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BRAIN EVOLUTION: PALAEOSCIENCES, NEUROSCIENCE AND ARTIFICIAL INTELLIGENCE

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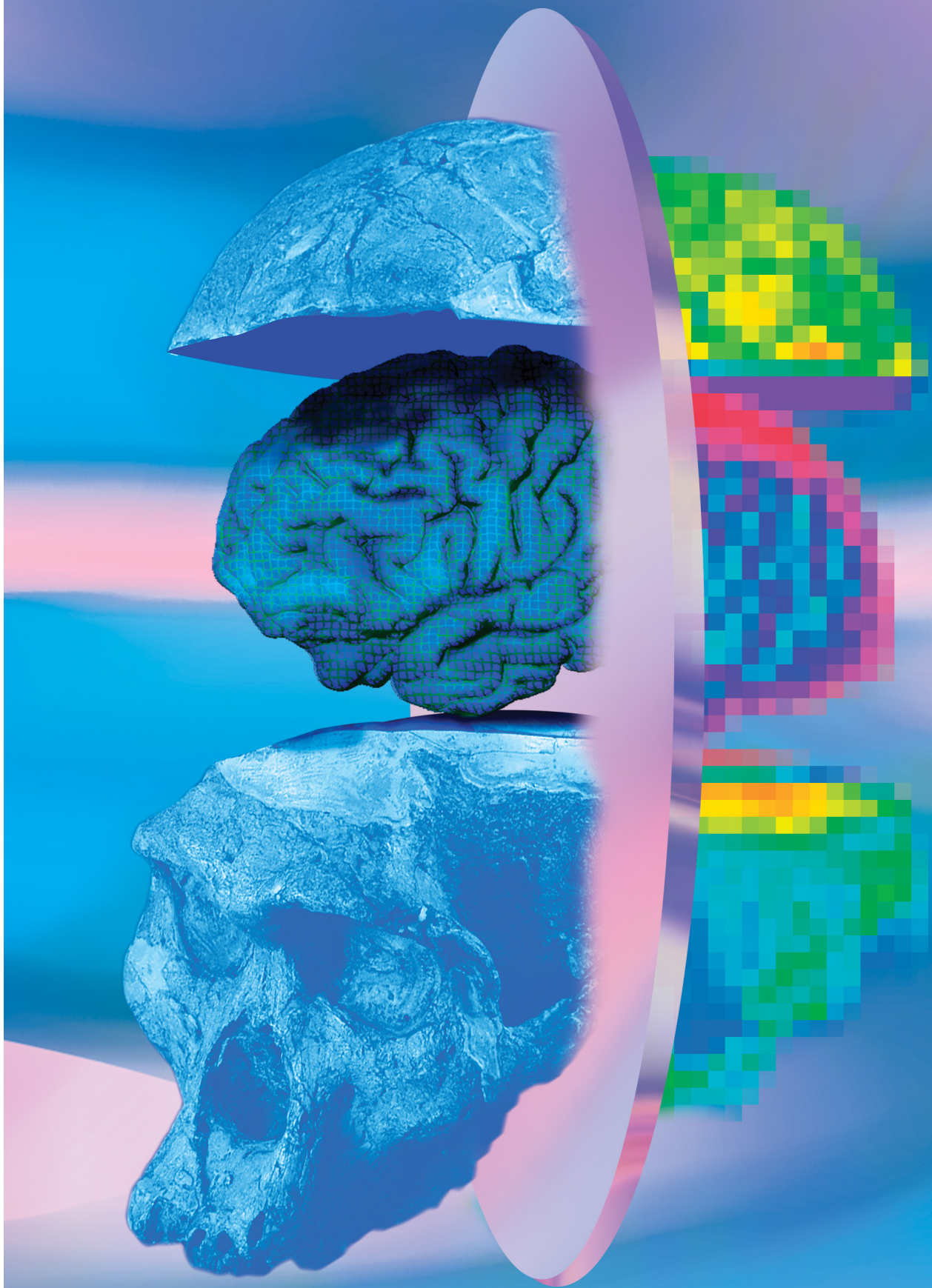
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BRAIN EVOLUTION

PALAEOSCIENCES, NEUROSCIENCE
AND ARTIFICIAL INTELLIGENCE

LES EDITIONS



LESEDI: *pronounced Leh-SEH-di | Meaning “light” in Sesotho, Setswana and Sepedi*



IFAS-Research, established in 1995 in Johannesburg, is one of the French Research Institutes Abroad (UMIFRE), under the joint supervision of the Ministry for Europe and Foreign Affairs and the CNRS (French National Centre for Scientific Research). As UMIFRE 25, it is associated with research institutes of IFRA-Nairobi, IFRA-Nigeria and SFDAS within CNRS UAR 3336. In addition, it shares its premises, part of its operations as well as transversal projects, with the French Institute of South Africa, whose mission is to ensure the French cultural presence in South Africa.

The mission of IFAS-Research is to initiate, support and carry out research projects in the human and social sciences, in conjunction with its many partners in southern Africa, France and Europe. Its activity is carried out within the framework of its regional mandate, which includes twelve countries in southern Africa, from the Republic of Congo to Mozambique.

As both a research laboratory and an institutional and logistics support platform for research, it particularly supports young researchers, innovative research fields and bilateral or multilateral scientific cooperation projects.

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FORWARD

Avant-propos

Comment notre cerveau a-t-il évolué ? Quels caractères distinguent notre cerveau de celui des chimpanzés et bonobos, nos plus proches parents, et comment sont-ils apparus ?

Pour répondre à ces questions, nous devons nous pencher sur le registre fossile qui documente les 7 derniers millions d'années d'évolution humaine. Contrairement à l'os et aux dents, les tissus mous de l'organisme ne fossilisent que très rarement et les informations concernant le cerveau de nos ancêtres et parents se limitent aux impressions que cet organe laisse sur la surface interne de la boîte crânienne (c'est-à-dire l'endocrâne). Ces empreintes sont notoirement difficiles à décrire, analyser et interpréter.

Dans ce contexte, nous avons développé dans le cadre du programme Protea des partenariats Hubert Curien (*National Research Foundation of South Africa*, Ambassade de France en Afrique du Sud, Ministère de l'Europe et des Affaires Étrangères, Ministère de l'Éducation Nationale, de l'Enseignement Supérieur et de la Recherche) le projet « EndoMap: Mapping the brain of our ancestors ». Ce projet a pour but de rassembler les compétences des neuroscientifiques (Centre de Recherche Cerveau et Cognition) et informaticiens-mathématiciens (Institut de Mathématiques) à Toulouse (France), ainsi que les paléontologues (*School of Geography, Archaeology and Environmental Studies of the University of the Witwatersrand*) de Johannesburg afin de mettre au point de nouveaux outils permettant une relecture des endocrânes fossiles (voir l'article d'E. de Jager dans ce numéro).

Cette approche s'est révélée fructueuse avec la publication de plusieurs articles scientifiques (de Jager et al., 2019, 2022 ; Beaudet & Fonta, 2020 ; Beaudet & de Jager, 2023), la participation à des conférences internationales (*British Association for Biological Anthropology and Osteoarchaeology*, *Cortical Evolution*, *Federation of European Neuroscience Societies*, *European Society for the study of Human Evolution*) et l'organisation de réunions scientifiques (*From Fossils to Mind* en ligne, *BrAIn Evolution* à

Johannesburg), mais également des activités de dissémination avec la présentation de la paléontologue sud-africaine Mirriam Tawane au Muséum de Toulouse (voir premier article de ce numéro).

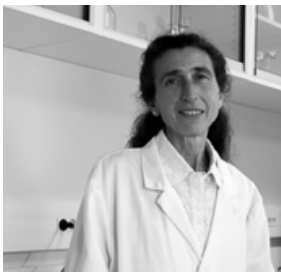
Cependant, l'avancement des travaux d'EndoMap fait face à des obstacles à la fois méthodologiques et conceptuels qui nécessitent de se tourner vers d'autres disciplines. Comment faire face aux données manquantes qui résultent de la nature fragmentaire du registre fossile ? Comment quantifier et interpréter la variation au sein des échantillons ? Les membres du projet EndoMap ont alors invité des spécialistes de différents domaines à échanger et réfléchir aux possibles apports et contributions d'une technologie comme l'intelligence artificielle à ces questions (voir dans ce numéro les articles de J. Shock & R. Catzel, J. Aramendi & L. Courtenay, B. Rosman & D. Stratford) et des disciplines qui traitent du comportement (psychologie, bioarchéologie) (voir dans ce numéro les articles de V. Williams, Z. Pretorius & K. Cockcroft, S. Prat).

Dans cette optique, l'équipe d'EndoMap et l'IFAS-Recherche ont organisé les 22-23 novembre 2023 à Johannesburg le colloque *BrAIn Evolution: Palaeosciences, Neuroscience and Artificial Intelligence*. En plus de communiquer le bilan des travaux réalisés dans le cadre du projet EndoMap, ce colloque a posé les fondements de nouvelles collaborations entre la France et l'Afrique du Sud et ouvert de nouvelles perspectives sur le développement d'une approche résolument interdisciplinaire présentée dans l'article qui ouvre ce numéro. Ce vingt-sixième numéro de *Lesedi* vise ainsi à rendre compte des échanges menés et des différents projets qui ont contribué à cette réflexion collective et pluridisciplinaire.

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BrAI Evolution: palaeosciences, neuroscience and artificial intelligence



Caroline Fonta & Amélie Beaudet

Caroline Fonta is a senior CNRS scientist at the CerCo (Brain and Cognition Research Center, UMR 5549, CNRS / Paul Sabatier University) in Toulouse, France. She is interested in isolating markers to characterise and predict brain ageing in a Non-Human Primate model (marmoset monkey *Callithrix jacchus*). She mainly uses non-invasive imaging to explore brain parenchyma and vascular network structure and function. She coordinates the EndoMap project.



