studies (Rogers et al. 2007), and brain activation studies show that empathic brain responses are not absent but may be modulated by differences in thinking for example (e.g. alexithymia [Bird et al. 2010] and appraisal differences [Hadjikhani et al. 2014]). Nonetheless, faced with a complex emotionally charged social situation those with AS show reduced expressed or intuitive empathy (Grove et al. 2014) and have difficulties identifying complex social emotions (Wright et al. 2008). They may go through continual cognitive re-appraisal (Hadjikhani et al. 2014; Torralva et al. 2013) and depend on logic (Hill, Sally, and Frith 2004) to search for appropriate ways to respond, which can lead to an apparent lack of caring (Hadjikhani et al. 2014). Though not lacking in pro-social motivation the *strategy* of pro-social engagement associated with AS becomes distinctive, and in turn leads to suitability for certain roles. For example individuals with AS are often valued for their logical response in a crisis (Rodman 2003). They may stay true to principles rather than being influenced by a need to maintain social standing (Cage 2015).

Specific kinds of social interaction of those with AS are thus distinctive. Such Individuals tend to rely on logic, rules (Gleichgerrcht et al. 2013), patterns, and memory (Sahyoun et al. 2009) as well as environmental and sensory information (O'Connor & Kirk 2008; Baron-Cohen 2000) in social interactions and tend to focus on scientific and analytical discussions, contributing new knowledge (Bauminger et al. 2008), or discussing particular shared interests with similar minded friends. They may prefer to employ material culture or technology to communicate (Ochs and Solomon 2010; Grinker 2010) rather than engage in face-to-face sharing of narratives or emotional displays (Fitzgerald and O'Brien 2007; Baron-Cohen 2012). Although often uninterested in social reputation (Izuma et al. 2011), a distinctive focus means that those with AS often attain notable roles in society (Howlin 2007), particularly in the fields of medicine, engineering, mathematics, physics and information technology (Baron-Cohen et al. 1998; Rodman 2003; Fitzgerald 2004; Fitzgerald and O'Brien 2007). Evidence for rule-based *morality* associated with AS deriving from a logical approach to relationships can also be found in the literature (De Vignemont 2007). The intuitive and empathetic theory of mind of those who are neurotypical may facilitate *agreeableness*, yet this very same trait makes it difficult to resist authoritarian controls (Bègue et al. 2014). In a pertinent study of enhanced perceptual abilities and resistance to social conformity (Yafai, Verrier, and Reidy 2014), which compared people with autism with neurotypical individuals in the Asch conformity paradigm (Asch 1951), those with autism were found to resist changing their spontaneous judgement to an array of graphic lines despite social pressure to change by conforming to the erroneous judgement of an authoritative confederate. Whilst a logical and moralistic approach to social interactions may not lead to fluid conversations, pleasing comments or a natural ability to put others at ease, a tendency to be whistle-blowers, and to counteract aggressive behaviour through adherence to *moral principles*, gives individuals with AS a certain respect in a collaborative social context. A willingness to police cheats and counteract dominance is highly regarded in hunter-gatherer contexts (Boehm et al. 1993). Likewise in modern contexts individuals with AS are often drawn to careers in law (Rodman 2003; Fitzgerald and O'Brien 2007) and in past contexts to the imposition of social norms and rules. Clearly agreed rules are essential to intergroup collaboration in modern hunter-gatherers. Amongst the Yamana individuals with a reputation for adherence to rules are given authority to impose order at initiation ceremonies for example (McEwan, Borrero, and Prieto 2014), and equally the strict imposition of highly complex and precise rules, known as *niqaiturasuaktut*, allow collaboration and division of carcasses during collaborative winter seal hunts amongst the Netsilik (Balikci 1989).

A niche within wider communities for a certain number of individuals with AS, bringing with them a focus on technical skills, the furtherance of knowledge or the upholding of rules, seems evident.

