Peer review history for:

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The original manuscript for review is appended below.

Reviewer 1: Round 1

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Reviewer 2: Round 1
Date completed: 15 August 2025
Conflicts of interest: None

Recommendation: Accept / Revisions required / Resubmit for review / Resubmit elsewhere / Decline / See comments
REVIEWER: Accept
Does the manuscript fall within the scope of SAJS? Yes/No
REVIEWER: Yes
Is the manuscript written in a style suitable for a non-specialist and is it of wider interest than to specialists alone? Yes/No
REVIEWER: Yes
Does the manuscript contain sufficient novel and significant information to justify publication? Yes/No
REVIEWER: Yes
Do the Title and Abstract clearly and accurately reflect the content of the manuscript? Yes/No
REVIEWER: Yes
Is the research problem significant and concisely stated? Yes/No
REVIEWER: Yes
Are the methods described comprehensively? Yes/No
REVIEWER: No
Is the statistical treatment appropriate? Yes/No/Not applicable/Not qualified to judge
REVIEWER: Not applicable
Are the interpretations and conclusions justified by the research results? Yes/Partly/No
REVIEWER: Yes

Please rate the manuscript on overall contribution to the field
Excellent/Good/Average/Below average/Poor

REVIEWER: Excellent

Should this manuscript be expanded and considered rather as a Research Article?
Yes/No

REVIEWER: No

Please rate the manuscript on language, grammar and tone
Excellent/Good/Average/Below average/Poor

REVIEWER: Excellent

Is the manuscript succinct and free of repetition and redundancies?
Yes/No

REVIEWER: Yes

The number of tables in the manuscript is
Too few/Adequate/Too many/Not applicable

REVIEWER: Not applicable

The number of figures in the manuscript is
Too few/Adequate/Too many/Not applicable

REVIEWER: Adequate

Are the results and discussion confined to relevance to the objective(s)?
Yes/No

REVIEWER: Yes

Is the supplementary material relevant and separated appropriately from the main document?
Yes/No/Not applicable

REVIEWER: Not applicable

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REVIEWER: Excellent

Is appropriate and adequate reference made to other work in the field?
Yes/No

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Is it stated that ethical approval was granted by an institutional ethics committee for studies involving human subjects and non-human vertebrates?
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REVIEWER: Not applicable

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REVIEWER: Yes

Are you willing to review a revision of this manuscript?
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REVIEWER: Yes

Comments to the Author:
This is an interesting and intriguing piece that seeks to hi-light the role of the precuneus in hominid (specifically Homo sapiens) cognitive development. I also like the intriguing link to the emergence of bow hunting within the African record as an explicit example of the real world implications. In many ways this is great short paper as it stands that does not (in my opinion) require any further work.

I do think however that there is scope for a larger and longer paper if the author wanted to expand on this

and I would certainly like to read this wider work. For example, I'd be interested to know how the mirror neuron system would link to the function of the precuneus especially (for example) in the attention of imagining the bow shot.

A great paper thank you for the opportunity to review.

Author response to Reviewer 2: Round 1

I thank the reviewer for taking the time to comment on the manuscript, and for suggesting 'a larger and longer paper', that paper has now been published elsewhere, and I added the reference to this manuscript (see https://doi.org/10.1007/s10816-025-09716-6)

Pleistocene bowhunting in Africa and the human mind

Abstract

Advances in genetic research and palaeo-neurology, together with a better understanding of the African archaeological record, demonstrate that the sapient mind evolved in Pleistocene Africa. Complex, bimanual technologies, operated over a distance – such as bowhunting – may provide a window into human cognitive evolution. I report on recent inter-disciplinary research, drawing on: a) the development of the human precuneus as brain region that facilitates visuo-spatial integration; b) sport psychology and cognitive-motor neuroscience; and c) neuro-genetic adaptations towards human attention. It highlights the role of the precuneus and attention in modern archery, and variation in the genetic development of attentional resources in African *Homo sapiens vs* the Neanderthals and Denisovans of Eurasia, which may explain why bowhunting was an African Pleistocene invention.

Significance:

The bow-and-arrow may have been invented in sub-Saharan Africa sometime between ~80 and 60 ka. Complex technologies of this time depth have the potential to inform on the evolution of the human mind. I highlight the precuneus as brain region, and at least 14 'attention genes' selected for in the *Homo sapiens* genome, that may have facilitated early African bowhunting.