Amélie Beaudet is a palaeoanthropologist and CNRS junior professor at the University of Poitiers (PALEVOPRIM, UMR 7262, CNRS / University of Poitiers) in France. Her research mainly focuses on the palaeobiology of early hominins and the adaptive and evolutionary contexts in which our own genus (*Homo*) emerged (www.ameliebeaudet.com). She coordinates the EndoMap project.

Context

By receiving inputs from the sensory organs and sending outputs to the muscles and other organs, the brain provides crucial information about the interactions between our ancestors (i.e., fossil hominins) and the environment in which they lived and evolved million years ago in Africa. However, to date, there is no consensus on how the human cerebral specificities emerged. Because brain tissue is not preserved in the fossil record, palaeontologists have to rely on brain endocasts to reconstruct the organisation of the brain and infer functional implications.

Indeed, the endocasts retain traces of the sulci of the cerebral cortex, which are hallmarks of the anatomo-functional organisation of the brain. As such, the study of fossil hominin endocasts has the potential to yield evidence on the emergence of critical human-specific functions and behaviours, such as speech capacity and toolmaking. Unfortunately, palaeoneurological studies are hampered by the fragmentary nature of

the fossil record. Within this context, on the 22nd and 23rd of November 2023 the “BrAI Evolution” workshop brought together researchers from palaeosciences, neuroscience and artificial intelligence (AI) for in-depth discussion on how to apply newly developed methods in neuroscience and AI to palaeontology to better understand the origins of the human brain.

Background

Besides its relevance for palaeoneurological studies, deciphering the timing and process of brain evolution within the human lineage is critical for understanding how our ancestors became humans, which include cerebral and behavioural specificities. However, assessing human brain evolution and cognitive capacities is significantly hampered by both technical limitations and the fragmentary nature of fossil endocasts. The integration of high-resolution 3D methods in the traditional investigative toolkit of palaeoneurology discloses new perspectives for reconstructing extinct neural conditions.

Within this context, we developed the “EndoMap: Mapping the brain of our ancestors” project that integrates the use of cutting-edge imaging techniques (X-ray microtomography) and image and data analyses, as well as the study of extant and fossil primate samples for unravelling the evolutionary history of the human brain (www.endomap.org). In particular, the main aim of the project was to virtually investigate the variation pattern of extant human endocasts using density maps before interpreting evidence from the fossil record (de Jager et al., 2019, 2022).

In 2020, the EndoMap project received funding for two years from the PROTEA program — *Partenariat Hubert Curien* coordinated by the *Ministère de l'Europe et des Affaires Etrangères*, the *Ministère de*

l'Education Nationale, de l'Enseignement Supérieur et de la Recherche and the National Research Foundation of South Africa — which was renewed for a third year in 2023. Initiated in 2017 by a 6-month Master internship in Toulouse through the Erasmus Mundus program AESOP+, this multidisciplinary project was part of a collaboration between the *Centre de Recherche Cerveau et Cognition (CerCo)*, in cooperation with the Institute of Mathematics of the University of Toulouse (France), and the School of Geography, Archaeology and Environmental Studies (GAES) of the University of the Witwatersrand (South Africa) (Figure 1).



Figure 1. The EndoMap team in France (top left) and South Africa (top right: Medical School, bottom left: Evolutionary Studies Institute, bottom right: Sterkfontein), credit: Amélie Beaudet.

The GAES, which also subsumes the Origins Center, houses archaeologists and geoarchaeologists as well as a vast array of palaeoanthropological and archaeological materials. The GAES works closely with the Evolutionary Studies Institute (ESI), which is a South African centre of excellence in palaeosciences that develops an approach combining palaeontology, palaeoanthropology, molecular biology, genetics, geosciences, archaeology, geography, biology, ecology and climatology. Some of the most iconic fossil hominin specimens are curated at the ESI, including “Little Foot” and the “Taung Child”. The imaging platform of the ESI, one of the few in South Africa, is equipped with a microCT scanner and workstations for the analysis of 3D objects. GAES and ESI can be considered as leaders in the field of palaeosciences in South Africa.

The CerCo is a joint laboratory between the CNRS and the University of Paul Sabatier Toulouse 3, housed in the Purpan University Hospital in Toulouse. Researchers at the CerCo work on the mechanism of perception, mainly in the visual, auditory and vestibular modalities, as well as of the major cognitive functions such as memory, mental states, among others. Scientific questions are explored by combining different methodological approaches (e.g., anatomy, brain MRI, electroencephalography, functional near IR spectroscopy, oculometry, brain inactivation, PET scan, psychophysics, electrophysiology, deep learning tools, artificial neural network) and various animal models, essentially human and non-human primates.

As part of the Toulouse Mind and Brain Institute (TMBI), the CerCo benefits from the close relationship between the various players involved in integrative neuroscience research on healthy humans, patients and animals, as well as from the support for interdisciplinary collaborations between neuropsychology, physiology, ethology, psychology, linguistics, ergonomics, clinical neurology, pharmacology, philosophy, computer science, artificial intelligence, etc.

Outcomes and next step

The synergy between palaeosciences and neurosciences, which share common concepts (e.g., changes in cerebral functional anatomy, on the scale of life vs. the scale of evolution) and methodologies (e.g., analysis of scarce and fragmentary data, variability formalisation) has been demonstrated through the publication of newly revealed data (see in this volume the paper from de Jager, see also de Jager et al., 2019, 2022; Beaudet & Fonta, 2020; Beaudet & de Jager, 2023), communications at international conferences (British Association for Biological Anthropology and Osteoarchaeology, Cortical Evolution, Federation of European Neuroscience Societies, European Society for the study of Human Evolution), organisation of scientific meetings (From Fossils to Mind, BrAIn Evolution), student internships, and several research trips by the members of the EndoMap team in France and South Africa. Through the project website, our density maps are shared with the scientific community and can be downloaded freely to be used as a resource for future studies of fossil endocasts (www.endomap.org). Additionally, with the financial support of the CerCo and the *Muséum de Toulouse*, the EndoMap team was pleased to invite Mirriam Tawane, the first black South African female palaeoanthropologist, to give a public lecture at the Museum of Toulouse on the 7th of June 2023 (Figure 2).

In parallel, we have been developing further our study of fossil hominin endocasts (e.g., Beaudet and de Jager, 2023). Throughout this process, the issue of fragmentary specimens and missing data emerged. As such, we decided to organize a conference in collaboration with IFAS-Research in November 2023 in Johannesburg (South Africa) entitled “BrAIn Evolution: palaeosciences, neuroscience and artificial intelligence” (<https://www.ifas.org.za/research/2023/colloque-international-brain-evolution-22-23-novembre-international-conference-brain-evolution-novembre-22-23/>) for discussing future challenges in the field of palaeoneurology (Figure 3). This conference was the opportunity to open discussions between palaeontologists, neuroscientists and computer scientists.



Figure 2. The EndoMap team invited Miriam Tawane to present her work at the Museum of Toulouse on the 7th of June 2023, credit: Amélie Beaudet.

From the brainstorming sessions with the participants and speakers emerged promising perspectives on how to integrate machine learning and deep learning tools, including data augmentation procedures, as well as probabilistic models (Bayesian approach) and mathematical methods (graph theory) that could be implemented and adapted to help addressing issues and/or overcoming limiting factors at various stages of the analyses in palaeoneurology (e.g., image analysis, data analysis, production of cerebral endocrania, phylogenetic projections). The present volume is a synthesis of the different contributions that delineate our current knowledge on African human origins, issues and perspectives (keynote by D. Stratford) and highlights how multidisciplinary initiatives can benefit the field of palaeoneurology and palaeontology as a whole. In

particular, we emphasized how new technologies such as artificial intelligence (see in this volume papers from J. Shock & R. Catzel, J. Aramendi & L. Courtenay, and D. Stratford & B. Rosman) as well as behavioural studies (see in this volume papers from V. Williams, Z. Pretorius & K. Cockcroft, and S. Prat) may contribute to improve our knowledge of human brain evolution.



Figure 3. The “BrAI Evolution: Palaeosciences, Neuroscience and Artificial Intelligence” conference was held in Johannesburg on the 22nd and 23rd of November 2023 at the French Institute of South Africa, credit: IFAS-Research.

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Exploration of the Sterkfontein Caves: 120 years of discoveries and the future



Dominic Stratford¹ & Benjamin Rosman²

Dominic Stratford is an Associate Professor at the School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Johannesburg and Guest Researcher at the Department of Anthropology, Stony Brook University, Stony Brook, USA. As Coordinator of Research at Sterkfontein, Dominic is passionate about developing a new era of research at the site – applying cutting edge digital techniques and multidisciplinary approaches to understand better the caves themselves, the ancient deposits that fill them, and the fossils and archaeological materials that have been excavated.

Benjamin Rosman is a Professor at the School of Computer Science and Applied Mathematics, University of the Witwatersrand, Johannesburg. In his role as the Director of the Robotics, Autonomous Intelligence and Learning (RAIL) Laboratory, Benjamin spends his time coordinating research projects that enable decision-making machines such as robots to learn more efficiently and be able to generalise their knowledge better to new environments, as typified by the caves.



