Neanderthals and *Homo sapiens*: Cognitively different kinds of human?

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Abstract Membership of an extensive social network is imperative for human survival. However, maintaining network cohesion is particularly challenging for hunter-gatherers because they are dispersed over large home ranges, and need to keep track of absent social partners for extended periods. The archaeological record suggests that compared to Neanderthals, contemporary modern humans maintained social ties between greater numbers of individuals over greater distances. I argue that such differences would have influenced neural development, driving differences in brain structure and the degree of social complexity that each taxon could sustain cognitively. Following recent suggestions that modern humans' larger parietals might suggest an enhanced ability to create a 'virtual inner world', I hypothesise that this capacity allowed them to monitor larger numbers of absent social partners and thus maintain larger dispersed social networks than their Neanderthal counterparts. Larger social networks would have boosted the ability of modern humans to insure against local resource failure, sustain demographic stability and conserve cultural innovations.

The importance and challenges of maintaining social networks

Social relationships are crucial for human survival. Indeed, the number and quality of such ties are positively related to life-expectancy, and the protective effect on health is greater than well-known factors such as giving up smoking and doing exercise (e.g.

Holt-Lunstad, Smith, & Layton, 2010). Furthermore, being part of a cohesive social network improves not only an individual's health, but also that of their children (in humans: Adams, Madhavan, & Simon, 2002; Iaupuni, Donato, Thompson-Colón, & Stainback, 2005; and in baboons: Silk, Alberts, & Altmann, 2003). Since social behaviour impacts on individuals' genetic fitness it is likely to be under strong selection and is therefore fundamental to understanding the evolutionary history of primates such as modern humans and Neanderthals (Pearce, Shuttleworth, Grove, & Layton, 2014).

For mobile hunter-gatherers, maintaining friendly links with other social units minimises the risk of conflict with other groups as they move around the landscape. Moreover, maintaining connections with individuals who habitually reside in distant regions provides insurance against local resource failure. Such long-distance contacts provide access to both up-to-date information on the distribution and yields of alternative resources in different areas, and the resources themselves (e.g. Pearce & Moutsiou, 2014). Furthermore, a large network is better able to conserve knowledge and transmit innovations (e.g. Pearce, 2014). Given such advantages, those with more extensive social connections will generally do better in a changing environment, especially if those changes are unpredictable: they will hear news more quickly and have more numerous independent sources of help as a safety net (Whallon, 2006). Consequently, the size of social network that Neanderthals and

contemporary modern humans were able to maintain would have had major implications for their survival.

Ensuring that social networks remain connected is particularly challenging for hunter-gatherers given their fission-fusion social system, whereby units periodically disperse and re-aggregate according to changing resource distributions (Grove, Pearce, & Dunbar, 2012). When residential bands are dispersed, individuals need to factor in their absent social partners' perspectives in decision-making and keep tabs on them over extended periods, so that they know who they can currently count on and where they are. These abilities relate to the capacity for creating a 'virtual inner reality' (Bruner, 2010b; Devlin, 2000). Such 'offline thinking' is required in order to imagine alternative solutions to challenges and has to happen in the face of interference from 'online' events (what is happening in the here and now) by switching routine tasks to autopilot. In order to have the cognitive capacity for off-line thinking, individuals require sufficient neural architecture in the associated brain areas, which, as described below, are predominately located in the upper parietal lobe.

In this chapter I propose that positive feedback between their social environment, neural architecture and sociocognitive capacities, allowed modern humans to gradually enlarge their social networks relative to those of the Neanderthals (Figure 1). Such feedback may

have occurred in a similar way to Iriki & Taoka's (2012) 'triadic niche construction' (ecological, neural and cognitive) model, which they proposed this specifically in relation to tool use. Although the exact sequence and direction of causality remains unclear, the conservative hypothesis proposed here is that differences in social environment led to altered neural architecture, but it is possible that neurocognitive differences initially drove these social disparities (for a discussion of different possible mechanisms of neural change see Bruner & Iriki, 2016). I first review the archaeological evidence indicating that compared to Neanderthals, contemporary modern humans had larger social networks. I then use studies on neural plasticity in living humans and macaques to propose that the consequently more complex social environments in which modern humans lived became reflected in their brain structure and their associated cognitive capacities. In particular, I propose that the enlarged upper parietals demonstrated by the fossil record allowed modern humans to maintain cohesion in larger dispersed tribes by enabling them to keep track of more social partners in their 'mind's eye'. Finally, I suggest possible ways of starting to test the proposed hypothesis and discuss the implications of social network size for hominin survival.