Keywords: Precuneus, genetic selection, *Homo sapiens*, cognitive evolution, attention

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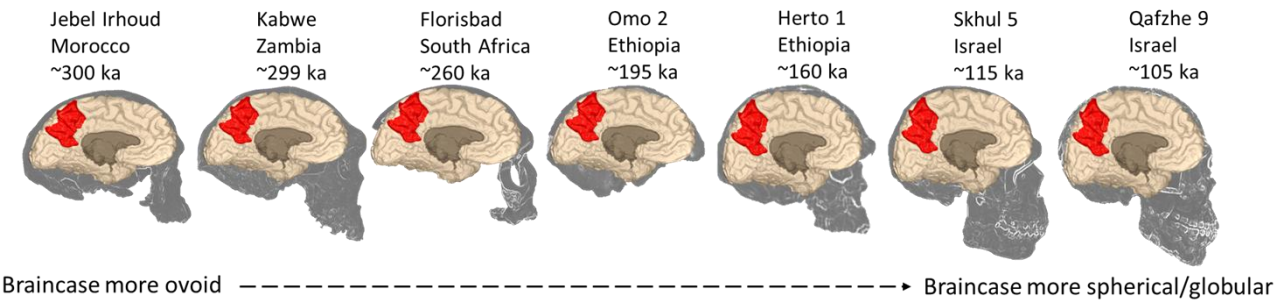
Introduction

Until recently, it was thought that Africans who lived during the Middle Stone Age about 300-30 ka were ineffective hunters lacking the bow-and-arrow[1], perhaps because they lacked the necessary cognitive capacity. Yet, Middle Stone Age faunal remains of tell a different story (see SOM data 1 in[2]), as does the human fossil record (Fig. 1 top). The African *Homo sapiens* genetic record also stretches back to between ~350-260 ka[3], with behavioural modernity recognised since ~100 ka[4]. The oldest evidence for hunting with stone-tipped weapons currently comes from South Africa at ~500 ka.[5] Cold phases possibly stimulated weapon development, so that by MIS 12 (478-424) African *Homo heidelbergensis* preferred hunting with thrusting spears complimented by stabbing spears.[2] By MIS 8 (300-243 ka) with the appearance of *Homo sapiens*, people seem to have started experimenting with javelin hunting over a longer ranges, and by MIS 5 (123-71 ka) we may see the first tentative experimentation with bowhunting, which seems to become well-developed by MIS 4 (71-57 ka).[2]

We cannot excavate the ancient human mind, but complex techno-behaviours such as bowhunting may reveal something about its evolution in Africa. Malafouris[6] applies Material Engagement Theory to explain how the use of technology shapes the brain and how it thinks. The things we do habitually are expressed in both our technologies and our brains, and changes in one may prompt changes in the other.[6] Today, cell phones, computers, gaming and social media are changing human brains, behaviours, and perhaps the evolution of our species.[7] If technology is changing our brains today, there is no reason to think it did not happen in the past.

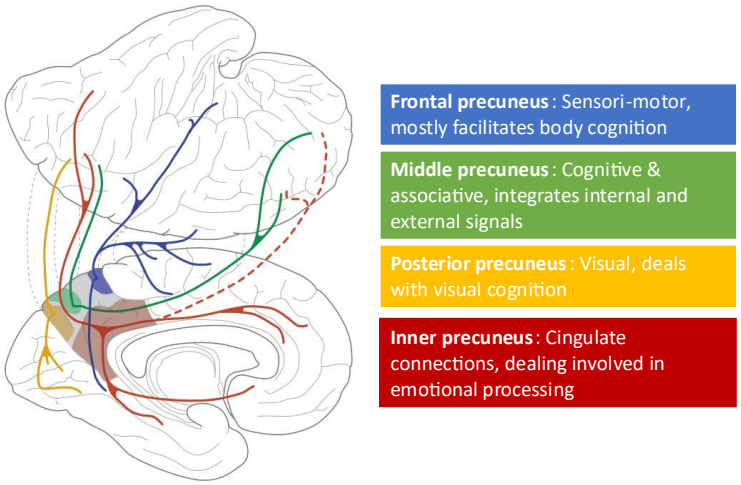


Source: Image created by [author]

Figure 1: Top: *Homo sapiens* cranial fossil record, showing the globularisation of the human brain and expansion of the precuneus.

