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Interpopulational variation in human brain size: implications for hominin cognitive phylogeny

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ABSTRACT: Throughout the hominin lineage brain size is believed to have increased threefold – increase which, it is argued by some researchers, results in the enhanced brain power that distinguishes humans from any other living being. However, as we demonstrate in this article this supposed increase is the result of comparing the species mean of contemporary humans with other great apes and fossil hominins. This method obscures both interpopulational variation among modern humans, and the fact that the putative increases in the mean are the result of an increase in the upper limit in some populations, which has the result of obscuring the relative stasis in the lower limit over the last 600k years. For example, populations such as Aboriginal Australians have a range that is more different from Danes than it is from that of Asian *H. erectus* over the last 600ka. Yet Aboriginal Australians, whose unique anatomy seems to be related to the climatic conditions of Australia, possess all of the socio-cognitive traits characteristic of all other modern-day populations – yet they seemed not to have undergone increase in brain size to the degree that many other populations have. In this instance brain size seems to be unrelated to cognition. In this article we present a statistical analysis of interpopulational variation in contemporary humans and why such an analysis is crucial for our understanding of hominin cognitive, social and technological evolution. We also suggest how such variation may add to our understanding of hominin ontogeny or life history. Additionally, we develop a model based on humanity's unique form of embodied social cognition that results from our upright bipedal posture and hand morphology. This model is then used to explain the results of our statistical analysis and the possible factors underpinning the human emergence.

KEY WORDS: Brain size, variation, cognition, archeology, embodied cognition, life history, *H. erectus*

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Interpopulational variation in brain size and the fallacy of comparing species means

The hands are intelligent and full of silent knowledge
(Lundborg 2013, p. 49)

In the literature on human brain size it has been frequently cited that the average cranial capacity for *Homo sapiens* is approximately 1400 ml. This had led to the view that our brain is three times the size of other great apes such as chimpanzees and early hominins such as the Australopithecines (Diniz-Filho et al. 2019; González-Forero and Gardner 2018; Verendeev and Sherwood 2017). It has also been argued that such increase is related to our enhanced brain power – power that distinguishes humans from any other living being (Diniz-Filho et al. 2019). However, when the range of variation of different populations of modern humans is taken into consideration, the validity of such assertions becomes problematic. For example, when considering the lower limit of brain size in modern humans, there are many people who have the full range of human cognitive adaptations, but whose brains are less than twice that of the upper limit of the chimpanzee brain. That is the upper limit of chimpanzee brain size is 500g/ml yet numerous modern humans have brain size below 900 g/ml (Hechst 1932; Tobias 1971: 36)[1]. For those researchers who propose a threefold increase in brain size is what distinguishes humans from other primate species, it is incumbent upon them to explain how numerous modern humans possess the full suite of cognitive adaptations characteristic of our species without having undergone so much as a twofold increase in brain size.

There are three issues which we will explore in this article which seem to have led to a misunderstanding among researchers studying brain evolution. The first is comparing the species means of *H. sapiens* with both earlier hominins such as *H. erectus* as well as with other great apes. Secondly, and related to this issue, is the failure to adequately explore how certain populations of modern humans differ from one another more than they do from fossil hominins. Thirdly, the increase in the species mean for *H. sapiens* seems to be a result of an increase in the upper limit relative to earlier species such as *H. erectus*, whereas we do not see a corresponding increase in the lower limit. Further, as we demonstrate, some populations of modern humans show very little increase in the lower and up-

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[1] In order to undertake the analysis in this paper, we used data from different populations that were reported using different systems of measurement such as grams, cubic centimetres or millilitres. This does not present any significant problems. For example, various researchers report cranial capacity measured in millilitres (equivalent to cubic centimetres) or brain weight measured in grams. However, given cranial capacity measured in millilitres is numerically similar to brain weight measured in grams – that is specific brain density is about 1.036 g/ml (Haug 1987) – we felt justified in making a comparison of different populations using both of these measures. Jerison (Jerison 1973) and Martin (Martin and Martin 1990) produced different equations for converting mammalian brain weights to endocranial capacities, but their use produces differences of the order of 5% while precise estimates may differ depending on internal morphology of the braincase and its overall size. Therefore we assume that details of how brain size was measured in various samples, will not obscure obvious, extensive similarities and differences in brain size distributions of those samples.

per limits when compared to samples of *H. erectus* over the last 600ka.

One of the factors involved here seems to be an overrepresentation of Europeans in many samples. For example, Beals and colleagues have argued that the figure of 1400ml noted above results from using larger brained Europeans as a model and that when non-European populations are included 1350 ml is more accurate (Beals et al. 1984, p. 305). In this context it is worth noting that Schoenemann estimates the range of cranial capacity for *Homo sapiens* as being between 1156 and 1775 ml (Schoenemann 2013). However, if this putative species range is compared with non-European samples a very different picture emerges. For example, it has widely been noted that Aboriginal Australians have cranial capacity significantly smaller than Europeans, which is most likely related to subsistence patterns and smaller body size associated with specific adaptations to Australia's unique climate and ecology (Beals et al. 1984; Harper and Mina 1981; Smith and Beals 1990; Woollard 1929). These differences are evident when we compare the range and variation of Aboriginal Australian and European samples and how these samples compare with putative species ranges and means. For example, in a sample of 63 adult Aboriginal Australians, with a range from 943 ml to 1399 ml (Milicerowa 1955), 44.5% of those individuals have a cranial capacity below Schoenemann's lower limit of 1156 ml. This indicates that putative species averages or ranges may tend to obscure the significance of interpopulational variation in models of human brain evolution.

One of the main aims of this study is to critically analyse the differences evident between Europeans and other populations of *H. sapiens* and the relevance of this variation for our understanding of brain evolution. For Europeans we acquired data on Danes (Pakkenberg and Voigt 1964) and Hungarians (Toth 1965). The importance of interpopulational variation is evident if we compare the above Aboriginal Australian sample with a range of 943 ml to 1399 ml (Milicerowa 1955) with these European populations. For example, Pakkenberg and Voigt reported over one thousand Danish brains with a range of 1298–1713 g for males and 1120–1393 g for females (Pakkenberg and Voigt 1964). Significantly, the Australian sample comprises 38 males, 29 (76%) of which are below the Danish lower limit of 1298 ml, with the smallest being 1074 ml. With the Australian females out of 28 individuals 20 (62.5%) are below the lower limit of the female Danish sample of 1120 g/ml. The smallest Australian is a female, having a cranial capacity 943 ml. This is 177 g/ml smaller than the smallest female in the Danish sample as well as being 213 g/ml smaller than the putative lower species limit of 1156 ml noted by Schoenemann.