The archaeological record

Several lines of evidence suggest that although Neanderthals had large social networks compared to other primates, they nonetheless had smaller ones than contemporaneous modern humans (e.g. see Pearce & Moutsiou, 2014). Although social behavior can only be studied indirectly in past populations, archaeological indices of social group or network size have been proposed and I examine these below. Although there would have been variation in network size, here I address the maximum network size that each taxon was able to maintain: what might be considered the 'best case scenario' for each.

The size of residential bands can be approximated from archaeological sites using the area of occupation and the number of 'sleeping hearths' (Hayden, 2012). For Neanderthals, these proxies suggest that residential groups most often comprised 12-14 individuals but could number up to ~30 (Hayden, 2012). Tentative support for the former value comes from the twelve El Sidron Neanderthals, who are purported to represent a single social group (Lalueza-Fox et al., 2011). In contrast, the butchery evidence for Neanderthals at Mauran suggests a minimum of 30 individuals, and perhaps an aggregation of several hundred (Farizy, 1994). Unfortunately, these estimates suffer from the palimpsest nature of the archaeological record: even single archaeological strata do not necessarily signify occupation by a single group. Despite this, these

data seem to match recent modern human hunter-gatherer group sizes fairly well: the median size of a recent hunter-gatherer residential band size is 14 during the most dispersed phase of the seasonal round and 37 during the most aggregated phase, whereas the median size of periodic aggregations of a number of bands is 150 (data from Binford, 2001). However, despite the archaeological group estimates suggesting a Neanderthal band size of up to ~30 individuals, ethnographic data for recent hunter-gatherers suggests that the average band comprises 37 individuals. Modern humans may thus have had larger bands than Neanderthals (Hayden, 2012). Although this difference may seem minimal, even an incremental difference at the level of the band might actually have had substantial implications in terms of survival. This is due to the organisation of human social networks, which comprise a series of cumulative nested layers (the residential band, the personal network, the mating pool and the tribe) in which each layer contains approximately three times as many members as the previous one (e.g. Pearce & Moutsiou, 2014; Zhou, Sornette, Hill, & Dunbar, 2005). Due to this scaling, even a small difference in band size at the inner layers may have translated into marked differences at the level of ethnolinguistic tribe, the outermost layer comprising the largest identifiable social unit in hunter-gatherers (Pearce & Moutsiou, 2014). For instance, a conservative difference of 7 individuals at the level of the band would have translated into a difference of 21 members of an individual's personal network, a difference of 63 individuals at the level of the mating pool (that is, 31 fewer potential

mates) and a difference of 189 at the level of the tribe. In this conservative case, modern humans would have been able to count on help from ~5 more bands than Neanderthals if their local resources failed, or for support in competition for resources. Although the exact impact that having 189 more, or fewer, people who could be called on in times of need and act as reservoirs of cultural knowledge, remains to be modelled and tested, the effect could have been substantial, particularly if such differences were sustained over time.

This suggested difference in the size of Neanderthal and modern human tribes appears to be borne out by evidence that Neanderthals exploited smaller geographic regions than contemporary modern humans living in similar habitats (e.g. Burke, 2012; Pearce & Moutsiou, 2014). The maximum distance over which raw materials move from their geological source to an archaeological site can give an indication of the maximum area covered by a social network, either through directly representing face-to-face exchanges or by representing potential interactions between individuals or subgroups exploiting the same geographic area (Pearce & Moutsiou, 2014). Whereas Neanderthals transferred obsidian up to 300km, European modern humans from similar dates transferred obsidian more than 400km, a distance that accords well with the geographic areas exploited by recent hunter-gatherer tribes living in analogous habitats (Pearce & Moutsiou, 2014). This difference indicates that

Neanderthal tribes probably exploited smaller areas than modern humans. Moreover, Neanderthals seem to have lived at lower population densities (Mellars & French, 2011). Given larger home ranges and higher population densities, it is likely that modern human tribes comprised greater numbers of individuals than the tribes of contemporary Neanderthals (Pearce & Moutsiou, 2014).