The evolutionary basis for inclusion of AS in an evolutionary context

Mate choice and reproductive success with AS

We might imagine that AS would confer limited reproductive success, but this is not the case. Limited abilities at 'nested' mentalising and the understanding of complex emotions may make social relationships less fluid. However in modern hunter-gatherer contexts such traits are rarely of primary significance in mate choice. Amongst the Hadza for example the most significant trait affecting female mate choice is being 'a good hunter' (Marlowe 2004). Food is shared widely so that hunting prowess does not confer direct nutritional advantage to one's kin; however, good hunters are more reproductively successful in attracting mates (Smith 2004). Intelligence is also significant and the primary consideration for someone to be seen as 'nice' is not astute social skills but non-violence (Marlowe 2004).

In a modern context, those with AS are known to have families and children thereby maintaining the genes associated with AS in the gene pool (Baron-Cohen et al. 1998; Lau and Peterson 2011). There may be some element of assortative mating, with AS individuals often selecting a similar partner to themselves (Baron-Cohen 2006). Even so, individuals with AS are also attractive to those who are neurotypical. The marital satisfaction of neurotypical spouses of individuals with AS has been shown to be within normal limits (Lau and Peterson 2011). There may be advantages in selecting a mate with AS that offsets costs related to the lack in complex social understanding, such as the ability to focus on securing practical resources, and a long-term commitment to both mates and offspring (Del Giudice et al. 2010).

Genetics

The genetics of autism are complex, with over a thousand genes currently implicated, and more research is needed to be conclusive (Liu et al. 2014). However, in broad terms, genetic research supports the argument that autism without intellectual impairment (AS) became a significant adaptive strategy that was selected for recently, perhaps after 200,000 years ago, and was subsequently maintained in human populations at low levels.

Autism in some form has a long evolutionary history. Genes associated with autism have been argued to appear in apes (Dumas et al. 2012), as they are also implicated in both ape and human brain expansion (Marques-Bonet and Eichler 2009). Autistic-like behaviours apparent across populations and with a genetic component have been recorded in macaques and in chimpanzees (K. Yoshida et al. 2016; Marrus et al. 2011; Faughn et al. 2015). About 30% of the cases of autism occur spontaneously rather than as a result of selection; these are cases where *autism with intellectual impairment* derives from spontaneous de novo copy order mutations (Iossifov et al. 2014; Ronemus et al. 2014). A propensity for such copy order variations (though not the variations themselves) appears to be part of human genome evolvability (Thomas 2014). Separately from these cases however we see a proliferation of genes associated with ASD relatively late in human evolution, sometime after 200,000 years ago. As Bednarik (2013) notes, two genes (AUTs2 and CADPs2) implicated in autism, are found in modern humans but not Neanderthals (Green et al. 2010). DNA flanking 15q13.3 is also associated with autism and exists only in modern humans and not the Neanderthal genome (Antonacci et al. 2014). In addition, uniquely human copy number variations (CNVs) in 16p11.2 are associated with autism, which are likely to be unique to modern humans as they arose in the past 183,000 years (Nuttle et al. 2014). Whereas some of these genes may be maintained despite being disadvantageous, it remains plausible that in recent evolutionary history certain autistic genes, particularly associated with ASD without intellectual impairment, were being selected for in certain contexts. Cross cultural comparisons in modern contexts confirm a consistent low percentage of autistic traits present across modern cultures (Wakabayashi et al. 2007).

Variable selection

AS might seem an obvious adaptive strategy, particularly with many arguing for the condition as a difference rather than a disorder (Jaarsma and Welin 2012). However, identifying the evolutionary dynamics of AS has been hampered by the conflation of AS and autism with other impairments including intellectual disability. Evolutionary approaches thus attempt to explain *autism* as a broad category and as an *asocial* extreme of normal behaviour, with low fitness (Ploeger and Galis 2011; Crespi and Badcock 2008; Shaner, Miller, and Mintz 2008). The logic-based theory of mind seen in AS, however, remains to be explored as a *pro-social* strategy integrated within communities and arising from, and influencing, wider cognitive, emotional and social factors.