The implications of the Eurocentric bias in sampling intimated by Beals and colleagues are thrown into stark relief by these comparisons. It should be noted that these population level differences in cranial capacity were used in the past to justify racist ideologies and the hierarchical ranking of human groups according to putative correlations between brain size and intelligence (Gould 1996). This view is now rejected by contemporary theorists of human evolution, with interpopulational variation in brain size most likely being related to differences in body size and the attendant thermoregulatory responses to different climatic zones (Beals et al. 1984). However, brain size is still considered to be important to human evolution with the above-mentioned increase assumed to be relevant to humanity's unique cognitive power. It should also be added some authors have developed a two-step model, where brain size fell within the range of modern humans at 300ka, but fully modern cognition as indicated by globular skull and brain shape evolved between 100–30ka (Neubauer et al. 2018).

What is significant in this context is that numerous theorists, in contrast to the above reserachers, have argued that human social and cognitive uniqueness is not necessarily related to encephalisation but to changes in breeding and social systems and the up–regulation of prosocial neuro-chemicals that occurred prior to increases in brain size in *Homo erectus* (Clark and Henneberg 2017; Hawkes 2006; Isler and van Schaik 2012; Lovejoy 2009; Raghanti et al. 2018). This perspective, grounded in the evolution of social structure as opposed to individual brains, is important as it may help explain why modern humans with cranial capacity below 1000 ml possess fully modern socio-cognitive ability unencumbered by small brain size – in fact unencumbered despite being 1,100 ml below the upper limit for all humanity which is 2,100 ml (Beals et al. 1984).

A similar pattern of interpopulational variation as noted above when comparing European and non-European populations, is also evident when comparing various European populations. For example, Toth's sample of Hungarian measures (N= 6,700) has a female range of 880–1775 g and a male range of 1000–1900 g (Toth 1965). This represents a lower male limit 298 g lower than the Danish male lower limit and for females 320 g lower than the lower Danish female measure. Significantly, Toth's lower limit of 880 g is 276 g/ml below Schoenemann species lower limit of 1156 ml.

Other examples exist of humans with brain sizes lower that 900 g who show no noticeable cognitive and behavioural impairment – for example, as noted by Hechst, an indivdual of normal intelligence was found to have possessed cranial capacity of 850 g (Hechst 1932). Interestingly, the largest recorded cranial capacity of a chimpanzee is 500 ml (Tobias 1971: 36). This measure is only approximately 350ml less than the brain cited by Hechst, 380ml less than Toth's lower limit and 443ml less than the smallest Australian female. In all these cases we have examples of members of *H. sapiens* who have cranial capacity less than double that of larger brained chimpanzees, and far less than the tripling in size often suggested based on species means. The implication is that these people possess the complete suite of socio-cognitive adaptations characteristic of modern humans without having tripled the chimpanzee upper limit – in fact they have not even doubled it. The implication is that human socio-cognitive uniqueness cannot be explained by brain size expansion alone. Additionally, in describing that uniqueness we would also need to explain why small brained members of *H. sapiens* do not differ significantly from their large brained counterparts in cognitive capacity despite very large differences in brain size. Or to put it another way: why are very small and very large brained members of *H. sapiens* similar in their socio-cognitive adaptations despite being over 1000 ml different in relation to the upper limit of chimpanzees and differing from each other by more than 100% in brain size (that is 880 ml compared with the upper limit for humanity of 2100 ml)? That is the largest chimpanzee brain is more similar to that significant portion of humanity with small brains than those small brained humans are to many large brained members of *H. sapiens*.

One of the consequences of pooling different populations of modern humans and comparing the species mean with fossil hominins, is it obscures the relative stasis in the lower limit of brain size over the last 600ka. As we will illustrate in the statistical analysis that follows, while the upper limit for *Homo sapiens* exceeds the upper limit of *Homo erectus* over the last 600ka by more than 500 ml, the lower limit for *Homo sapiens* and *Homo erectus* is virtually the same. This means the putative increase in mean brain size is the result of an increase in the upper limit which changes the mean despite very little change in the lower limit. And that increase in the upper limit seems to be in part due to the very large brains of some European populations with large body sizes relative to other populations.

For example, the Danish sample ranges from 1120 to 1713 g (Pakkenberg and Voigt 1964), the Hungarian sample from 880 to 1900 g (Toth 1965) while the Australian Aboriginal sample ranges from 943 ml to 1399 ml (Milicerowa, 1955). These ranges can be compared with Schoenemann's sample of Asian *H. erectus* over the last 600k years which is 876–1225 ml (Schoenemann 2013). The largest difference with *H. erectus* is represented by the Danish sample where both the lower and upper limit are significantly higher – although the upper limit more so than the lower limit – that is 876 g/ml and 1120 g/ml for the lower limit which is a difference of 244 g/ml while the difference in the upper limits of 1225 and 1713 is 488 g/ml. However, the Hungarian sample shows very little difference in the lower limit compared with *H. erectus* – but a significant increase in the upper limit. For example, the Hungarian lower limit of 880 g is virtually the same as the *H. erectus* lower limit of 876 ml while the upper limit of 1900 g represents a 675 g/ml increase. Significantly, the Aboriginal Australian upper and lower limits differ very little from those of the *H. erectus* sample – that is the range for the *H. erectus* sample is 876–1225 ml while the Aboriginal Australian sample is 943–1399 ml. In this instance there is only a 67ml increase in the lower limit and 174ml increase in the upper limit – which contrasts with the Danish difference in the upper limit when compared to *H. erectus* of 488 g/ml and the Hungarian increase 675 g/ml. This suggests that the apparent increase in mean brain size in *H. sapiens* may be at least in part explained by a greater increase in the upper limit relative to the lower limit– an increase that seems to be more pronounced in European populations. And this increase in the upper limit is going to change the mean, with this mean obscuring relative stasis in the lower limit.

Brain size, life history and cognitive archaeology

The issues we analyse in this article relating to brain size evolution provide fresh ways of thinking about cognition, the archaeological record and the evolution of hominin life history – which as we will suggest are interrelated phenomena. In this section we will briefly explore research in cognitive archaeology, hominin life history and other potential factors that may explain humanity's psycho-social uniqueness that are not dependent on brain size. Then we will move on to a statistical analysis of our data set, which will be followed by a discussion of the implications of our results for our understanding of the human emergence.

The evolution of the hominin brain has important implications for how we understand our unique adaptations as a species. The rise of contemporary technological and scientific accomplishments has its original genesis in the first hominin tool makers, which are believed to have existed among Australopithecines which have cranial capacity within the chimpanzee range (Harmand et al. 2015; McPherron et al. 2010). Given such tool making presupposes a specific hand and locomotor morphology it is worth considering the degree to which the unique nature of hominin anatomy facilitated technological innovation (Lundborg 2013). The approach we develop finds support from the field of embodied cognition, which postulates human cognitive capacities emerge not so much from the brain itself but from the brain's existence within bodies which are themselves embedded in the objective world of nature (Chemero 2011; Gallagher 2006; Grafton 2009; Stewart, Gapenne and Di Paolo 2014).