The higher frequency of ‘symbolic’ artefacts in the modern human record, such as ornaments and figurines, also supports their networks being larger than those of Neanderthals. Such artefacts can stand as a mnemonic for social ties as well as creating obligations to reciprocate and maintain that tie, so face-to-face interactions can be less frequent and more ties can be maintained (e.g. Gamble, 1999). Moreover, material culture representing group membership can create connections between personal networks with no overlapping members, through ties to a shared group such as a tribe. Consequently, if modern humans made more use of ‘symbolic’ artefacts as a mechanism of social bonding than the Neanderthals did, they would have been able to sustain more extensive social networks.

Although there are purported examples of non-utilitarian artefacts in the Neanderthal record, apparently demonstrating that they did have the cognitive capacity for such creative behaviour, these are far less prevalent and diverse than those attributed to modern humans. For

example, Neanderthals have been linked with possible examples of ornamentation (e.g. Finlayson et al., 2012; Zilhão et al., 2010), ochre use (e.g. Roebroeks et al., 2012) and some examples of cave art date to the overlap between the last Neanderthals and the earliest European modern humans (Pike et al., 2012). Nonetheless, the Neanderthal symbolic record appears very modest compared to the many shell beads from modern human sites (e.g. d'Errico, Henshilwood, Vanhaeren, & van Niekerk, 2005; Vanhaeren & D'Errico, 2006), the distinctive regional tool styles of modern humans (e.g. McBrearty & Brooks, 2000) and the figurative art and evidence for music found in Europe from the earliest modern human occupations onwards (Conard, 2009). Collective music-making is a powerful way of bonding large groups of individuals simultaneously, and so far musical instruments have only been found associated with modern humans (Morley, 2013; Pearce, Launay, & Dunbar, 2015; Weinstein, Launay, Pearce, Dunbar, & Stewart, 2015). Though it remains possible that we simply cannot recognize objects used by Neanderthals to support large-scale community cohesion, the contrast in the archaeological records between the two taxa suggests that although Neanderthals may have been technically capable of creating 'symbolic' objects, they did not do so to the same extent as contemporary modern humans. Given the Neanderthals' consequent need to meet social partners face-to-face rather than being able to rely on material culture to support their social ties, this may have limited them to smaller networks.

Taken together, the archaeological data suggest that modern human bands and tribes were larger than those of contemporary Neanderthals living in similar habitats. This implies that Neanderthals, though by no means asocial or isolated, would have interacted with fewer individuals both daily and across their lifespans. Consequently, a modern human would have had to function in more complicated social contexts that the average Neanderthal, and this likely had implications for their brain structure.

Neural plasticity

The fact that the relatively recent cultural innovations of reading and arithmetic are processed in well-defined cerebral areas suggests that neural circuitry that evolved for a particular function can be co-opted to support a different, though probably related, function associated with novel behaviours, at least within certain limits (the neuronal recycling hypothesis: Dehaene, SCohen, 2007). Along similar lines, engaging in maintaining more extensive, and more complex, social worlds may have had repercussions for how neural circuits were allocated in the modern human brain. Support for the impact of behavioural and environmental variation on brain structure comes from the findings that extensive use of complicated cognitive maps leads to enlargement of the posterior hippocampus in London taxi drivers (Maguire et al., 2000), and that the longer a taxi driver

has been working, the more their brain changes (Maguire et al., 2003). Thus, even during adulthood routine tasks can have a marked impact on brain structure. For instance, when adults learn to juggle there is selective structural change in brain areas underpinning the complex processing of visual motion (Draganski et al., 2004). That neural plasticity happens across primates is illustrated by the finding that macaques trained to use tools show increased grey matter in specific regions of their parietal and temporal lobes (Quallo et al., 2009). If neural plasticity occurs in both living humans and macaques as a result of training, it may also have occurred in Neanderthals and their modern human contemporaries, particularly since cortical organisation seems to be more plastic in humans compared to other primates (Gómez-Robles, Hopkins, Schapiro, & Sherwood, 2015).