Introduction

The Sterkfontein Caves represent one of hundreds of caves found within the UNESCO World Heritage Site called the Cradle of Humankind. The boundary of the Cradle of Humankind covers an area of about 47,000 hectares, stretching from the town of Muldersdrift to the Hartbeestpoort Dam, and attempts to protect fossil- and artefact-bearing cave sites that have yielded evidence of human, ecological and landscape evolution spanning about the last 3.5 million years. All the fossil-bearing cave sites have formed in the late Archaean dolomitic limestones of the Malmani Subgroup, a sedimentary carbonate rock that formed in an inland sea that occupied the area about 2.5-2.4 billion years ago (Eriksson, Altermann, Catuneanu, Van der Merwe & Brumby, 2001; Martini, Wipplinger, Moen & Keyser, 2003). Dissolution of cavities and passages formed large subterranean karst networks that eventually opened to the landscape surface perhaps as long as five million years ago. Once open, the caves acted as

traps for sediments, bones and stone tools that fell into the cavities through tall, narrow shafts. Over hundreds of thousands of years, or even millions of years, huge deposits of sediments can accumulate that contain fossils of the animals that lived on the landscape in the past. At some sites, like Sterkfontein, Swarktrans, Kromdraai, Cooper's Cave and Drimolen, stone and bone tools made by our early ancestors in the vicinity of the well-vegetated entrances fell into the caves and provide additional evidence of the technology of these species from just over two million years ago.

The Sterkfontein Caves represent one of the earliest sites of fossil discovery in the Cradle of Humankind. Research at the site over the last 88 years has yielded a remarkably rich fossil record that starts at about 3.6 million years ago and includes discoveries of some of the most important fossils of human ancestors in the history of human origins research. Amongst many sig-

nificant discoveries, some of the better known include: the first adult *Australopithecus*, discovered by Robert Broom in 1936 (Broom, 1936a, b); Mrs Ples – one of the most complete *Australopithecus* skulls (Broom, 1947); the first partial skeleton of an *Australopithecus* (Broom & Robinson, 1947); and ‘Little Foot’ – the most complete skeleton of an *Australopithecus* yet discovered anywhere in the world (Clarke, 1998). In addition, the ancient cave deposits at the Sterkfontein Caves have yielded two large Earlier Stone Age lithic assemblages, the Oldowan, which dates to 2.18 million years ago, and the Early Acheulean, which dates to about 1.4 million years ago (Kuman & Clarke, 2000; Granger et al., 2015; Kuman, 2023). Research continues at Sterkfontein, and new advances in technology are providing exciting new opportunities to further explore the fossils that are yielded from the ancient deposits, and the caves themselves.

Discovery, exploitation and destruction

The earliest reports of fossils in the Cradle of Humankind were made by Mr D. Draper of the South African Geological Society in 1895 (Draper, 1895; Malan, 1959). Draper’s report documents fossils at ‘Kromdraai Caves’, which are located about 5 km west of Sterkfontein. Here, ancient fossil-bearing deposits were exposed on the landscape surface, and this site became famous over 40 years later when Robert Broom discovered the first specimen of a new species of human ancestor he named *Paranthropus* (Broom, 1939) in 1938. At this point in time, miners were quarrying exposed calcium carbonate deposits from the hillsides of the area to be made into lime and transported to Johannesburg for use in various industries. The calcium carbonate cave deposits (also known as speleothems and include stalagmites, stalactites and flowstones) grew into huge formations in the undisturbed ancient caves and over millions of years of gradual landscape erosion were exposed on the landscape surface. Mining continued in the Cradle until the early 1940s. At Sterkfontein, blasting related to the mining of calcium carbonate deposits exposed on the landscape broke into the massive underground

cave system at some point between June 1896 and June 1897 under the direction of Mr G. Martinaglia. Draper’s subsequent reports to the South African Geological Society in 1897 mention accessing the caves and observing remarkable speleothem formations that warranted the cave’s protection from destruction. It seems that at this point, Draper had arranged for the underground areas of the caves to be protected by the company that owned the mining rights for the property. The extent of the Sterkfontein Caves system was, at this point, unknown, but it appears from both local and international reports that members of the public could access the cave system and explore (Malan, 1959), with some reports mentioning passages over a mile long. The beauty of the speleothem formations, before their destruction in 1921, was probably best documented in an article published in the French Journal ‘Cosmos’, in which a Marist Brother and seven colleagues describe their exploration of the caves with the property manager, Mr H Thomasset, and note the variety and abundance of intact speleothem deposits that filled the cavities. Interestingly, their article also notes the discovery of a ‘large fossil jaw with all the teeth of a large antelope’ (Malan 1959; 322).

Following the destruction of the cave’s speleothem deposits by the public and their deliberate destruction in 1921, larger-scale mining continued inside the caves. The extent of this mining has undoubtedly destroyed not only the natural beauty of the caves, but also potentially hundreds of fossils that were caught in the blasting process. Large mining dumps were created not only on the landscape surface but also underground. It is in these dumps that the earliest fossil discoveries were made at Sterkfontein, initially by students of Raymond Dart in 1935, and then momentarily by Robert Broom in August 1936 when the first adult *Australopithecus* was found (TM1511) (Broom, 1936a, b). The discovery of TM1511 would demonstrate South Africa’s fundamental role in the global search for human origins and stimulate the following 88 years of research at Sterkfontein and in the area. These mining dumps have continued to yield remarkable fossils, none more so than ‘Little Foot’, the most complete *Australopithecus* skeleton yet dis-

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covered (Clarke, 1998; Clarke, Pickering, Heaton and Kuman, 2021), parts of which were recovered from a dump on the floor of the Silberberg Grotto.

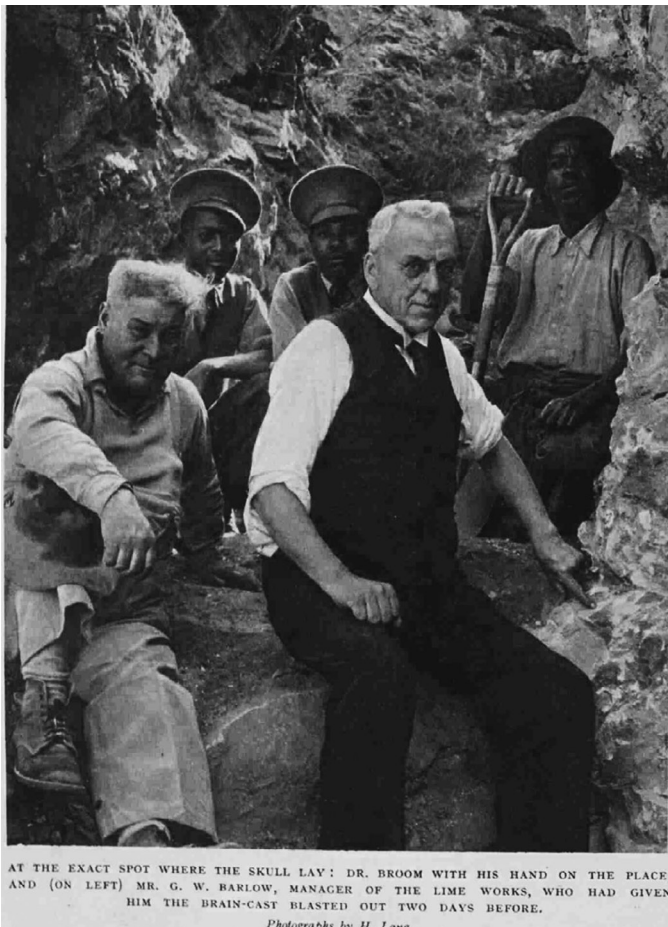


Figure 1. Robert Broom at the site of the discovery of TM1511 next to quarry supervisor Barlow (Broom 1936b). (Photograph courtesy of the British Newspaper Archive; brightness and contrast adjusted from digital scan of original).

1936 onwards: research and exploration of the Sterkfontein Caves

Mining continued after the discovery of TM1511, and it was only after the lime mining industry had collapsed during World War II that systematic research excavations were started by Robert Broom and John Robinson. Broom used similar methods to those practiced by the lime miners. He would use dynamite to break the heavily cemented sediments and release

fossils from the area where parts of TM1511 were discovered (Figure 1), an area named the ‘Type Site’, which is located in the northeast of the Sterkfontein site. In the early 1950s, Robinson and Bob Brain discovered some stone tool implements in loose deposits about 30m west of the Type Site. Excavations in the area by Revil Mason and John Robinson (Robinson & Mason, 1962) yielded Earlier Stone Age lithics that would contribute new perspectives on the behaviours of human ancestors in the Cradle of Humankind.

In 1966, a new phase of research excavations was started by Phillip Tobias. Approaching the site in a methodological manner and with long-term research goals, Tobias and site manager Alun Hughes conducted vegetation surveys, established a new excavation grid and finer survey control, removed the *ex-situ* ‘overburden’ to reveal *in situ* deposits and stratigraphic relationships, surveyed the mining dumps in the vicinity of the caves, and started systematic excavation of *in situ* deposits (Tobias & Hughes, 1969). The careful documentation and processing of the miners’ dumps yielded a large sample of fossil fauna, including new human ancestor fossil materials. Even in the early 21st century, some of these dumps are still being processed, and fossil discoveries are still being made from this work. Until the late 1960s, all human ancestor fossils (with the exception of StW 13 and StW 14) were yielded from mining dumps, and it wouldn’t be until the late 1970s when the first human ancestor fossil discoveries were made from *in situ* deposits. As excavations, led by Alun Hughes, progressed eastwards, a very large area of soft *in situ* deposits was found in the middle of the site, between the stone tool-bearing area that Robinson and Mason excavated and the human ancestor fossil-rich Type Site. Excavations of this area, to be named by Tim Partridge as Member 4 (Partridge, 1978), progressed quickly from the early 1980s, and huge assemblages of fossil fauna, including those of human ancestors, were yielded. In addition, the first fossil wood was found in the southern part of Member 4 and suggested that at some point during the formation of that deposit, dense woodland extended over the site (Bamford, 1999). Human ancestor fossil finds included another partial *Australopithecus* skele-

ton and 700 pieces of *Australopithecus*, which Clarke has proposed represents two species of the *Australopithecus* genus (Clarke et al., 2021).