Also important for our analysis is research in the field of cognitive archaeology which has sought to link the evolution of the human brain to artefacts in the archaeological record in order to determine the cognitive capacities of the hominins who made those artefacts (Coolidge 2009; de Beaune, Coolidge and Wynn 2009; Pargeter et al. 2019; Stout et al. 2018; Stout et al. 2015). Significantly, one of the contributing factors to the emergence of such technological innovations is believed to be the increase in brain size throughout hominin phylogeny (de Beaune et al. 2009, pp. 15 and 115). We will also provide a critique of this position.

Other important research germane to these issues are studies that have found strong correlations between brain size and various milestones of primate development – correlations which can help illuminate the evolution of hominin life history. For example, a relationship between cranial capacity and the uniquely hominin life history pattern has been postulated, with cranial capacity being taken as a possible means of estimating life history milestones such as age of first birth in extinct hominins (Bogin and Smith 1996; Smith, BH 1991; Smith and Tompkins 1995). Significantly, it has been argued that an extension of ontogeny, which resulted in a childhood phase of development during which social learning could occur characterised *H. erectus* – an extension of the period of learning that seeks to account for evidence of complex tool manufacture in the archaeological record (Bogin 2003; Sterelny 2012). It has also been argued that an adolescent stage of development may have evolved in later *H. erectus* during the middle Pleistocene as 'life histories near those of living humans would be expected to arise as hominid brain size crested 1000 cc' (Smith and Tompkins 1995: 264).

Additionally, researchers have argued that cooperative or allo-parental care of offspring characterised the social and breeding system of *H. erectus* – a system which is believed to underpin both the increases in brain and body size we see in this group of hominins as well as its putative demographic expansion out of Africa (Hawkes and Coxworth 2013; Hrdy 2009; O'Connell et al. 1999). Such increases in brain and body size are also thought to be associated with an extension of ontogeny which requires increased metabolic allocation to infant and childhood growth from other individuals of the social group in addition to the mother. (Clark and Henneberg 2015). Additionally, it has been argued that such changes in social and breeding systems were necessary prerequisites for the demographic expansion of the genus *Homo* out of Africa and into the unoccupied temperate and tropical regions of the Old World (Hawkes and Coxworth 2013). Further, it has also been argued that *H. erectus* possessed high levels of phenotypic plasticity that enabled modification of development in response to environmental conditions (adaptability), resulting in variation in adult anatomy that is not genetically canalized (Antón et al. 2016). In this sense, changes in life history and the plasticity enabling adaptation to myriad environmental niches, are thought to be associated with the demographic expansion of *H. erectus*. It is important to note that such plasticity did not evolve in a brain abstracted from bodily, social or natural processes, but unfolded in the context of a rich interaction between cognition, the body and the objective world.

In support of such an embodied conception of hominin phylogeny, it is worth noting the significant anatomical and behavioural similarities between *H. sapiens* and *H. erectus*, which suggest the possibility of similar abilities associated with the manufacture of lithic technologies; as one group of researchers writes when commenting on similar tool making abilities in modern humans and ancient hominins: '*…past and modern humans share a common body structure and the same physical constraints*' and that consequently the uniformity '*between current and extinct populations can provide a fundamental way of understanding manufacture technologies of stone tools from all periods.*' (Chen and Chen 2016, p. 93). Significantly, the ability to learn how to manufacture complex Acheulean technologies of the kind *H. erectus* is presumed to have made, is thought to require an extended life history akin to modern humans – that is a period of apprenticeship during which culturally accumulated technical knowledge is transferred from one generation to the next (Sterelny 2012).

However, other researchers have argued against the existence of such affinities, claiming for example that *H. erectus* had not yet evolved a modern life history pattern. This position is based on comparison of measures of perikymata in the detention of modern humans and *H. erectus*. This research suggests that the growth curve of *Homo erectus* was unique, that it differed from that of modern humans in the direction of chimpanzees and that truly modern dental development emerged relatively late in human evolution (Dean et al. 2001; Dean and Smith 2009). Additionally, compared with chimpanzees, neocortical myelination is developmentally protracted in humans, with slower myelination during childhood and a delayed period of brain maturation that extends beyond late adolescence (Miller et al. 2012). Based on such findings, it has been argued that a significant amount of adaptive changes affecting the brain most likely took place in the past '*few hundred thousand years along the evolutionary line leading to extant modern humans*' and that consequently the '*life-history pattern and brain ontogeny of extant humans emerged only recently in the course of human evolution*' (Hublin et al. 2015, pp. 8 and 1). Additionally, the extension of ontogeny throughout hominin phylogeny that resulted in an adolescent stage of development is believed to be unique to *Homo sapiens* (Bogin 2003). In contrast to researchers who propose a modern life history pattern was evident in *Homo erectus*, these theorists argue it is a recent evolutionary innovation unique to *Homo sapiens*.

It is unclear from the extant literature which of the above two views is correct. However, evidence of the complex tool making capacities of *H. erectus*, the attendant capacity for nuanced spatial cognition and prescriptive technical procedures, and the associated social structures facilitating intergenerational transfer of such skills, suggests these early hominins may have possessed cognitive, social and behavioural traits we associate with modern humans (Chen and Chen 2016; Shen et al. 2016; Sterelny 2012)

In this paper we are interested in exploring variation in cranial capacity that exists between populations of *Homo sapiens* in order to explore the degree of overlap evident between *Homo erectus* and specific populations of *Homo sapiens*. Such an analysis offers an alternative to models that compare only the species means of *Homo erectus* and *Homo sapiens* – models that may underestimate overlap in variation that becomes evident when specific populations are compared with *H. erectus*. We also argue such an analysis is important for our understanding of hominin life history, social psychology and technological development. More specifically, if it is shown that populations of *H. sapiens* overlap with *H. erectus* to a degree significantly greater than species means would suggest, there is also a possibility that life history patterns may also have overlapped. Consequently, this analysis may contribute to the debate as to when in hominin phylogeny a modern form of life history and cognitive ontogeny emerged.