Since the cognitive processes which individuals engage in habitually appear to influence their brain structure, it seems likely that the more often someone processes complicated social stimuli, the larger and more interconnected their associated brain regions would become (Figure 1). This is indeed the case for macaques: monkeys housed with a larger number of cage-mates show increased grey-matter volume in the specific regions of their temporal and prefrontal cortices that underlie social cognition, as well as more connectivity between them (Sallet et al., 2011). Both personal social network size and the capacity to understand the mental states of others are

associated with the size of analogous areas in humans (J. Powell, Lewis, Roberts, Garcia-Finana, & Dunbar, 2012; Van Overwalle, 2009). In humans these associations between social environment and brain structure are only correlations, so the direction of causality remains unclear. However, the macaques were not free to choose how many conspecifics they lived with and this means that the size of the macaques' social networks *caused* the development of more neural tissue dedicated to processing social information, rather than vice versa (Sallet et al., 2011). Accordingly, given the archaeological indicators that modern humans maintained links with more individuals, neural networks associated with processing social complexity may have been enlarged in modern humans relative to Neanderthals.

Since neural plasticity seems to continue into adulthood, a Neanderthal living in a modern human group and exposed to large dispersed social networks might have developed the requisite neural architecture and sociocognitive abilities to keep track of them. However, it seems likely that the majority of Neanderthals would have remained in Neanderthal groups, and thus would have developed the social brain areas that went along with these less complicated social milieus. In living humans, the fine-tuning of the neural and cognitive processes for handling complex social information continues into early adulthood (Deeley et al., 2008; Dumontheil, Apperly, & Blakemore, 2010). Consequently, if

Neanderthals matured more quickly than modern humans (Smith et al., 2010), this might have limited the refinements they could make to cognitive processes dealing with social complexity. In contrast, modern humans were interacting within the context of more extensive social networks throughout their longer adolescences, and would have developed larger and more interconnected 'social brain' structures to cope with this added social complexity. Although the issue of causality requires much further debate (cf Bruner & Iriki, 2016), even if neurological differences were not the initial reason for differences in social complexity between these taxa, they would have arisen as a consequence.

Virtual worlds

Although Neanderthals and their modern humans contemporaries had similarly large brains in terms of absolute volume, this does not necessarily mean that they were organised identically. For instance, Pearce et al (2013) proposed that modern humans had smaller visual brain areas compared to contemporary Neanderthals and therefore that more of the modern human brain could be taken up with processing of social information, allowing modern humans to deal with greater social complexity, including larger cohesive groups. The suggestion of differential brain organisation is supported by external brain shape differences between Neanderthals and modern humans that are present from early postnatal development (e.g.

Gunz, Neubauer, Maureille, & Hublin, 2010). I have suggested that differences in brain structures underlying social cognition might arise through training, but such early ontogenetic cranial differences between modern humans and Neanderthals seem to suggest that these brain differences were inherited traits rather than purely being the result of varying (social) environments. It is possible that as modern humans started to disperse out of Africa and across the globe, adaptive learning (and neural changes associated with such learning) allowed them to increase their fitness by enlarging their social networks (illustrating the Baldwin Effect: Sznajder, Sabelis, & Egas, 2012). This enhanced social capacity might then have become inherited through genetic (selection for gene variants that either coded for enlargement of 'social brain' regions per se, or for genes that regulated phenotypic plasticity and sensitivity to the social environment) or epigenetic (changes of gene expression driven by environmental factors) processes (see Bruner & Iriki, 2016). Whatever the exact mechanism, interactions between social environment, neural architecture and sociocognitive capacity (Figure 1) are likely to have occurred throughout hominin evolution.