We argue here that, after the rise of collaborative morality, a potential social niche arose for a low proportion of individuals with AS whose logic-based theory of mind facilitated the release of cognitive resources. In small-scale collaborative hunting and gathering contexts, a positive social reputation for making a contribution to group wellbeing and survival becomes a key selective pressure for evolutionary success. As a result, AS becomes a viable alternative perceptual strategy to a 'neurotypical' complex theory of mind, bringing with it valued social and technical talents. The emergence of technological or social innovations (such as systems of laws and rules) which improve survival, in turn, create a niche to which the characteristics of those with AS are particularly suited.

Following potential inclusion of AS in a community through collaborative morality, selection pressure may have varied according to particular context and the cultural or ecological setting. Collaborative morality is fiercely upheld in modern hunting and gathering groups; however, alternative competitive social contexts where those with AS might be exploited can arise (Boehm 2012). Specific ecological influences may have been significant. For example, mid to high latitude and variable environments associated with unpredictable resources might have been particular 'hotspots' where traits of autism were most valued. In such situations complex technology, with a focus on detail and a high level of standardisation to ensure maintainability and reliability, is essential for survival (Oswalt 1976; Bleed 1986), and emerging specialised roles would provide the scaffolding for such autistic traits to be developed and valued, and the cultural niche (Laland and O'Brien 2012) into which autistic traits are particularly well adapted. Abilities at focusing on and providing technological solutions will have been particularly valued, especially where changing environments put survival at risk. Moreover, subsistence in such environments often depends on large mammals. In such situations (as seen in modern whale-hunting groups) survival depends on formal rules to collaborate between groups, and cultures place the greatest emphasis on supporting others (Heinrich et al. 2004). When more than one group collaborate in hunting or in agricultural endeavour they cannot rely on empathy only, with rules and traditions taking a more central role in successful collaboration. This, alongside the technological innovations necessary to trap and kill the prey.

Archaeological evidence

The emergence of long-distance networks of raw material movement and of alliances, with materials exchanged along such networks, is perhaps our best material evidence for collaborative morality, shared across whole regions. Such evidence appears after the emergence of our own species around 200 to 150,000 years ago in Africa, appearing after 100,000 years ago in south African and north African archaeological sites (Bouzouggar et al. 2007). Global expansion after 100,000 years ago is argued to also reflect collaborative morality (Spikins 2015b).

Archaeological evidence for the first emergence of notably complex technical innovations supports the argument that an inclusion of traits of autism and of individuals with AS occurred in this time frame and was particularly significant in certain ecological contexts. Notable and novel technological innovations first appear in southernmost region of south Africa at a time of environmental variability after 100,000 years ago for example. These include the heat treatment of flint to improve knapping precision (Brown et al. 2009), new standardised and precise project point technology (Shea 2006), microlithic and compound technology (Brown et al. 2012), complex adhesives demanding an understanding of chemical reactions (Wadley, Hodgskiss, and Grant 2009), and poisons (d'Errico et al. 2012). Novel precise and standardised beadworking, interpreted as evidence of large-scale networks, appears in northernmost Africa at around 80,000 years ago (Bouzouggar et al. 2007).

Following dispersion out of Africa further novel technologies appear after movements into the northern latitudes of ice age Europe (after 40,000 years ago) where hunter-gatherers faced particularly variable and challenging environments. As well as new technologies (such as spear throwers, scaffolding, fat based lamps, storage facilities and intensive processing of starchy foods) there is also evidence for other new analytical ways of perceiving the world including mathematical notation, maps and calendrical systems (Hayden and Villeneuve 2011). The Abri Blanchard plaquette for example shows the phases of the moon and its position in the sky, and must have been recorded over many sequential nights using some type of recording grid (Spikins 2015a). AS has even been argued to have influenced the precise, accurate style of Upper Palaeolithic art, with some graphic elements of Upper Palaeolithic art and savant autistic artists showing similarities (Kellman 1998; Humphrey 1998; Spikins 2009).