Materials and Methods

Our aim in this study is to compare specific *H. sapiens* populations with fossils of *H. erectus*. We obtained data from the literature on individual cranial capacities, dates and locations of *Homo erectus* specimens (Rightmire 2013; Schoenemann 2013)(Appendix 1), Ugandans (Górny 1957), medieval Polish (Wokroj 1953) and Aboriginal Australians (Milicerowa 1955). For other populations, such as Danes (Pakkenberg and Voigt 1964) and Hungarians (Toth 1965) data were only available as averages and standard deviations or ranges. Since distributions of human brain sizes do not differ from the normal distribution (Holloway 1980) in order to illustrate overlaps of brain size distributions using these parametric data, we used a random number generator that produced 500 individual datum points for each group based on probabilities of the normal distribution. These distributions were then graphed for comparison. Further, as already noted, our data set contained brain sizes either in the form of cranial capacities or brain weights yet given the two variables are roughly comparable we felt justified in carrying out such a comparative analysis (Haug 1987).

We used these methods to compare samples of all *H. erectus,* Asian *H. erectus* and a more limited sample of Asian *H. erectus* spanning the last 600ka years, with various populations of modern humans. Although a similar analysis could have been performed using different dates and fossils from other regions such as African *H. erectus*, we chose this region and period as it corresponds to the early stages of the Middle Pleistocene. This period in Asia has a rich record of both *H. erectus* fossils, as well as evidence of complex stone tools – artefacts which are believed to be indicative of a flexible adaptation to the mental and technological constructs of tool manufacture that may help evaluate the knapping and cognitive capabilities of early hominins (Li et al. 2014).

To quantify overlaps of brain size distributions in more detail we used Linacre's method (Linacre 1996: 487). This method allows us to calculate the degree of overlap of two normal distributions with different means and standard deviations using combinations of probability distributions of normal curves. We have also determined the overlap between the ranges of brain sizes calculated as the ratio of two values. For example, as can be seen in Table 1, we have presented two measures of overlap with below the diagonal being overlap of distribution and above overlap of ranges. These were calculated as the difference between two arithmetic means of compared distributions divided by three standard deviations of less variable distribution, and, three standard deviations of the more variable distribution. The ratio of the larger of the two values multiplied by 100 to the smaller one is the index of the range overlap.

In our analysis we sought to determine the degree to which *H. sapiens* shows a distinct difference in cranial capacity from *H. erectus*. We also sought to test the hypothesis as to whether such differences justified taxonomic distinctions between the two putative species. Demonstrating such a difference is an important issue in palaeoanthropology as cranial capacity is one of the traits frequently cited when taxonomic distinctions between *H. sapiens* and earlier hominin species such as *H. erectus* are made (Diniz-Filho et al. 2019; Gómez-Robles et al. 2017; González-Forero and Gardner 2018).

Results

Figure 1 illustates the results of our analysis. As can be seen Asian *H. erectus*

Table 1. Overlap in brain size/cranial capacity

	N	Mean	Sd	All humanity	Erectus	Asian erectus	Erectus 600 ka	Aborigines	Uganda	Poland	Danes	Hungarians
All humanity	>10,000	1350	157		52	67	78	95	99	97	100	94
Erectus	33	953	171	27		88	100	96	70	60	61	56
Asian erectus	23	1023	127	33	79		93	81	62	54	54	72
Erectus 600 ka	13	1090	113	33	60	78		85	75	63	63	84
Aborigines	67	1173	106	47	40	50	70		93	76	64	99
Uganda	165	1286	134	82	27	32	40	61		80	80	100
Poland	218	1397	137	79	14	20	20	34	69		93	100
Danes	667	1388	134	89	15	21	21	40	70	98		100
Hungarians	2132	1372	175	95	23	24	30	43	77	89	88	

Overlap between distributions and ranges (Mean ±3SD) of brain size/cranial capacity in various human populations and *Homo erectus*. Distributions (below the main diagonal) and ranges (above the main diagonal).

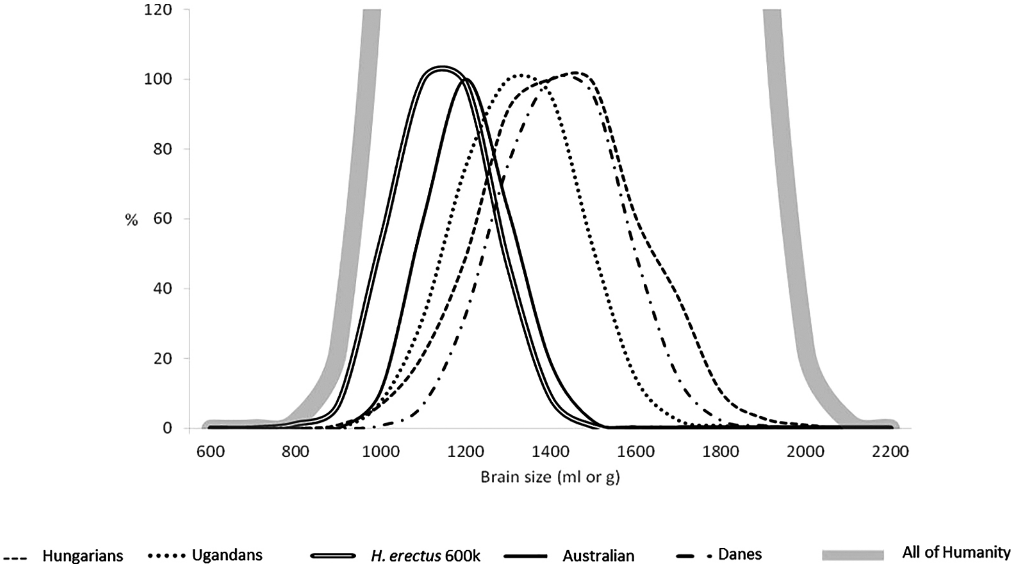

Fig. 1. Brain size distributions in *H. erectus* and various modern populations
Distribution of brain size comparing *H. erectus* with various modern human populations. Note the greater degree of difference that exists when comparing the Danish sample and the Australian Aboriginal sample than when comparing the Aboriginal sample with *H. erectus*. This greater degree of overlap between specific populations of *H. sapiens* and *H. erectus* when compared with that evident between specific populations of *H. sapiens*, should not occur if cranial capacity were the defining feature of modern humans.

from the last 600k years shows signficant overlap with all popualtions of *H. sapiens*. However, this overlap is less pronouced in the two European samples than in the Ugandan and Aboriginal Australian samples. For this reason, in the interest of clarity of presentation, we have not shown the distribution of Polish cranial capacities in Figure 1 as it overlaps with the two other European distributions – however we do include the Polish smaple in our more detailed analysis of overlap in Table 1. Further, out of all the popualtions analysed, the Aboriginal Australian sample has the largest amount of overlap with *H. erectus* with a mean that is closer to *H. erectus* than either of the European samples.