If, as the archaeology suggests, modern humans had larger social networks and more complex social environments compared to Neanderthals, we might expect differences in 'social brain' areas in the frontal and temporo-parietal regions. Although both Neanderthals and modern humans display wider frontal lobes than

other hominins (Bruner & Holloway, 2010), there is some suggestion that modern humans had relatively wider orbitofrontal regions (Bastir et al., 2011) as well as differences in their temporal lobes that might reflect differing mentalising and social memory capacities between these taxa (Bastir et al., 2011; Bastir, Rosas, Lieberman, & O'Higgins, 2008; cf Olson, McCoy, Klobusicky, & Ross, 2013). However, frontal and temporal morphology is influenced by other regions of the skull, so these apparent differences may be associated with secondary structural variations rather than neural function (Bastir, Rosas, & Kuroe, 2004; Bruner & Ripani, 2008; Lieberman, Ross, & Ravosa, 2000).

Despite these controversies, what is generally accepted is that modern humans have larger upper parietal lobes than Neanderthals (Bruner, 2010a; Bruner, Manzi, & Arsuaga, 2003). The upper parietals have strong connections to the frontal lobe and integrate multimodal information to represent an individual's body and the world (Bruner & Iriki, 2016; see Bruner et al, n.d., this volume). The superior parietal lobule is involved in working memory tasks requiring information manipulation, visual attention and spatial orientation (Culham & Valyear, 2006; Koenigs, Barbey, Postle, & Grafman, 2009), and the intraparietal sulcus dividing the superior and inferior parietal lobules is thought to play a role in directed action and interpreting the goals of others, visuospatial working memory, and processing symbolic numerical information (Cantlon,

Brannon, Carter, & Pelphrey, 2006; Hamilton & Grafton, 2006). In addition, the retrosplenial cortex (RSC) is linked to navigation, episodic memory of recent autobiographical information, and planning (Vann, Aggleton, & Maguire, 2009). Moreover, the medial precuneus is involved in reflective self-awareness as part of the 'default mode network', which is active during daydreaming, thinking about the past, or planning, and overlaps 'social brain' areas associated with understanding others (e.g. Cavanna, 2006; Land, 2014; Mars et al., 2012). Peer et al (2015) found that both differentiated and overlapping areas in the precuneus and inferior parietal lobes are activated when someone is orientating to a person, to space and to time, forming *"a specific brain system with a highly ordered internal organization, closely related to the default-mode network"*. Although the default mode network was active for all three orientation domains, it particularly overlapped with brain areas linked to person-orientation in terms of thinking about how emotionally close another individual is to oneself (Peer et al., 2015). In sum, the upper parietal cortex integrates memory with the manipulation of sensory information to allow navigation, mental orientation towards other people and interpretation of their goals, as well as replaying of past events and simulation of possible future ones. As I discuss further below, these spatial integration, memory and imaginative functions are likely to be imperative to cognitively representing a dynamic and extensive social network distributed across space, whose membership needs to bear each other in mind in order to maintain social connection despite only infrequently

meeting face-to-face (see also Bruner et al, n.d., this volume). Parietal differences between hominin species might point to differences in the ability to do this.

However, a note of caution is required is relation to interpretations of the fossil record with regard to parietal anatomy and function: since both the precuneus and the RSC are located deep within the brain, it is impossible to study their anatomy directly from fossil endocasts. Nonetheless, recent work indicates that precuneal morphology has a strong influence on midsagittal geometry and that much of the difference in mid-brain morphology between humans and chimpanzees is attributable to differences in the size of the precuneus, which is enlarged in humans (Bruner et al., 2014; Bruner, Preuss, Chen, & Rilling, 2016). These findings suggest that internal differences in parietal organisation do affect surface shape. Consequently, external differences between the parietals of Neanderthals and modern humans are likely to reflect internal differences as well.