Bowhunting in the human precuneus

The globularisation of the sapient cranium, with an expansion of the Precuneus, becomes recognisable in the Old-World *Homo sapiens* fossil record between ~160-100 ka[8], long after our split from the Neanderthals and Denisovans ~700-500 ka (Fig. 1). The precuneus is active during cognitive processing in modern archers[9], serves as interface between action and cognition in higher-order, bimanual coordination[10], and damage to the precuneus causes impairment in bimanual synchronisation[11]. Such coordination develops incrementally into adulthood, improving with inter-hemispheric communication *via* the corpus callosum, and with the ability to focus attention through time and across space.[12] The precuneus, with other parts of the human brain, also shows the most activation when spatial attention is needed during tool use.[13] It is part of the brain's default-mode system, with extensive network activity and structural connectivity.[14] The frontal region mostly facilitates body cognition, the posterior region visual cognition, the middle portion integrates internal and external signals, and the inner area links to emotional processing (Fig. 2). The result is visuo-spatial integration functioning as a bridge between embodied experience, emotion and cognition.[15]



Source: Adapted from Beldenpoint CC-BY-3.0, annotations by [author]

Figure 2: Inter-connectivity of the human precuneus (adapted from[14]), with intra-precuneal functional regions.

During modern archery, visuo-spatial integration facilitates: a) The space-time understanding of physical body-environment coordination; b) the assimilation of visual images with conscious, self-centred episodic memory recall; and c) multi-variate mental experiments or imagining 'what if' scenarios when planning a shot. During bowhunting, the precuneus with its network, would be involved in: a) Storing visuo-spatial information about limb and hand positions, and hand-tool interactions; b) facilitating shifts in attention between the embodied location of the hunter and the location of the prey animal on the landscape; c) predicting the flight of the arrow and prey movement; and d) focusing the mind to take an accurate shot.[8] According to Bruner[16], similar levels of visuo-spatial integration, conscious embodied experience, emotional control, attentional shift and focus, i.e., similar 'mindfulness', is not possible without the developments observed in the sapient precuneus by ~100 ka. Today, our ability to focus attention in multiple ways enables us to conduct both mundane and complex tasks. It is key to successful bowhunting. Yet, it is difficult to sustain attention without training.

Attention in the archer's brain

Liu et al.[17] demonstrated how 45 minutes of Chinese archery affects the ability to control attention, emotions, working memory, and cognitive flexibility in pre-adolescent children. Sport psychology and cognitive-motor neuroscience can assess variation between expert and novice performances and their neuro-anatomy.[18] Practicing archery stimulates the selective, yet simultaneous, processing of both internal and external information, so that the archer's attention becomes focussed on multiple aspects relevant to firing a successful shot, whilst ignoring or buffering distractions.[19] The ability to pay attention in such a complex manner is key to sapient cognition today. Neuro-cognitive work suggests that repeated practice and improvement in aiming accuracy result in plastic changes in brain areas associated with spatial attention.[9] Kim et al.[20] performed an fMRI study, comparing

variation between expert and novice archer neural networks during the aiming process. They found that the precuneus was one of the areas with significantly higher activation compared to other regions in the brains of expert archers, and even more active in the brains of novice archers compared to experts when aiming.[18,20] This suggests that the sapient precuneus probably also plays role in bowhunting (Fig. 3), and that attention-demanding tasks such as bowhunting may stimulate development/changes in the precuneus and its associated attentional networks.

Source: Arri Raats (19919656433) CC-BY-2.0

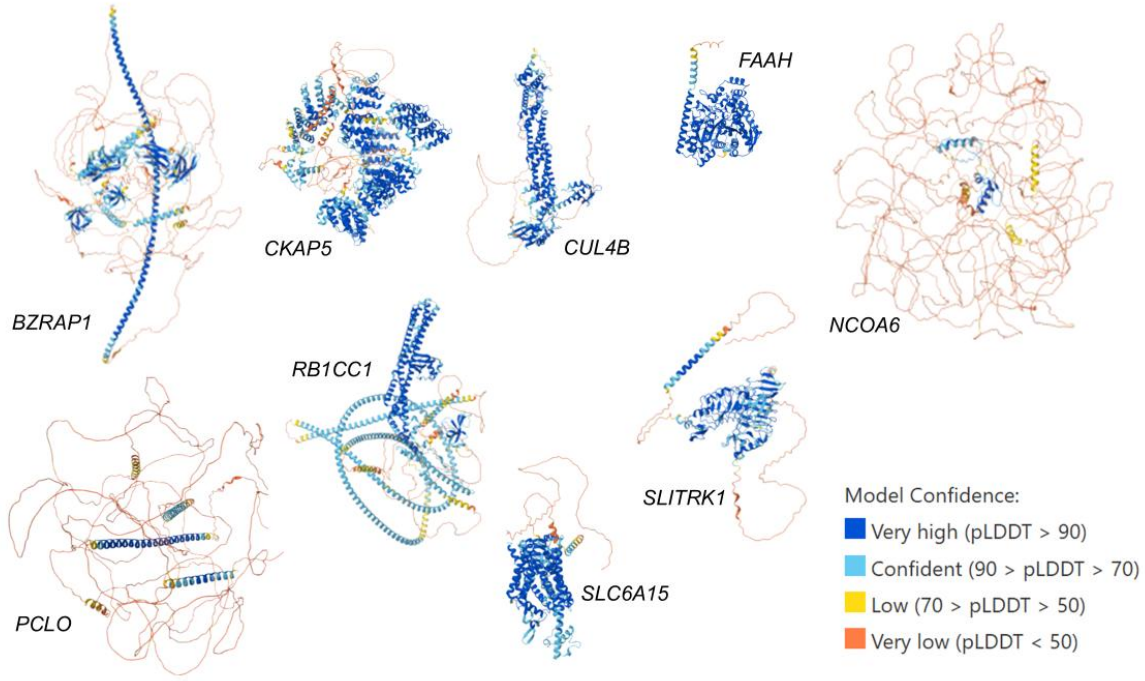
Figure 2: Kalahari Khomani San, Boesmansrus Camp, Northern Cape, South Africa.