In Table 1 we present the results of our more detailed analysis of degrees of overlap using Linacre's method (Linacre 1996: 487). What is worth noting below the diagonal, where we have illustrated overlap of distributions, is the differences in the degree of overlap when comparing different modern populations with *Homo erectus*. For example, the Polish sample has the least amount of overlap with Asian *Homo erectus* of the last 600ka with just 20%. The Danish sample has 21%, with Hungarians 30%, Ugandans 40% and Aboriginal Australians 70%. Significantly, when we look at the overlap between the populations of *Homo sapiens* – for example between Europeans and Australians – we find the Polish sample overlaps with Australians the least with a measure of 34%, Danes at 40% and Hungarians at 43%. The Ugandan sample shows greatest overlap with the Australian sample with a result of 61%. And when we compare different European populations the degree of overlap is much greater than when comparing those populations with non-European populations – for example Danes overlap with Poles at 98% and with Hungarians at 88%.

The significant observation about these results is that the Aboriginal Australian sample overlaps with the *Homo erectus* sample more than it does with the Danish sample. For example, the overlap between the Australian sample and *Homo erectus* sample is 70% whereas the overlap between Danish and Australian sample is 40%. This means that the differences between two distinct populations of *Homo sapiens* are significantly more than the differences between one specific population of *Homo sapiens* and our sample of *Homo erectus*. In other words, the Aboriginal sample shows greater affinity with *Homo erectus* than with Danes. Similar conclusions can be drawn from looking at the overlap of ranges above the diagonal line. Given such overlap between *Homo erectus* and specific populations of *Homo sapiens*, we suggest that species distinctions based on cranial capacity are unwarranted. Of course, other characters may provide evidence for a species distinction between *Homo erectus* and *Homo sapiens* – but the results of our analysis suggest cranial capacity is not one of them.

Some important points flow from these observations. Firstly, when we look at specific popualtions of *Homo sapiens* as opposed to species means, we see signficant overlap with *Homo erectus*. It is important to note that this overlap only occurs at the lower limit of the range for the whole of humanity and at the lower limit of specific populations. Further, while *Homo erectus* shows affinity with the lower range in the *Homo sapiens* dsitrubution, the overlap is evident predomianantly in the Australian sample. Additionally, there is no comprable overlap with *H. erectus* in the upper range of *Homo sapiens* in any of the samples – although, as noted, the upper limit of the *H. erectus* sample and the Austrralian sample are not substantially different. In other words individual members in the lower range of the distribution, as well as populations more genrally in the lower range of *Homo sapiens*, show overlap with *Homo erectus* – yet there is no such overlap in the upper range of the *Homo sapiens* distribution. Another way of framing this phenomenon is that *Homo sapiens* seems to have extended the upper limit of cranial capacity while the lower limit seems to differ very little when compared with *H. erectus* over the last 600k years.

The increase in the upper limit, with signficantly less change in the lower limit, may be related to selection for themoregualtory adaptations to different climatic regimes resulting in interpopulational variation in both body and brain size (Beals et al. 1984). It is worth noting that brain weight and body weight correlations for individuals within a population are weak and insignificant (Holloway 1980; Pakkenberg & Voigt 1964). However, the correlation between brain weight and body weight when comparing populations is quite strong (r = 0.63) which suggests interpopulational variation may be related to regional adaptations to local climate (Beals et al. 1984). This phenomenon may account for the larger brain and body size in the Danish sample when compared with the Aboriginal sample – populations which inhabit very different climate zones. It also suggests that variation in brain size is related to the bodies those brains are contained in and the ecosystems such embodied brains have their existence in.

Our analysis of interpopulational variation when comparing *H. erectus* and *H. sapiens* derives from a Darwinian approach to biological variation. For example, such an approach considers variability as an essential biological feature, which when applied to brain sizes of two putative human species, as opposed to comparisons of means or averages, yields a significant amount of overlap and commonality. Consequently, given such overlap, the hypothesis of cognitive differences between these two species deriving from putative differences in cranial capacity, is falsified.

Implications for Taxonomy and Brain Evolution

The taxonomic distinction between *H. erectus* and anatomically modern *H. sapiens* is based on differences in numerous characters, from putative schedules of dental development, skull shape and cranial capacity to associated life history trajectories (Dean et al. 2001; Dean and Smith 2009; Detroit 2000; Hublin et al. 2015). Our results, however, indicate that such a distinction is not warranted based on the trait of cranial capacity – although such taxonomic distinctions may be valid when considering other traits. Additionally, if a different sample were chosen somewhat different results may be obtained. For example, in Table 1 we have given data for a larger sample of Asian *H. erectus* with a mean of 1023 ml that includes older fossils, as well as a global sample with a mean of 953ml. A comparison of those samples with other populations of *H. sapiens* – which we have not undertaken in any detailed manner – would give somewhat different results.

In this context it is worth noting that in the extant literature on hominin brain evolution, numerous researchers have postulated an accelerating expansion of brain size from *H. erectus*, through so-called *H. neanderthalensis*, *H. heidelbergensis* and present day humans (Diniz-Filho et al. 2019; Gómez-Robles et al. 2017; González-Forero and Gardner 2018).

Our analysis, however, does not support the notion of a brain size based taxonomic distinction between our *H. erectus* sample and modern humans. Further, if we remove the confounding factor of a shift in the upward limit of modern humans – a shift which seems at least in part attributable to pooling large brained and bodied European populations with non-European populations – then the differences between *H. erectus* and specific modern human populations seem less significant than the work of the above researchers would suggest. In other words, when comparing specific populations with our sample of *H. erectus* as opposed to the global mean, the differences between specific populations of *H. sapiens* and *H. erectus* are insignificant.

There are two ways of interpreting our results. The first would involve designating those populations, such as Aboriginal Australian, which show greater affinity with *H. erectus* than the large brained Danish sample, as members of *H. erectus* – a designation it should be added that is only based on the one character of cranial capacity. This option, however, seems problematic for several reasons, not least of which is the fact that we know Aboriginal Australian to be members of the same species as Europeans, with the full suite of cognitive, linguistic and social adaptations characteristic of modern humans.

The second option would involve designating what have traditionally been classified as *H. erectus* as members of *H. sapiens*. This approach was adopted by Campbell decades ago who designated the Ngandong fossils as a subspecies of *H. sapiens* with the nomenclature of *H. sapiens soloensis* (Campbell 1962). Echoing this view, in more recent times it has been suggested that *H. erectus* be included in *H. sapiens* (Henneberg 1990; Wolpoff 1999). Our analysis supports these claims but only in a very limited sense; that is, they only apply to the very specific trait of cranial capacity. It is worth noting however, that in our analysis of globularity included in this issue, we found that skull shape has changed much less in the transition from *H. erectus* to *H. sapiens* when compared with changes in the cranial base. For example, we found significant overlap in skull shape evident between *H. erectus* and *H. sapiens* when compared with differences in the cranial base and mastoid region. This suggests that changes in skull shape are related more to changes in the jaw and associated muscle attachment areas in the base and mastoid region associated with dietary factors, than actual selection on the brain and shape of the cranial vault (Clark and Henneberg, this issue, pp. 467–485). Significantly, these changes seem to be related to dietary factors associated with environmental context, diet and food preparation practices. It should be added that the differences we analyse in this paper seem to be also related to the environmental and climatic context of brain morphology and somatic evolution.