Given their associated functions, the larger superior parietal lobules of modern humans are likely associated with an enhanced capacity to create a 'virtual inner reality' compared to other hominins (though it should be noted that Bruner, Román, de la Cuétara, Martin-Loeches, & Colom, 2015 did not find associations between precuneal size and some cognitive abilities *within* living humans).

Such an ability as this would support individuals to take account of absent social partners in decision-making, as well as in the spatial tracking of network members across a home range (that is, knowing where they are), and the navigation required to travel to their location to meet them. For instance, Burke (2012) argues that modern humans translated egocentric navigation based on detailed knowledge of the local landscape into a cognitive representation resembling an aerial map (interestingly, the RSC has been associated with switching between these egocentric and allocentric frames of reference: Vann et al., 2009). If correct, such a shift in spatial perspective may have allowed modern humans to mentally map their social partners across the landscape and be able to find them more easily if the need arose. The development of such search and navigational abilities would have required abstract spatial representation and the capacity to follow ordered sequences of navigational cues, processes involving various regions of the parietal lobe. In addition, a distributed cognitive system may have developed through pooling information on the changing spatial distribution of the collective network: for example, through different residential bands sharing gossip on encountering each other (Hills et al., 2015). Repeated engagement in these visuospatial cognitive processes is likely to have been accompanied by upper parietal enlargement.

Spatial cognition is not only relevant to social network maintenance in terms of locating members, but also seems to be key to cognitive

processes underlying face-to-face social engagement, such as empathy: mentally ‘putting yourself in someone else’s place’. For example, the way in which another’s body is represented in relation to the self seems to drive associated attitudes, and increasing the sharing of bodily representations has been shown to increase positivity to members of an out-group (Maister, Slater, Sanchez-Vives, & Tsakiris, 2015). Differences in spatial cognition between Neanderthals and modern humans may thus also hint at differences in the degree of self-other distinction and associated interpersonal traits such as empathy.

As well as tracking the spatial distribution of their network, hunter-gatherers need to factor-in absent partners during their current interactions. This would engage at least the precuneus/RSC (incorporating social memories and planning) and the intraparietal sulcus (visuospatial integration to understand the goals of self and others) (Bruner et al., 2014). The more social partners an individual needs to keep in their mental picture, the more complicated that picture and the larger the precuneus/RSC and intraparietal sulcus required. In addition, individuals need to visualise social partners despite interference from their current surroundings, requiring enhanced working memory and focused attention (e.g. Coolidge & Wynn, 2005). Again, this extra cognitive burden on working memory would probably require enlarged superior parietals. Overall, the larger parietal lobes exhibited by modern humans, and in

particular the expansion of the precuneus, may be linked to their more complex social environments, which would have required the development of enhanced capacities for imagination, including complex processing of spatial and goal-related information (Bruner, 2004; Bruner et al., 2016; Coolidge & Overmann, 2012).

The lateral widening of the Neanderthals' superior parietal lobules (Bruner et al., 2003), implies that Neanderthals may have found off-line thinking easier than their *Homo heidelbergensis* ancestors. However, Neanderthals do not show upper parietal enlargement to the same extent as modern humans and thus may have been less specialised for spatial and social processing (in terms of keeping track of the spatial distribution of their social network and taking account of absent social partners in their decisions). As mentioned above, although this parietal difference could be purely developmental, arising each generation in response to social environments, over time the globularisation of the modern human brain associated with enlargement of the precuneus (Bruner et al., 2014), seems to have become an evolved trait that arises soon after birth and deviates from the general allometric hominin trajectory (Bruner et al., 2003; Gunz et al., 2010). Either way, it is likely that the complexity of the social environments inhabited by Neanderthals and modern humans would have been manifested in their respective brain structures, and this in turn may have fed back into differential cognitive limits on social network size (Figure 1).