Ron Clarke continued Tobias and Hughes' excavations from the early 1990s and focused on excavating the stone-tool bearing area known as Member 5 (Partridge, 1978) and refining the stratigraphic control of the major deposits. Clarke's excavations yielded a large Oldowan assemblage associated with *Paranthropus robustus* fossils and an important Early Acheulean collection of artefacts that were associated with *Homo ergaster* (Kuman and Clarke, 2000). Clarke also started exploring some of the underground chambers of the Sterkfontein Caves and demonstrated the potential richness and age of these deposits with two significant discoveries: 'Little Foot', in 1997 (Clarke, 1998) in the Silberberg Grotto; and numerous human ancestor fossils from the Jacovec Cavern (Partridge, Granger, Caffee & Clarke, 2003). Recent dating efforts have proposed that these two deposits are the oldest currently known at Sterkfontein and in the Cradle of Humankind, dating to about 3.6 million years old (Granger et al., 2015; Granger et al., 2022). What was clearly demonstrated from these initial exploratory excavations in the depths of the Sterkfontein Caves is that the extensive cave network, with passages and chambers stretching over 5 km, has the potential to yield some of the oldest and best-preserved human ancestor fossils in southern Africa. Clarke's research program not only extended excavations into the deeper chambers, including the Silberberg Grotto, Name Chamber and Jacovec Cavern, but keen observations of the stratigraphy allowed finer control to be established over known deposits, which provided researchers opportunities to understand associations between faunal assemblages, stone tools and sediments more accurately (e.g., Clarke, 1994; Kuman and Clarke, 2000).

2015 onwards: exploratory excavations and innovation at the Sterkfontein Caves

Following the large-scale excavations of Tobias and Hughes, and Clarke, Dominic Stratford's tenure as director of research sought to continue aspects of Clarke's research question by conducting exploratory excavations in more remote areas of the caves and applying fine-resolution stratigraphic approaches to refining deposit associations and sedimentary processes. To link the new underground excavations with the surface-exposed deposits of Member 4 and 5, Stratford developed a large survey control framework that would enable excavators to document the locations of single artefacts, fossils, deposit features or chambers and passages into a single, global coordinate system (Stratford, Merlo & Brown, 2016). This network of survey control datums spanning the landscape surface and underground cave system has enabled intricate three-dimensional models to be built and layers of fine-resolution data to be documented by a wide range of specialists (Figure 2). These models have the potential to augment and be incorporated into virtual reality environments, or used to generate accurate spatial data for geologists, geomorphologists, archaeologists and science communications applications. As excavations have progressed in more remote areas of the caves, it is possible to locate individual specimens on global maps that include detailed metadata and can be linked to photographs, three-dimensional artefact models and databases in customised GIS (Geographic Information System) environments. Various postgraduate students are dedicating studies to exactly these problems and the development of sophisticated visualisation and analytical tools to help researchers and science communicators.

The complexity of the cave system has hindered the ability to incorporate all areas of the caves. To date, about 20% of the dry Sterkfontein Cave network has been mapped (another 5kms of passages and chambers are underwater). Surveying and laser mapping require a huge investment in time and equipment and in many areas the passages and chambers are just too narrow

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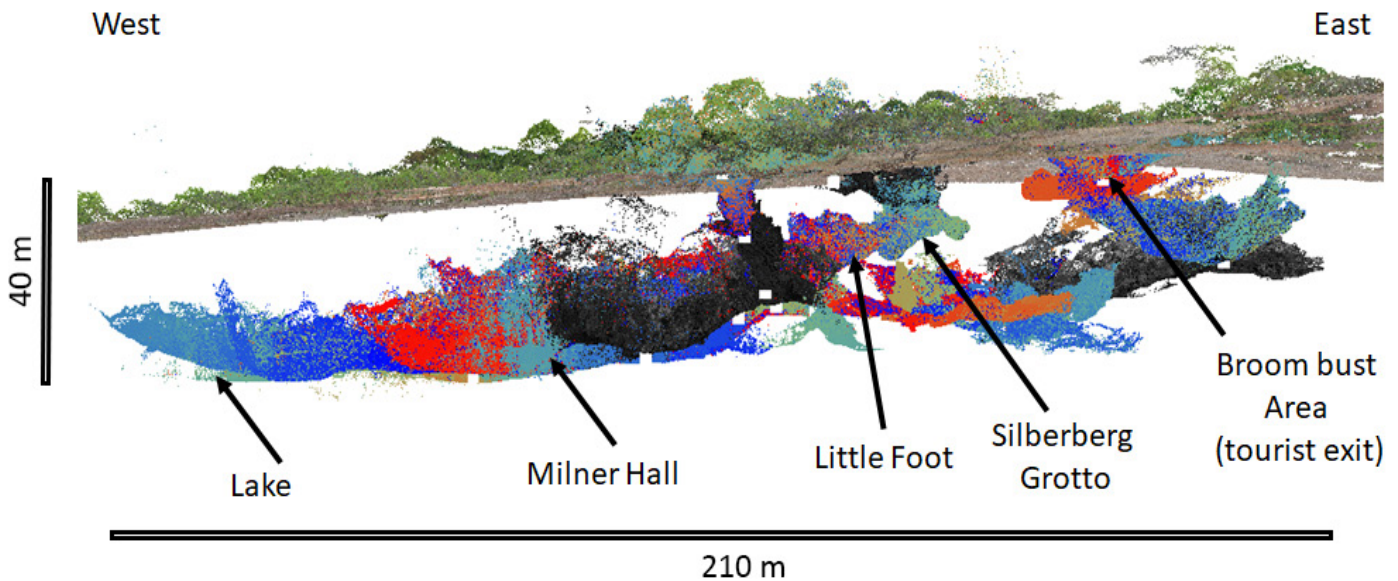


Figure 2. A dense three-dimensional points cloud generated through multiple laser scanning initiatives presenting an east to west profile through Sterkfontein hill and part of the underground cave system with some important areas of cave exploration and excavation labelled. The different coloured point clouds represent different scanning events. White squares represent survey control datum locations. Image credit: Dominic Stratford.

or tight to allow conventional LiDAR (a laser sensing device that measures the distances to objects) mapping tools. To address this challenge, in 2023, a joint project with the School of Computer Science and Applied Mathematics at the University of the Witwatersrand was established with the aim of deploying robots into the Sterkfontein Cave network to build detailed maps of the caves.

Robot mapping typically requires that the robot can localise itself within the environment, whilst simultaneously building a map of the regions it has already explored. This is a particularly difficult task in the cave setting, owing to the lack of GPS, the poor lighting conditions, and the complex physical characteristics of the spaces through which the robots must travel (for example Figure 3).

The unique challenges presented by the terrain in the caves necessitate a three-pronged approach to thoroughly explore the space. The main chambers can reach up to 36m in height. These have been mapped in the past by fixed position and handheld devices. To map the full extent requires aerial vehicles, or



Figure 3. Natural lighting in the Lincoln Cave, part of the Sterkfontein Caves network. Note the rock-strewn floor and irregular walls and ceilings. Image credit: Dominic Stratford.

drones, fitted with LiDAR scanners. The difficulty is that, because of the irregular shape of the chambers, the drones must be autonomous, and thereby able to avoid collisions with rocks (e.g., Ackerman, 2022).

The passages between the chambers are long, narrow, and winding, which makes them best traversed by terrestrial vehicles. These robots will be both legged

and wheeled, with the exact choice coming down to the size of rocks in each passageway, and the size crevasses in the ground. These, again, would carry LiDAR sensors to create 3D maps of the environment. Finally, a later phase of the project will involve deploying aquatic vehicles into the underwater sections of the caves. These regions remain completely unexplored. The augmentation of human scientists with robots in this way presents an exciting new chapter in the story of the caves.

The Sterkfontein Caves within the Cradle of Humankind represent a cornerstone in our understanding of human evolution, offering unparalleled insights into our ancient past. Over decades, this site has facilitated groundbreaking discoveries that have significantly advanced our knowledge of early human

ancestors, their behaviours, and their environment. The shift from manual excavation to the incorporation of advanced technologies and robotics for exploration and mapping illustrates the ongoing commitment to uncovering the secrets held within these ancient deposits. As research continues to evolve with these technological advancements, the Sterkfontein Caves promise to remain at the forefront of palaeoanthropological and archaeological research. The future of exploration in this unique and complex cave system holds the potential for uncovering further significant findings, thereby continuing to contribute to our collective understanding of human origins and the intricate history of life on Earth.

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Revolutionising palaeoneurology: Advanced analytics of sulcal imprints in fossil brain endocasts



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Introduction

The evolution of the human brain is characterized by a series of both allometric and non-allometric increases in brain volume, interspersed with significant reorganizational events. These events have involved several changes. Firstly, there has been a reduction of the primary visual cortex, which interprets basic visual information from the eyes. Secondly, there has been a relative expansion of the association areas in the prefrontal cortex. These areas are responsible for controlled and coordinated movement as well as orchestrating thoughts. Additionally, these evolutionary changes have been accompanied by an increase in cerebral asymmetries. Consequently, the modern human brain exhibits distinct differences in sulcal pattern (ravines on the brain) organization compared to our closest living relatives, the chimpanzees and bonobos (collectively referred to as extant *Pan*; Falk, 2014). Sulci provide a basic indication of the underlying functional architecture of the brain since they are closely related to the specific functional areas of the brain. For example, in humans, the area for speech and language (Broca's motor speech area) is located in the lateral prefrontal cortex, while the areas that help us understand what we see are mostly in the lateral occipital cortex, with a small part reserved for the primary visual cortex at the back of the brain. These areas in modern human brains have a unique sulcal

configuration compared to other primates. Palaeoneurologists are particularly interested in exploring the timing and mode of these derived cortical configurations in the fossil record.