Neuro-genetic adaptations towards human attention

We are also able to trace neuro-genetic adaptations in human cognitive evolution. Kaczanowska et al.[21] shows functional networks starting to shift from motor control to attention in ancient hominoids by >18 Ma and in ancestral homininae by >7 Ma. Much later (~700-500 ka), the Neanderthal split from a common *Homo* ancestor shows genetic selection for strategic thinking (prospection/theory of mind), working memory and mathematical skill.[21] The Denisovans who split from the Neanderthals after 500 ka clustered with functional networks for motor control, affective attention (introspection), affective processing (impulse/emotional control), active and passive attention, and action planning.[21] After ~300 ka *Homo sapiens* in Africa shows continued selection for working memory, fine motor control, language, emotion recognition, relational processing (causal cognition), abstract thinking and a notable emphasis on strategic thinking.[21]

Of 44 genes, listed as associated with Neanderthal, Denisovan, and *Homo sapiens* cognition[21,22], 26 are associated with attention[17]. Of these 'attention genes', none were selected for in all three groups.

We (*Homo sapiens*) selected for five attention genes (*ADAMTS9, ARHGEF11, CHL1, LAMB3, MKKS*) also selected by the Denisovans, and a different one (*ADGRV1*) selected by the Neanderthals. Fourteen of the attention genes (*ASTN1, BZRAP1, CKAP5, CUL4B, FAAH, LPHN3, MCPH1, NCOA6, NUP210, PCLO, PCNT, RB1CC1, SLC6A15, SLITRK1*), currently associated with neuro-genetic selection for human cognitive evolution[21,22], were selected for only in *Homo sapiens*. Nine of these (*BZRAP1, CKAP5, CUL4B, FAAH, NCOA6, PCLO, RB1CC1, SLC6A15, SLITRK1*) have been linked to cognitive processing in the precuneus (see Table 2 in[18]; Fig. 3) – which is associated with activation and neuronal pressure when bimanually aiming an arrow at a target through space[18,20]. These observations suggest different neuro-genetic pathways for developing the ability to pay attention amongst ancestral humans, and may explain why only *Homo sapiens* became habitual bowhunters during the African Pleistocene.



Source: Adapted from AlphaFold Protein Structure Database (CC-BY 4.0), https://alphafold.ebi.ac.uk, visited March 2025

Figure 3: Three dimensional protein structures from of genes selected for in *Homo sapiens* since our split from the Neanderthals and Denisovans that are associated with the precuneus and with attention (modified from the).

In conclusion

Interaction between brain, body and tools depends on a range of attentional resources to coordinate actions, motor planning and task orientation, and to integrate tools in the human body and neural schemes.[24] Noticeable changes in Pleistocene technology may demonstrate parallel changes in human attention, ultimately leading to the techno-behavioural complexity observed in the *Homo sapiens* hunter-gatherer record since ~100 ka.[4,24] The origin of bow hunting in Africa sometime between ~80 ka and 60 ka, represents a major change in human techno-behaviour that is, thus far,

exclusive to *Homo sapiens*. Neuro-cognitive work demonstrates how modern archery helps to develop attentional resources, and how paying attention during aiming an arrow stimulates the precuneus – a brain region that only reached its modern range by ~100 ka[15]. If we accept that practicing archery affects an archer's brain and how it pays attention, it is reasonable to suggest that ancient human brains went through similar neuro-plastic adaptations when using bimanual technologies that required attentional visuospatial training.

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