One issue that needs addressing is the confounding factor of brain size reduction throughout the Holocene. This occurred in Africa, Australia and Europe – although it seems to be only about 10% in all cases (Brown 1992; Henneberg 1988; Henneberg and Steyn 1993). This means that earlier populations of *H. sapiens* may have overlapped less with *H. erectus* than modern human populations do and that consequently our results may merely record the effects of more recent Holocene size reduction. However, even accounting for this factor, we still would see significant overlap between earlier populations on all three continents, and despite that overlap being approximately 10% less than the current level, it is still a significant amount. Consequently, our use of modern populations still demonstrates significant overlap with *H. erectus* that would only be reduced but not cancelled if earlier populations were included. Consequently, the problem of size reduction does not seem to undermine our assertion regarding taxonomy and cranial capacity. Additionally, the brains of modern humans are not especially variable neither in comparison to other mammals (Henneberg 1990) nor to earlier hominins (Henneberg and Thackeray 1995) – and given Asian *H. erectus* over the last 600ka sits comfortably within that range, cranial capacity does not seem to be a marker of taxonomic distinction.

From *Australopithecus* to Asian *Homo Erectus*: Archaeology, Embodied Cognition and Social Structure

In this section we briefly explore how brain size, life history and the archaeological record can be approached from the point of view of embodied cognition and the unique locomotor and hand morphology of hominins. As opposed to mere comparisons of brain size with chimpanzees, we focus on how human anatomical structure is unique among primates.

In this context many of the traits which characterise modern humans can also be found in early hominin species such as the Australopithecines – who while having brain size overlapping with chimpanzees differ distinctly in their anatomical configuration. We also explore how this may provide a means of interpreting the results of our data and analysis and the possibility that Asian *H. erectus* possessed cognitive abilities, and associated life history and social structures, akin to those of modern humans.

Researchers in the field of embodied cognition have emphasised the degree to which human cognition is a function of the kinds of bodies we have and how those bodies interact with the social and natural environments we exist in (Chemero 2011; Gallagher 2006; Grafton 2009; Stewart et al. 2014). Such a focus on the unique anatomical structure of human bodies has been developed by theorists focussing on the role of erect bipedalism in the hominin lineage – which not only emancipates the upper limbs and hands from locomotion, thereby facilitating the coevolution of hands and brain, but also enables modulation of the vocal tract and the consequent evolution of language (Clark and Henneberg 2017; Lundborg 2013; Wilson 1999).

What is also significant about our results is that they provide possible evidence that the life history of Asian *H. erectus* over the last 600 ka was little different from modern humans – that is if we accept the correlation between cranial capacity and life history trajectories such as those advanced by other theorists (Smith and Tompkins 1995). While it has been argued that modern human life history trajectories are of recent origin based on dental development and brain maturation (Dean et al. 2001; Dean and Smith 2009; Hublin et al. 2015) other evidence suggests a more ancient origin of the modern life history pattern, evidence that finds further support in the results presented in this study. For example, in contrast to the studies mentioned above, more recent work that takes greater account of the variation in dental development in modern humans, suggests that early *Homo* tooth formation does in fact lie within the range of modern humans (Dean and Liversidge 2015; Xing et al. 2019). Consequently, it has been argued that *'modern human dental growth and development evolved in East Asia before the appearance of fully modern human morphology'* (Xing et al. 2019: 1). Combined with our analysis of cranial capacity, and its putative correlation with life history, this evidence suggests that the ontogeny of *H. erectus* was not in any way different from that of modern humans. This assertion follows from the simple observation that the overlap in brain size evident when comparing specific populations of mod ern humans with our sample of *Homo erectus*, suggests the possibility of a similar overlap in life history trajectories associated with growth of the brain.

One of the ways of testing this hypothesis further would be to collate life history data on various European, African and Aboriginal Australian populations to establish if their maturational rates differ as much from each other as their cranial capacity does. If they did, this would provide indirect but very suggestive evidence that the variation in life history in some modern populations may in fact overlap to a significant degree with that of *H. erectus* in the same way that cranial capacity does. It would also be instructive to compare interpopulational variation in life history or ontogenetic trajectories in modern human populations with putative rates of maturation in *H. erectus*. Such an analysis, however, is far beyond the scope of this study.

Additional evidence that suggests a modern life history pattern was already evident in *H. erectus* comes from archaeological excavations and the field of cognitive archaeology. For example, an increasingly rich archaeological record in China and South East Asia comparable to the African Acheulean, suggests quite advanced tool making capacities associated with spatial cognition and prescriptive procedures as well as enhanced planning and technical competence well before 600k years (Li et al. 2014; Mishra et al. 2010; Pei et al. 2015; Yamei et al. 2000; Yang et al. 2017). Significantly, the ability to manufacture Acheulean tools is believed to require a modern form of spatial cognition (Wynn 1989), the capacity for prospection and goal directed motor control associated with the default mode network (Stout et al. 2015) as well as periods of sustained apprenticeship and the intergenerational transfer of technological and cultural traditions – transfer that may have required an extended period of learning and socialisation of the young akin to that of modern humans (Sterelny 2012).

Additionally, both fossil remains as well as stone tools have been found on Indonesian islands long before 600ka (Brumm et al. 2016). Significantly, colonisation of such islands would have required crossing the sea barrier demarcated by the Wallace Line. In this context it has been proposed that such colonisation would have required quite complex technical skills akin to modern humans such as the building and navigation of maritime craft (Bednarik 2015). Definitive proof for this thesis is yet to be provided – which may result from the fact that perishable materials of the kind used for such craft are unlikely to have survived in the archaeological record. Alternatively, these migrations may have resulted from passive dispersal not requiring complex forms of cognition or technological competencies (Dennell 2014; Leppard 2015).

It should be noted that when considering hominin cognitive evolution the manufacture of specific stone artefacts can only ever provide an indication of the minimum cognitive capacities of their manufacturers (Wang et al. 2012). Additionally, the relative absence of stone-based artefacts in Asia is by no means indicative of technological backwardness, as much of what was needed for everyday life could have potentially been made from perishable plant materials of which no trace is left in the archaeological record. This problem is a particularly acute one for theorists who propose maritime travel across the Wallace Line during the Pleistocene – although it should be noted this hypothesis seeks other forms of evidence that suggest such plant based materials would have been used if such a crossing did occur (Bednarik 2015).