Due to the delicate nature of brain tissue, it rarely withstands the taphonomic processes that the remains of our ancestors were subjected to. Consequently, we have to rely on the remains of cranial bones and their corresponding endocasts to study the evolutionary history of the brain in the fossil record. Cranial endocasts serve as a replica of the brain's "fingerprint" imprinted on the inner surface of the cranial vault. There are typically three types of cranial endocasts that can be studied in the fossil record. The first is a natural endocast, which is formed when fine sediments enter the cranium through foramina after death and over time this sediment will solidify to form an endocast. Notable examples of hominin natural endocasts include those of the "Taung child" and of Sts 60, respectively discovered from the iconic sites of Taung and Sterkfontein in South Africa, both attributed to *Australopithecus africanus*. The second type, synthetic endocasts, are created using moulding materials like liquid latex or silicon to form a mould, which is then used to create a cast, usually with plaster of Paris (Holloway, 2018). This method can be time-consuming and sometimes

harmful to the cranial remains, requiring expert palaeontological knowledge to produce a quality cast. The third and most recent type is the virtual endocast, generated using modern imaging techniques such as computed tomography (CT). Virtual endocasts are generated using non-destructive methods and are easily modifiable, and shareable, making 3D modelling the standard not only in endocast studies but also in other areas of palaeontology (Carlson, Rowe, Ketcham & Colbert, 2003).

Besides providing information on brain size and overall morphology, endocasts provide information about brain organisation through imprints that coincide with brain sulci. The study of brain sulcal imprints' convolutional anatomy on endocasts can reveal insights into the brain's underlying functional organisation, particularly the reorganisation of cortical areas over time. In particular, literature indicates a reduction in the primary visual cortex and an increased complexity in the frontal lobe's sulci, such as those around the Broca's region (Amiez et al., 2023). Research shows that the early hominin (i.e., non-*Homo* ancestors and relatives) brain exhibits a frontal lobe sulcal configuration similar to that of extant *Pan*, characterised by the Broca's area being anteriorly delineated by the fronto-orbital sulcus (Beaudet, Du & Wood, 2019). In some cases, such as the 2-million-years old (Ma) hominin remains discovered in South Africa and attributed to *Australopithecus sediba*, the fronto-orbital sulcus displays an intermediate pattern, bifurcating on the dorsal surface of the frontal lobe – a configuration also observed in brains of extant *Pan* (Hopkins et al., 2022). The modern human configuration first appears between 1.7 to 1.5 Ma in the fossil record, although there was considerable variation within *Homo* during this period (e.g., Dmanisi fossil crania from Georgia; Ponce de León et al., 2019; Beaudet & de Jager, 2023).

Similarly, the position of the lunate sulcus on early hominins, which is suggested to delimitate the visual cortex in non-human great apes, has been debated for many years. The debates surrounding the lunate sulcus primarily stem from a lack of consensus among researchers, exacerbated by inconsistent methods for

studying cortical imprints on endocasts. The advent of high-resolution imaging for generating endocasts enables the application of more precise methods to previously unstudied, fragmented fossil endocrania. Despite this, a notable portion of cortical imprint research still depends on the manual description of endocast imprints, necessitating extensive neuroanatomical expertise for accurate identification and labelling. In neuroscience, population-specific brain atlases have become instrumental in anatomically labelling and identifying brain structures across various platforms and modalities. Three main methods underpin these atlases, as described by Toga and Thompson (2001). First, the label-based approach involves manually segmenting large volumes of brain data after alignment. This allows for the creation of a probability map for structures of interest, based on the proportion of subjects assigned a given anatomical label at each voxel. Second, the deformation-based approach employs a warping algorithm to generate a deformation map from a scan, relative to a reference scan. This method is instrumental in elucidating anatomical differences between populations. Lastly, we utilize the density-based approach in our research. Its suitability for aligning images on a voxel-by-voxel basis makes it ideal for our samples, which exhibit high interindividual variation. Leveraging this foundation, we propose a method employing automated detection to identify and characterise the interindividual variability of cortical sulcal imprints on the surface of virtual endocasts, tailored for application in the fossil record.

Proposed method

Our proposed method encompasses four distinct phases: image acquisition, automatic extraction of endocast, automatic imprint detection and atlas creation, and finally, density map creation (Figure 1). In the image acquisition phase, we found that 3D surface scanning effectively scans both natural and synthetic endocasts, and it works well for partial cranial remains as well (Figure 2). For more complete fossil remains, high-resolution imaging techniques such as lab-based or synchrotron Micro Focus X-ray

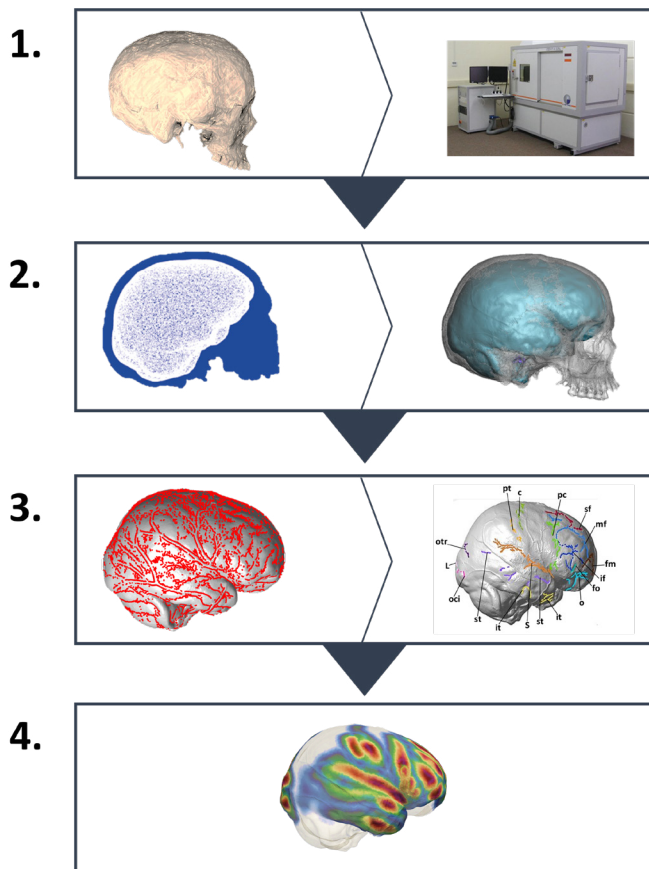


Figure 1. Schematic of the steps that form the foundation of the proposed method. *Step 1:* Image acquisition using micro-CT. *Step 2:* Automatic extraction of endocast. *Step 3:* Imprint detection and atlas creation. *Step 4:* Density map creation

Tomography (micro-CT) can be used to scan heavily mineralized fossil remains. These latter methods yield images of higher resolution, and they also generate correspondingly larger file sizes. Following this, we used an open-source, automated segmentation software, called Endex (<https://perso.liris.cnrs.fr/gilles.gesquiere/wiki/doku.php?id=endex>) to extract the endocast from the cranium. After the extraction of the endocast, we employed a crest line detection method, based on the algorithm by Shin Yoshizawa and co-authors (2008), to detect imprints on the endocasts. We then used a custom MATLAB (Mathworks) program to label crest lines indicative of sulcal imprints (Figure 3). We tested this approach on extant human endocasts, leading to the first description of sulcal imprints in this context (de Jager et al., 2019). The final phase involves the incorporation of brain atlas concepts to visualise

the inter-individual variation of sulcal imprints via a density map (de Jager, Risser, Mescam, Fonta & Beaudet, 2022; <https://www.endomap.org/>). To create a density map, we had to make sure that all our endocasts were aligned within a 3D space after which they were deformed towards each other to calculate the average endocast. Once the average endocast was calculated we could use the deformation values to project all the sulcal imprints onto the average endocast to create a density map.

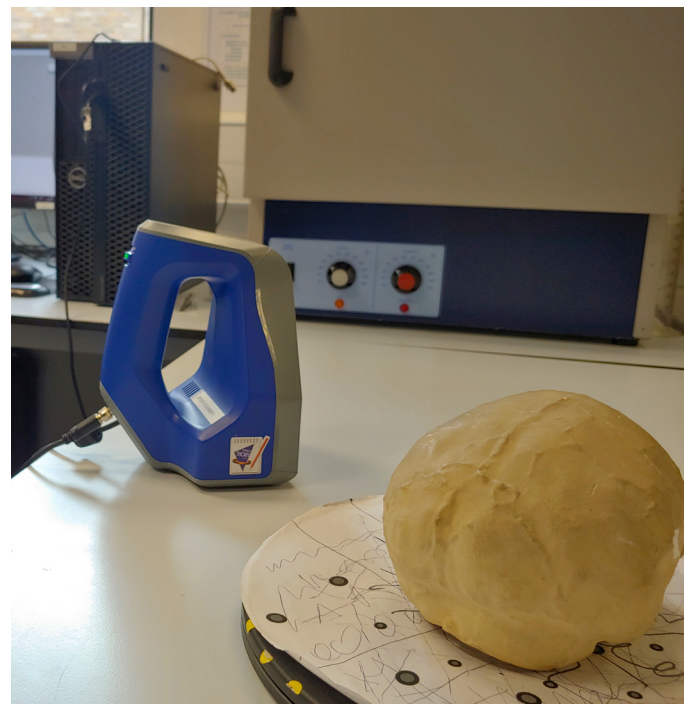


Figure 2. Surface scanning of Neanderthal plaster endocasts from La Quina, curated at the Duckworth collection in Cambridge, using Artec Space Spider 3D scanner.