Artefacts such as maps and calendrical systems stand out from a material record of past hunter-gatherers in which such highly analytical objects are extremely rare. It is tempting to infer that such unusual artefacts can only have been produced or influenced by individuals with AS. Similar precise records of the world made by individuals with AS in modern contexts (such as the record of weather patterns made by Kevin Phillips [Baron-Cohen et al. 2009] and lists produced by Chris Goodchild [2010]) are known to be not only interesting and often a preferred means of communicating but are also emotionally *comforting* to individuals with AS, in providing a much needed sense of *predictability*. However, we would argue that the inclusion of individuals with AS in society will have stimulated different ways of thinking and perceiving the world especially with regard to engaging with material objects, thereby providing social niches occupied by individuals with certain talents. No one single artefact indicates the presence of individuals with AS, but the appearance of novel, engineered, precise forms of technology and new analytical ways of perceiving the world in certain contexts is highly suggestive. In more modern times autism genes have been suggested to be important for aptitude in computerised technologies (Baron-Cohen 2012).

Modern patterns of diagnosis

Whilst we need to be cautious about interpreting modern patterns of diagnosis as these are prone to the effects of cultural differences (Grinker et al. 2012), nonetheless some broad patterns are in evidence. Autism is generally more frequent in societies occupying higher latitudes, with northern European descent populations have higher rates of autism than those of southern European descent (Elsabbagh et al. 2012). In turn, autism rates are notably higher amongst non-Hispanic than Hispanic communities in the US (Palmer et al. 2010). Rates of autism diagnosis in aboriginal and Torres Strait islander populations, archaeologically regions low in technological innovation despite cultural complexity, are also significantly lower than those in local populations of European descent and lower than might expected given diagnosis of other disorders (Leonard et al. 2003; Parker et al. 2014). The influence of cultures is also evident. Low rates of autism in cultures such as Brazil have been argued to reflect a greater cultural focus on gregariousness and sociability above individual talents compared to the experience of individuals in cultures such as the US and UK (Paula et al. 2011).

Further research would be needed to explore these patterns in detail. Nonetheless, once the emergence of collaborative morality created a potential niche for a low percentage of individuals with AS to exist within human societies, relative selection pressure affecting inclusion clearly reflects a complicated relationship between ecology, genes and culture, and their co-evolution.

Conclusions

We argue that the emergence of collaborative morality changed the selection pressures operating in small-scale hunter-gatherer societies by buffering vulnerabilities where these were associated with valued skills, and providing an opportunity for alternative pro-social strategies to emerge. Human personality variation could widen, and alternative adaptive strategies which did not depend on a complex or nested understanding of others' motivations could emerge. In highly collaborative contexts individuals with less complex social cognition would be protected from exploitation, and could be at a selective advantage in contexts where other talents compensated for any lack of social fluidity. Evidence for enhanced technical and social skills identified in autism without intellectual impairment (AS) is used to argue that AS became an adaptive strategy which contributed to individual and group fitness through a unique logic- and detail-based perception and understanding of the world. Roles for low levels of individuals with AS are seen in modern hunter-gatherers as well as industrialised contexts; individuals with AS are reproductively successful, and there is emerging archaeological and genetic evidence to support the notable inclusion of autistic traits and perception after 200,000 years ago and particularly in certain ecological and cultural contexts.

The dynamic interrelationship of different evolutionary strategies for developing a positive social reputation helps explain the relevance of autistic traits with regard to the rise of innovations in the technological sphere, and also has implications for understanding the appearance of large-scale social networks. Furthermore, in moving away from assuming that complex theory of mind abilities are necessarily pro-social and selectively advantageous we can begin to appreciate the complexity of different pro-social strategies and personality variation in human societies.

Disclosure statement

No potential conflict of interest was reported by the authors.

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