The importance of plant based technologies in the cultures of Pleistocene hominins, is also suggested by data from gathering and hunting societies where spears made entirely from wood are important parts of tool kits, being used alongside stone tipped spears (Allen and Akerman 2015). Further, wooden spears are thought to have preceded the development of technologies based on stone flaking in Australia (Walsh and Morwood 1999). Consequently, it is conceivable that perishable tool industries and the attendant cultural traditions were developed by *H. erectus* prior to the earliest evidence we have of stone tool manufacture. Of course, obtaining direct evidence one way or the other on this issue is difficult – and arguments have been presented for and against non-lithic technologies during the Asian Pleistocene (Brumm 2010; Watanabe 1985; West and Louys 2007). The reason we are highlighting this point is that our analysis is focused on the most recent solid evidence for the minimum cognitive capacities of Asian *H. erectus* – with the caveat that those capacities could have been far beyond what the very meagre archaeological evidence suggests, and potentially of much greater antiquity.

While earlier researchers had assumed that Eastern Asia lacked complex Acheulean tools, and was therefore technologically and culturally "backward" (Movius 1948) more recent research has shown this assumption to be incorrect. For example, traces of intentional manufacture, including striking platforms, bulbs of percussion, and edge modification have been dated to the early Pleistocene (Shen et al. 2011). Similarly, evidence of large-scale flaking of rock followed by intensive retouching, with production of Acheulean-like bifacial forms dated to 800ka is believed to signify an important advance in hominin behaviour involving enhanced planning and technical competence (Yamei et al. 2000).

Accruing evidence of this kind continues to emerge from China indicating quite complex and sophisticated lithic traditions (Kuman et al. 2014; Li et al. 2014; Wang et al. 2012; Yang et al. 2017). Significantly, there is also evidence of increasing complexity of tool manufacture throughout the Pleistocene, suggesting indigenous evolution of lithic traditions may have played an important role in early hominin cultural development in China (Shen et al. 2016). Such evolving traditions presuppose an "informational commons" – that is accumulative knowledge that is not the product of any single individual invention but which individuals inherit as part of their culture's 'essential cognitive capital' (Sterelny 2012: 76).

The internal cognitive representations required to preconceive, plan and execute the multiple steps required to make Acheulean tools are believed to require 'projective and euclidean spatial operations' (Wynn 1989, pp. 89–90). Additionally, fMR studies have suggested Acheulean toolmaking, in contrast to Oldowan, recruits brain regions associated with flexible prospection and planning, learning and social scaffolding, "central executive" working memory and "mental time travel" (Stout et al. 2015). Significantly, mental time travel, which involves the projection of the self into both past and future scenarios, is believed to be fundamental to the hunter-gatherer adaptation that led to the demographic expansion of the genus *Homo* out of Africa and into China some 2 million years ago (Corballis 2019).

The construction of such artefacts is unlikely to have been possible in the absence of intergenerational knowledge transfer, for the skills required to create them would not be acquired by each individual anew but were the result of cumulative cultural accumulation of technological competencies and knowledge. Social pedagogy, whereby such skills are transferred from old to young, is thought to play an important role in hominin technological innovation (Assaf et al. 2016; Bamforth and Finlay 2008; Grimm 2000). If *H. erectus* did possess a complex informational commons this would enable the intergenerational transfer of the technological, social and moral competencies necessary for prosocial cooperative foraging during the Pleistocene – that is the passing of technological and cultural knowledge from the old to the young (Sterelny 2012). Such apprenticeship of the young would be necessary to learn how to manufacture complex tools such as Acheulean hand axes, skills which require significant time to learn and which could not be acquired merely by individual effort or ingenuity. In this context Newton's famous comment that his achievements were due to standing on the shoulders of giants – that is his discoveries were a result of building on past discoveries – would apply as much to *H. erectus* tool makers as modern astrophysicists.

From this point of view, archaeological artefacts are not necessarily evidence of changes in hominin cognition – although these are undoubtably important – but more evidence for changes in the social structure within which cognitive ontogeny unfolds and blossoms. In this sense the social niche or structure in which the brain unfolds may be as important as the actual brain itself – which as we have noted is related to our unique life history configuration, the apprenticeship of young and the unique locomotor and hand morphology that characterises the hominin lineage.

Some researchers have argued that the evolution of unique hominin social structure, which represents a departure from the social structure of the last common ancestor, has very ancient origins in our lineage. For example, some authors have postulated changes in neurochemical pathways, with upregulation of prosocial neuropeptides such as oxytocin, which are central to social and sexual bonding, to have occurred at the base of the hominin clade (Clark and Henneberg 2017; Lovejoy 2009; Raghanti et al. 2018).

Although this perspective is speculative, it does account for the absence of aggressive male canine armoury in early hominins such as *Ardipithecus ramidus*, and the possible redirection of male mating effort from tournament behaviour to provisioning in the context of a prosocial mating and social system (Clark and Henneberg 2015, 2017). Whatever the merits of this model, it does provide the suggestion that a departure from the great ape form of social life occurred very early in the hominin lineage, millions of years before any noticeable increases in brain size and body size. And it is within the context of this social structure that the coevolution of individual brains, bodies and cultures would have developed.

This view is consistent with that advocated by Holloway (1973), who has argued that the brains of early hominins such as the *Australopithecinae* were reorganized to a human pattern despite their small endocranial capacities and that this change formed the basis of consequent selective regimes. As he writes:

> *The subsequent growth of the brain, from the australopithecines to modern man, was paralleled by an ever-increasing expansion of cultural complexity, reflected not only in the inventory and quality of stone tools, but also in the archaeological contexts, which show increased efficiency of hunting, utilization of more and larger animals, and possibly other cultural adaptations such as shelters, storage, and social structural adaptations* (Holloway 1973: 456).

According to Holloway, this process of "complexity management" involves a positive feedback process of continuing adaptation – adaptive processes that involve social behaviours such as less aggressiveness within the group and increased cooperation. Consequently, he argues that the production of stone tools was not necessarily a causal factor in hominin social and cognitive evolution but that they do provide '*clues to behavioural processes that are more extensive in the adaptive sense' involving selection favouring 'social behavioural factors which enhanced co-operative adaptive strategies.*' (Holloway 1973, p. 457). This perspective concurs with the hypothesis discussed above regarding evidence for reduced aggression and increased levels of prosocial behaviour in *Ardipithecus ramidus* – the difference being those authors postulate upregulation of prosocial neurochemicals whereas Holloway suggests neural reorganisation was the decisive factor.