Perspectives

Utilizing this method, we were able to visualize, for the first time, the complete anatomy of the fragmentary sulcal imprint distribution of the entire sample of modern human endocasts. Modern human endocasts are historically challenging to study due to their limited sulcal imprint visibility when analysed with older standard methods. However, by employing high-resolution micro-CT scanning combined with an automated detection method we successfully created an

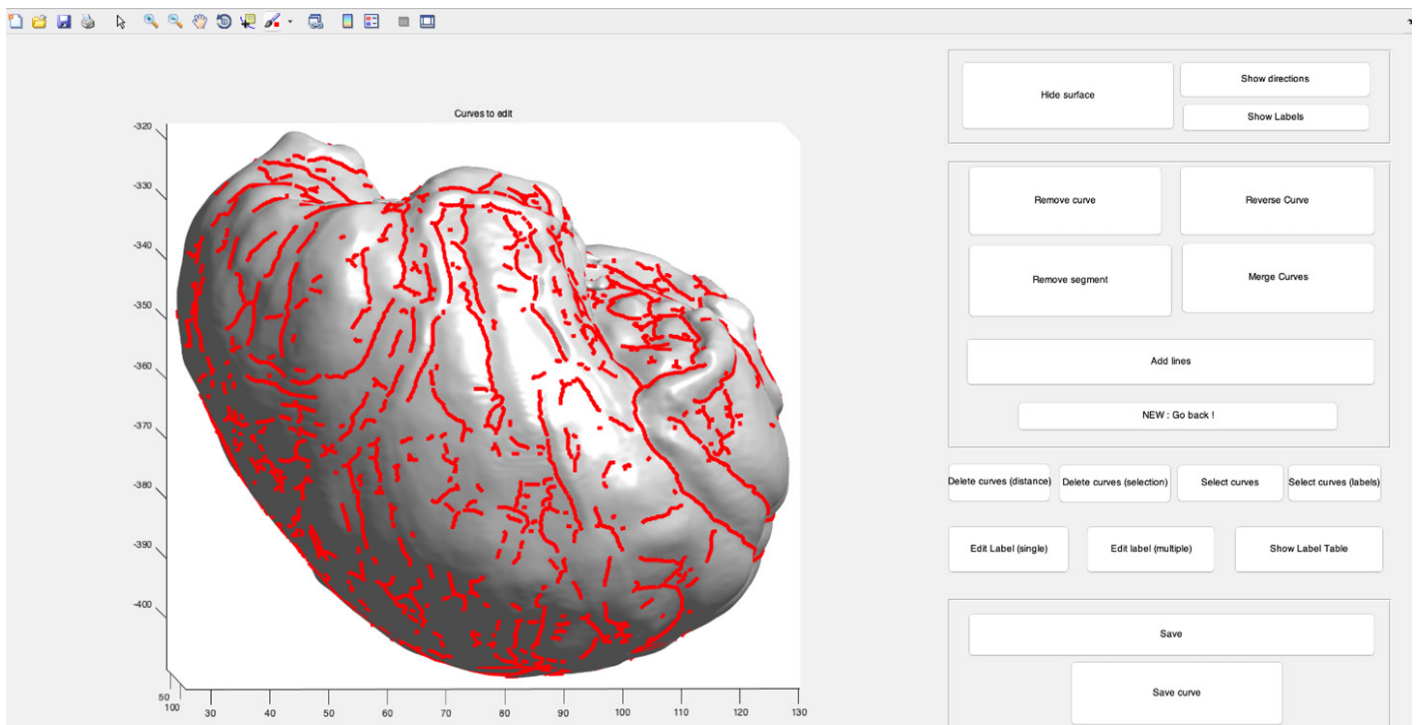


Figure 3. Interface of custom MATLAB software that was used to label curves.

atlas of sulcal imprints on modern human cranial endocasts (Figure 4). To test the correlation between endocast imprints and actual brain sulci in extant humans, Dumoncel et al. (2021) used CT scans and MRIs of the same individual, revealing an 80% correlation, with higher variability on the brain's superior surface. The reason for this lack of imprint formation on the superior surface of the brain is not yet fully understood. Given the method's effectiveness on extant human endocasts, we intend to expand our analysis to include our closest living relatives, extant *Pan*. Mapping the cranial endocasts of extant *Pan* will provide an updated reference of the ancestral brain morphology and sulcal patterns in the hominin lineage, offering a crucial baseline for future comparative studies of evolutionary changes in the fossil record. Once we have established a comparative database of extant *Pan* sulcal imprints on endocasts, we will be able to implement it in combination with the modern human sulcal imprint atlas to map various fossil hominin endocasts including *Australopithecus*, *Paranthropus* and members of *Homo*. We envisage that by imple-

menting this methodological approach we will be able to provide empirically validated descriptions of sulcal imprints in the fossil record and in the process solve long-standing debates in palaeoneurology.

Like any new analytical method, our proposed method has limitations and areas for improvement. Our approach still relies on manual labelling of imprints and endocasts, and there is ongoing debate regarding the nomenclature and identification of sulci, particularly the sulci of the occipital lobe in modern human brains. This issue can be mitigated in brain scans by using brain atlases and machine learning to standardise sulcal labelling and identification. The fragmentary nature of sulcal imprints on endocasts and the absence of a complete reference database for all sulcal imprints, combined with a small sample size, complicates resolving this issue using machine learning. However, the advancing development of AI technology and cross-platform imaging analysis methods will significantly enhance our study of cranial endocasts and the fossil record in the foreseeable future.

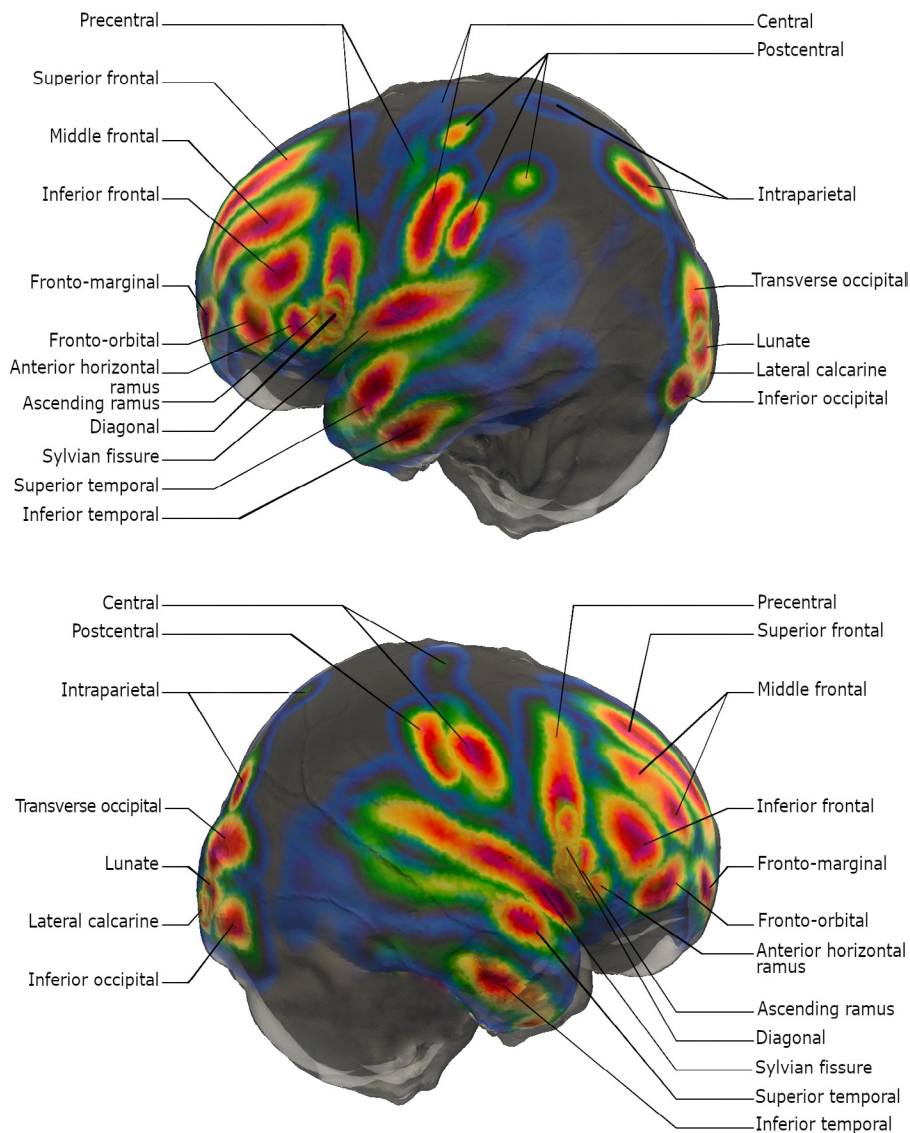


Figure 4. Density map of sulcal imprints on 20 modern human endocasts depicting the density distribution of sulci identified. The dark red centre indicates the highest probability of identifying a sulcus whereas blue indicates the lowest probability (de Jager, 2024).

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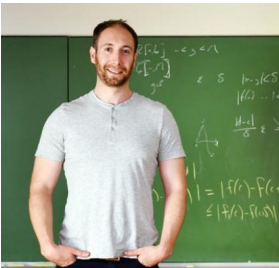
Using Machine Learning to Study the Aging Brain



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Introduction

Structural Magnetic Resonance Imaging (MRI) is a technique which allows one to study features of the whole brain at sub-millimetre scales in a non-invasive way. This can be used by radiologists to find pathologies and damage in the brain for which X-rays and CT-scans are insufficient. However, when there are many scans to look at or compare, or where the damage location is unknown, even experienced radiologists may miss the source of the problem. Over the last few years, machine learning techniques have been developed for analysing MRI scans and have shown great promise in detecting pathologies that may be missed by a human (Ahsan & Siddique, 2021), even though it is still vital to have a human in the process to validate the findings.