Although testing the hypothesis that differences in social environment drove brain differences between Neanderthals and modern humans would be challenging to say the least, some of the underlying claims could be investigated. Firstly, future work could explore whether better visuospatial capacities, particularly in relation to keeping track of conspecifics across space and time, in extant primates is associated with greater social complexity: the expectation would be that primate species with larger groups and/or fission-fusion social systems would have greater abilities of visuospatial integration, particularly in relation to social stimuli (for instance, in knowing the relative locations of conspecifics). However, solving how to collect comparable data on visuospatial capacities across species might prove challenging. Secondly, the hypothesis that better performance on visuospatial tasks is linked to having (i) larger networks and (ii) more spatially distributed social networks could also be tested within humans. For instance, one might expect mobile hunter-gatherers to out-perform individuals whose social networks are more clustered and sedentary: individuals who see the members of their social network regularly face-to-face (for example because they all reside in the same local area) might not develop their visuospatial abilities to the same extent as individuals who need to keep track of a spatially dispersed network. Thirdly, whether larger parietals are linked to larger social groups or networks, and greater visuospatial abilities, could be tested both across extant primate species and in humans (though the work of Bruner et al., 2015 suggests that this might not be the case in the

latter). Fourthly, longitudinal studies could examine whether childhood social environments impact on adult visuospatial abilities and brain morphology.

Cognitively different, but not stupid

Although the initial portrayal of Neanderthals as stupid proved incorrect, this does not necessarily exclude the possibility of some cognitive differences existing between Neanderthals and modern humans (Langbroek, 2012; Wynn, Overmann, & Coolidge, 2016). Since Neanderthals and contemporary modern humans exploited similar resources using similar subsistence strategies, regarding 'technical' cognition there may be little difference (Villa & Roebroeks, 2014). However, Neanderthals and modern humans still may have differed in their abilities to process complex social information. That social and technical intelligence relate to different cognitive domains is supported by the finding that chimpanzees do as well on mechanistic tasks as 2.5-year-old humans, but perform significantly worse on social tasks (Herrmann, Call, Hernàndez-Lloreda, Hare, & Tomasello, 2007). Moreover, individuals with autistic traits are often good at understanding abstract concepts and mechanisms ('technical' cognition) but either fail, or show marked developmental delays in passing, tasks requiring understanding others' mental states or identifying the emotional expression on human faces ('social' cognition) (Baron-Cohen, 2009). Given their

different social environments, Neanderthals and modern humans likely differed in their capacities to cognitively process social complexity.

Having the cognitive capacity to sustain more extensive social networks would have had a number of implications for modern humans. Even if differences with Neanderthals were initially relatively small, the impact of the associated effects would have built up over time. Firstly, larger modern humans social networks would have meant that contact could be kept with a greater number of bands inhabiting distant areas, providing more independent sources of help if local resources failed. Although Neanderthal bands could take refuge in new areas as well, without social ties to resident groups the incomers would have lacked local knowledge and up-to-date information about resources in those unfamiliar areas. Even if they could find available resources, they would risk violent altercations with other groups in order to access them and in such intergroup conflicts they would suffer through having fewer supporters to rely on to provide reinforcement. In contrast, if modern humans encountered competition for resources, they could either call on more coalitionary partners for support in order to win through brute force, or they could access resources in other areas where they knew friendly groups.

Secondly, larger modern human social networks would have been less vulnerable to demographic instability, for example by providing a larger pool of mates. In addition, any deaths would have had a proportionally smaller impact on the availability of individuals to forage, reproduce and provide specialist knowledge. A large social network thus decreases the risk of local population extinction and, ultimately, species extinction.

Similarly, larger social networks are associated with a decreased risk of losing cultural innovations and information due to a larger pool of experts and innovators, boosting the development of cumulative culture (Henrich, 2004; A. Powell, Shennan, & Thomas, 2009). In contrast, it may be that cultural innovations made by some local Neanderthal groups never spread or persevered due to their small social networks. Moreover, constraints on transmission of cultural innovations may have further limited Neanderthal network size, since exchange of 'symbolic' artefacts is a well-established means of sustaining social ties (e.g. Pearce, 2014). Taken together, these implications suggest that the ability to sustain larger social networks, particularly through 'offline' thinking, was a crucial factor in why modern humans could survive both unpredictable environments and intergroup competition for resources.

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Figure 1: The proposed interaction between social environment, neural architecture and sociocognitive capacity.