Further evidence for the emergence of uniquely human traits before the increases in brain and body size in *Homo erectus* is putative tool manufacture and possible hunting among *Australopithecus*. For example, stone artefacts with evidence of core reduction with battering activities have been dated to 3.3 Ma (Harmand et al. 2015) while stone-tool-assisted consumption of ungulates by hominins dated at 3.42–3.24 Ma has been attributed to *Australopithecus afarensis* (McPherron et al. 2010).

These abilities seem to be related to more fundamental aspects of hominin anatomical structure, such as erect bipedal locomotion and the attendant upper limb and hand morphology, which unlike other primates, are not used in locomotion (Napier 1993). The emanacipation of the hands from locomotion in erect bipedal hominins, is believed to have resulted in intensified selection for manual manipulation and precision grasping of the kind used in tool manufacture, and relaxation of selection for locomotion using the forelimbs (Almécija et al. 2010; Lemelin and Schmitt 2016; Richmond et al. 2016). Consequently, it has been suggested that human hand proprotions may not have evolved specifically as a reponse to stone tool use, as has been traditionally supposed, but that the relaxation of selection for the use of forelimbs for locomotion resulted in hand moprhology that could be later exapted for stone tool manufacture (Alba et al. 2003). Such maniupulative ability, combined with precise and complex integration of the hands with the brain's cogntive and affective neural systems, is believed to have given rise to human culture – from ancient forms of tool manufacture to classical piano playing, extreme rock climbing and professional juggling (Wilson 1999). This view of human brain evolution, grounded in our erect bipedal posture and unqiue hand morphology, postulates a coevolutinary process between the hands and brain that began at the origin of the hominn clade and which now manifests itself in our extraordinary social and technological comptencies (Lundborg 2013). In this sense what seems to be unique about human cognition is not so much the brain but our singular form of physcial embodiment. This appraoch provides a unique way of intergating paleoanthropology with cogntive neurosceince and attempts to move beyond the mind/body dualism charteristic of Western philosophy and sceince – that is an eco-centric view of cogntive evolution that sees the brain in terms of its embodied realtionship with the spatio-temporal structures of the natural word in which it evolved (Northoff 2018).

From this persecptive the increased technological competencies that developed in the hominin lineage seem to be relatd to erect bipedlaism, upper limb moprhology, changes in life history trajectories and the evolution of unique forms of embodied social cognition – and not nessarily brain expansion or increased cogntive power. This view is supported by evidence that chimpanzees outperform humans in numerical working memeory tasks (Inoue & Matsuzawa 2007) and that it is not general intelligence that distinguishes humans from the great apes, but specific socio-cultural adaptations for co-operative behaviour and social learning (Henrich 2015; Herrmann et al. 2007). Consequently, it has been claimed that our idiosyncratic cognitive ability is not necessarily due to our general intelligence, but a result of the fact that '*our brains evolved and expanded in a world in which the crucial selection pressure was our ability to acquire, store, organize, and retransmit an ever growing body of cultural information*' – a body of information that constitutes the 'collective brain' of culture (Henrich 2015: 5 and 12). Further, such capacity presupposes not only our unique form of embodied cognition but also an extended ontogeny and period of learning – an extension we suggest was already evident in *H. erectus*.

This perspective provides a useful gloss and theoretical orientation to interpret our results. The quite significant overlap between certain populations of *H. sapiens* and our *H. erectus* sample is quite understandable if selection on brain size, and hence increased cognitive power, is not the decisive factor under selection in our lineage. It would also account for why smaller brained members of *H. sapiens*, as well as populations which have a lower mean, do not differ in their socio-cognitive profiles from larger brained populations. The question that needs to be answered by those who argue that a tripling in brain size underpins our unique and increased cognitive power is: why do these small brained members of *H. sapiens* possess the full suite of socio-cognitive adaptations without having undergone such a threefold expansion?

Concluding remarks

If the argument we have presented in this article has any merit, then the question arises as to why the increase in mean cranial capacity seems to have occurred? As we have noted, the increase in the mean of *H. sapiens* cranial capacity is to a large extent due to an increase in the upper limit with a much less pronounced increase in the lower limit relative to our *H. erectus* sample. And this increase in the upper limit seems to be more pronounced in European populations – which may be a result of correlated increases in body size in addition to climatic factors. In this sense both the variation in brain size in *H. sapiens*, as well as the upward trend of the mean in the hominin lineage, may be related to factors impacting general growth trajectories of the body and the brain related to ecological niche and climatic factors. Other factors may include diet as hominins became co-operative foragers, with the increased metabolic allocation to infant and childhood growth that is believed to be a part of a cooperative or allo-parental breeding structure, resulting in larger mean body and brain sizes. Such increased metabolic allocation may have resulted in extension of life history and growth trajectories that would be necessary for intergenerational knowledge transfer – yet such extension would also yield larger brain and body sizes. Of course, none of these factors on their own explain the human emergence – but we suggest they may have been components of a more generalised adaptive suite. Our analysis also provides other researchers with the opportunity to test our hypothesis using different data sets to ascertain its falsifiability – and thereby further our understanding of the nature of the human emergence.

Authors' contribution

GC was the main author and primary researcher. Both authors collaborated on the data collection and analysis. MH assisted with the statistical analysis.

Conflict of interest

The authors declare no conflict of interests.

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Appendix 1

Data on *Homo erectus* cranial capacity used in this study. From Rightmire (2013) and Schoenemann (2013)

Specimen	dating (Ma)	CC (ml)	Location
ER 3733	1.8	848	Kenya
ER3883	1.6	804	Kenya
ER 42700	1.6	691	Kenya
WT 15000	1.5	880	Kenya
OH 9	1.4	1067	Tanzania
Daka	1.0	986	Ethiopia
D2280	1.7	775	Georgia
D2282	1.7	655	Georgia
D2700	1.7	600	Georgia
D3444	1.7	625	Georgia
Trinil	0.9	940	Java
San2	1.5	813	Java
San4	1.6	908	Java
San10	1.2	855	Java
San12	1.1	1059	Java
San17	1.3	1004	Java
SanIX	1.3	870	Java
Ngawi	?	870	Jawa
Sam1	0.8	1035	Java
Sam3	0.4	917	Java
Sam4	0.8	1006	Java
Ng1	0.1–0.5	1172	Java
Ng6	0.1–0.5	1251	Java
Ng7	0.1–0.5	1013	Java
Ng10	0.1–0.5	1135	Java
Ng11	0.1–0.5	1231	Java
Ng12	0.1–0.5	1090	Java
ZhouII	0.4	1030	China
Zhou III	0.6	915	China
Zhou V	0.3	1140	China
Zhou X	0.4	1225	China
Zhou XI	0.4	1015	China
Zhou XII	0.4	1030	China