There are other questions about the brain for which even a well-trained human is unable to answer with any reasonable accuracy. One such question is about the age of a brain. Over the lifetime of a healthy person, the brain changes, with certain parts growing,

and others shrinking (Figure 1). As an example, the ventricles (structures filled with cerebrospinal fluid) get larger as we age (Sachdev, 2003).

One reasonable question would then be whether it is possible to develop a machine learning algorithm to predict how old a person is based on an MRI image of their brain. Given a three-dimensional MRI image, the output of such an algorithm will be a number - the predicted age. If such an algorithm is trained on a large dataset of healthy people, where their brains are thought to be aging at a normal rate, the algorithm can 'learn' what the brain looks like at different ages. Thus, if a patient's brain is predicted to be older than the person is, this may indicate that there is some underlying pathological condition (Cole et al., 2016).

The difference between a person's chronological age and their predicted brain age is known as the brain age delta:

$$\Delta_{\text{brain age}} = \text{age}_{\text{predicted}} - \text{age}_{\text{chronological}}$$

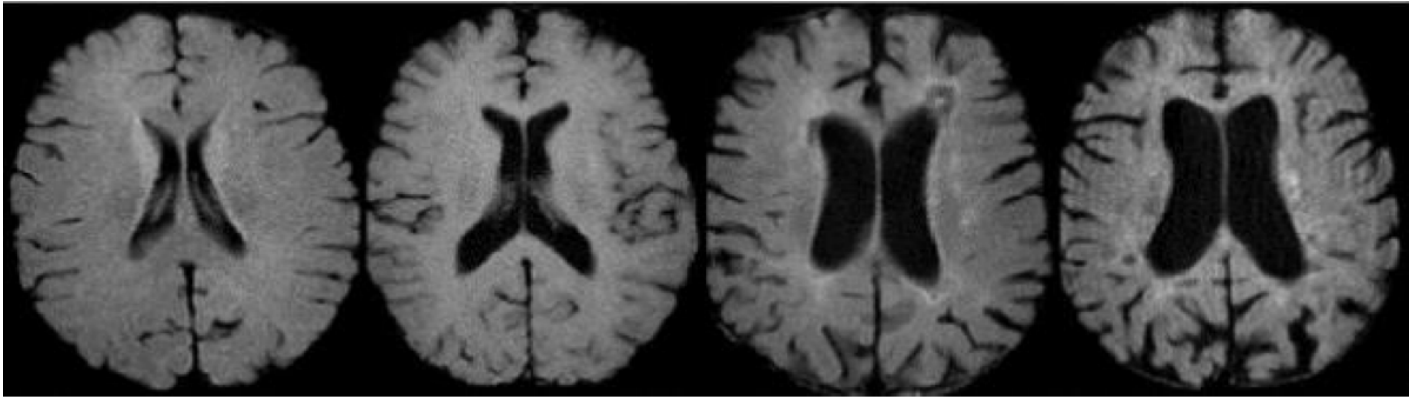


Figure 1. In these MRI images, one can clearly see the ventricles in the centre of the brain enlarging from younger to older patients (left to right). MRI images courtesy of the Oregon Brain Aging Study, Oregon Alzheimer’s Disease Research Center.

Those with brains that are aging at a normal rate should have $\Delta_{\text{brain age}}$ around zero, and those with more rapidly aging brains have $\Delta_{\text{brain age}} > 0$.

By training on a healthy population, and testing on a similar population, the so-called mean absolute error can be used as a metric for how good this algorithm is. The mean absolute error (MAE) is given by:

$$MAE = \sum_{i=1}^N |age_{predicted}^i - age_{chronological}^i|$$


where the sum is from participant $i=1$ to $i=N$, $age_{predicted}^i$ is the output of the algorithm (also referred to as model) for the i^{th} participant and $age_{chronological}^i$ is the true age of the i^{th} participant.

There are many factors that go into how accurate such a model is. These include the number of brain images in the training set (used to train the machine learning algorithm in the first place), and the distribution of ages of people in that training set (Bashyam et al., 2020). For instance, if a model has been trained on images of people who are between 20-40 years old, it is not expected that it would give accurate predictions for people aged 80 years. One of the central tenets of machine learning is that the distribution of

the training set should be as similar as possible to the distribution that the algorithm will be used on in practice. For example, a doctor whose patients are mostly elderly should be using an algorithm trained on an older population.

Finding datasets that are large enough, and with the right distributions for a given problem, can often be difficult. In this study, a two-stage process was used whereby the model was first pre-trained on a large dataset with a limited age distribution, and then further trained on a smaller dataset with a wider age distribution. This created a model which could then be applied to populations of patients over a wide range of ages. This method, known as transfer learning, involves pre-training on one dataset followed by further training on a more specific problem using the same algorithm. An analogue for this would be for a person to ‘pre-train’ by learning to read on very general material, and then to use these reading skills to learn about a new topic by reading up on that, specifically. The skill of reading is transferred to a new skill that one wants to acquire.

What actually are such machine learning models? The MRI images themselves are composed of three-dimensional pixels, known as voxels, each represented by a single number that indicates its brightness. This number corresponds to the strength of the signal detected by the MRI machine. For such complex three-dimen-



sional images, a neural network architecture known as a residual neural network (ResNet) is ideal (Jonsson et al., 2019; Kolbeinsson et al., 2020). These are machine learning architectures inspired by networks in the real brain (Fukushima, 1980), with features corresponding to real visual systems (so-called convolutional layers). These machine learning algorithms require powerful computers (using Graphical Processing Units to accelerate the computations) and very large amounts of data (often in the hundreds of gigabytes).

In this study, an adapted ResNet was designed and trained on around 15,000 brain images from the UK Biobank dataset (Sudlow et al., 2015). This dataset has around 21,000 images of participants in the age range from 45-82 years. After validating that the model had been accurately trained, the pre-trained model was then trained again on a smaller dataset called CamCAN which contains only 652 images but is over a wider age distribution of 18-88 years (Shafto et al., 2014; Taylor et al., 2017).

In the description above, there are a number of steps which have been missed. These include the steps of pre-processing the data, de-biasing the predictions and fine-tuning hyperparameters of the model. However, when all of this has been appropriately carried out, the predictions on the UK Biobank dataset were an MAE of just 2.57 ± 1.94 years, meaning that on average the predicted age was around 2.6 years from the chronological age, a result which is close to state of the art.

After pre-training on the large dataset, and then training on the smaller dataset, the results were an MAE of 3.54 ± 2.59 years. This number is higher than the 2.57 quoted above, but this is being applied to a smaller dataset with a much larger distribution of ages than the pre-training dataset. Had pre-training not been carried out, the MAE would have been 6.38 ± 5.30 years, showing a very significant increase in accuracy obtained using the transfer learning technique.

The techniques developed and discussed in this note may seem to be very specific to a particular problem, but in fact the process of transfer learning and automatic image analysis of three-dimensional scans can be applied to many problems, including those of archaeology and palaeontology. This could include the analysis of bone fragments, to pottery and beyond. We are at an exciting moment in integrating powerful machine learning techniques into many areas of science and the future of this work is definitely bright.

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Reconstructing incomplete fossil long bones – The Reverse Engineering method



Julia Aramendi & Lloyd A. Courtenay

Julia Aramendi is a postdoctoral researcher at the University of Cambridge funded by the British Academy (NIF22\220310) for her project titled “Exploring locomotor and biomechanical diversity in the hominin fossil record based on long bone external morphology”. Her research focuses on the development of new techniques for the study of fossil hominin long bones, combining the techniques within virtual anatomies and artificial intelligence.



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Context and study aims

The anatomical study of our ancestors and close relatives (i.e., hominins) has traditionally focused on cranio-dental remains, but recent attention has shifted to the postcranial skeleton, that is the skeletal elements located behind or beneath the cranium, as it has been proved to be essential to comprehend many behavioural (i.e., locomotion, tool use and making) and social aspects (i.e., pregnancy, group structure). However, understanding bone morphology and function is challenging due to various factors such as genetics, posture, activity, and pathologies that may influence the external bone shape and be responsible of the evolutionary trends observed in the fossil record (e.g., adaptations, retention of ancestral traits, convergence). Additionally, the study of living primate species (chimpanzees, gorillas, orangutans, humans), which has been widely used to make biomechanical inferences on the human fossil record, is not as straightforward as researchers would wish. First, the link between form and function is still not clear among extant groups and second, fossil specimens often present unique features

that are not observed in extant species and are thus difficult to interpret.

The difficulties in properly understanding the biomechanical capabilities of our ancestors also lie in the scarcity and poor preservation of the fossil record. The availability of hominin remains in the archaeo-palaeontological record is quite limited, even more so in the case of Pliocene (5 to 1,6 million years ago) and Early Pleistocene (2,6 to 0,8 million years ago) sites, like the ones of the “Cradle of Humankind” in South Africa. Moreover, hominin fossil bones do not only appear quite rarely, but they are usually discovered in a fragmentary way, which limits our understanding of human evolution.

Researchers have tried to cope with the fragmentary nature of the human fossil record in diverse ways, including the use of statistical methods to predict bone length (see review in Reno et al., 2005), and perform overall reconstructions using a variety of computa-

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tional techniques, that are fundamentally based on the use of symmetrical structures, like those found in the cranium (Gunz, Mitteroecker, Neubauer, Weber & Bookstein, 2009). These methods are thus based either on the availability of other complete or almost complete fossil remains subsumed in the same fossil taxon, on the use of symmetry to reconstruct missing bone areas, or on the extrapolation of data collections on modern samples. From this context, three methodological questions emerge:

- 1) How should palaeoanthropologists deal with the reconstruction of fragmentary remains, when no other similar specimen is available, or the taxonomy is ambiguous?
- 2) How should we proceed with those remains that lack symmetry, like limb long bones?
- 3) Up to what point are modern data valid for the reconstruction of extinct species considering they do not accurately represent ancestral morphologies?

In light of the difficulties that palaeoanthropologists must face when studying postcranial remains, the present project is designed to provide a replicable quantitative method to reconstruct incomplete fossil remains. More specifically, our project focuses on the development of innovative techniques, including 3D virtual methods and advanced computational tools, for reconstructing hominin long bones of the upper (humerus and radius) and lower (femur and tibia) limbs.

Reconstructed information would offer palaeoanthropologists novel ways for anatomical comparison, effectively addressing the bias introduced by the lack of homology among hominin specimens. Furthermore, this reconstructed data could contribute new evidence to the enduring discussions surrounding the emergence and identification of key features typically associated with humankind, such as tool use and manufacturing, terrestrial bipedal walking, and the assessment of biomechanical capabilities within the Plio-Pleistocene hominin taxa.

Methodological approach

The methodological approach combines the use of data gathered in the form of landmarks, as defined in geometric morphometrics (GMM), with Artificial Intelligence (AI) models to reconstruct missing bone portions.

GMM is a widely used technique in palaeoanthropology based on the identification of landmarks (O’Higgins, 2000), i.e., specific homologous points that contain morphological information in the form of Cartesian coordinates (Bookstein, 1991; Dryden & Mardia, 1998). In the case of long bones, analyses are usually limited by the preserved area of the specimen under study since anatomical reference points are located on the long bone ends. In the present study, alongside the commonly used fixed anatomical landmarks, a dense point net made up of sliding semilandmarks is projected onto the diaphyseal region – the shaft or central part of a long bone – to gain as much information as possible from the preserved region in complete and/or fragmentary specimens. Semilandmarks are particularly useful in those cases where no or few anatomical landmarks have been defined (Bookstein, 1997), as it is the case of the long bone shafts. Semilandmarks thus make it possible to quantify homologous surfaces and analyze them together with fixed landmarks. Homology is achieved through the sliding algorithm which mitigates the effects of arbitrary landmark distribution by “optimizing” the positioning of semilandmarks relative to the average shape (Gunz & Mitteroecker, 2013).

First, the long bones of complete modern great apes, including humans, chimpanzees, gorillas, and orangutans were digitised using surface scanners, achieving a maximum resolution of 0.15 mm (Figure 1). Additionally, we selected several *Homo naledi* (Berger et al., 2015) humeri and femora available in Morphosource (<https://www.morphosource.org/>), that present different levels of fragmentation and represent different bone portions. *Homo naledi* is a hominin species found in the Rising Star Cave System (South Africa) that is dated to ca. 230.000 years ago (Dirks

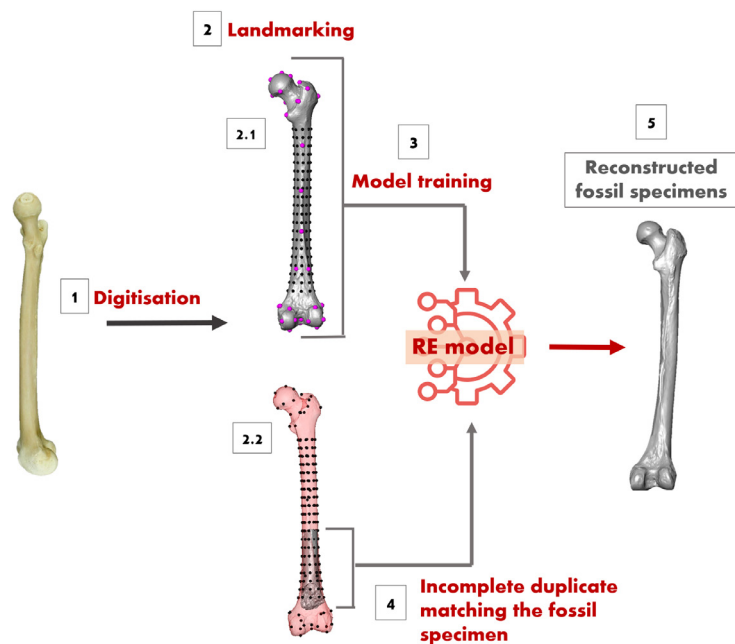


Figure 1. Workflow of the Reverse Engineering approach.

- 1) Digitization of the original extant primate long bones;
- 2) Landmarking of both (2.1) complete modern long bones and (2.2) incomplete fossil bones, including both landmarks (pink) and semilandmarks (black);
- 3) Model training based on the information gathered from complete extant specimens;
- 4) Generation of a sample duplicate that only includes the landmarks and semilandmarks represented in the fossil specimen to be reconstructed (excluding the landmarks that correspond to the bone portions depicted in red);
- 5) Estimation of missing bone portions in fragmentary fossil long bones, and generation of a complete fossil specimen considering the original and reconstructed landmarks and semilandmarks.

et al., 2017) and that presents anatomical adaptations in its limbs that have been linked to both terrestrial bipedalism and climbing (Feuerriegel et al., 2017; Marchi et al., 2017). Then, all 3D models were landmarked using both Avizo (v. 2020.3.1) and the Evan ToolBox (v.1.75), following the same strategy, though the fossil group is represented by a reduced number of landmarks as bone portions are missing (Figure 1).

To estimate the missing landmark in each fossil specimen, the morphological data gathered from modern specimens in the form of superimposed landmark configurations – that is after rotation, translation and scaling as usually performed in GMM (Goodall, 1991; Rohlf, 1999) – are introduced into the reconstruction model. The method has been preliminarily named the Reverse Engineering (RE) approach and is based on establishing the relationship between a set of morphological variables, describing the preserved portion of bone represented by each fossil, and the corresponding landmark configurations that represent the complete bones in our modern reference collection (Figure 1).

The mathematical function can be defined by using a series of supervised regression problems, leverag-

ing tools provided by AI to improve model accuracy, including standard and robust linear regression, regression trees, Support Vector Machines, Neural Networks, and Meta-learning regression algorithms. Once this mathematical function is defined, it can be employed to predict the morphology of the entire bone corresponding to each *Homo naledi* humerus and femur remains.

Preliminary results and future perspectives

Using RE, we were capable of successfully reconstructing all fragmentary *Homo naledi* remains (Figure 2), providing complete sets of landmark configurations for each specimen. In that way analytical problems related to the lack of homology among fossil specimens could be solved, providing new perspectives to the study of hominin long bone remains.

According to our results, the use of meta-learning algorithms holds particular promise for the reconstruction of hominin long bones. This approach is capable of

Reconstructing incomplete fossil long bones – The Reverse Engineering method

generalizing the information collected from complete modern groups and utilizing the acquired knowledge to reconstruct fossil specimens that might present different anatomical features. That means that the RE approach does not just replicate the information of the modern specimens used to train the model, but it can identify morphological patterns and apply them to unknown specimens, such as those represented here by *Homo naledi*.

In the context of this project, we have also compared the RE approach to state-of-the-art methods for estimating missing landmarks in modern great ape long bones. This primarily included Gunz and colleagues' (2009) Thin Plate Spline approach, and Brown and colleagues' (Brown, Arbour & Jackson, 2012) Bayesian Principal Component Analysis algorithm, among others. Error estimations were computed through various experiments on modern reference samples using Leave-One-Out Cross Validation. This involved iteratively excluding one individual from the reference sample, removing a portion of landmarks, and utilizing the remaining individuals as reference to predict the position of the missing landmarks. Our findings suggest that the RE approach outperforms other methods that were tested in terms of accuracy for reconstructing missing landmarks on extant great ape long bones (Figure 3). These differences in performance become particularly remarkable when the bone area to be reconstructed is large. These results imply that our method excels in handling situations with a high degree of missing information, making it a valuable choice, especially when dealing with small long bone remains.

The method's preliminary success suggests its potential application to other skeletal elements, making it a valuable resource for a broader spectrum of palaeoanthropologists. Digital resources for other researchers will be created in the form of open-access software, including packages and libraries in both R and Python, which are open-source programming languages that do not require a licence to operate or use and that are well known in the palaeoanthropological community.

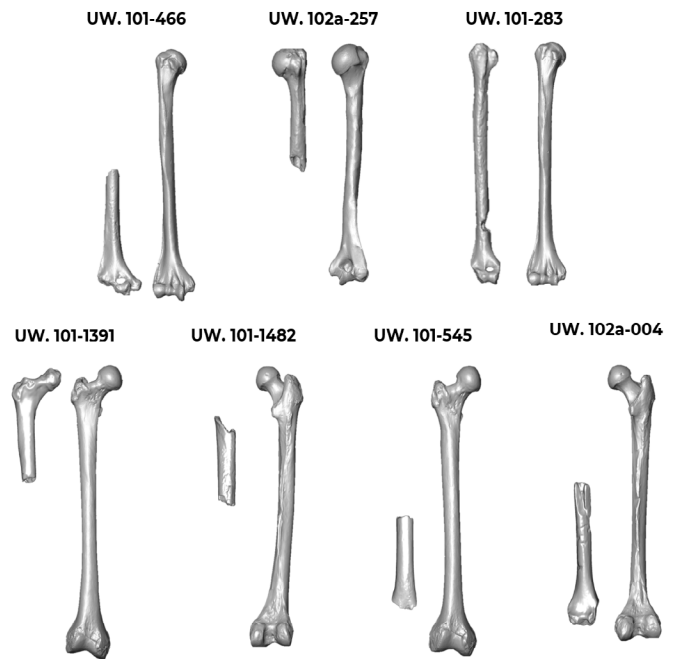


Figure 2. Original and reconstructed humeri and femora of *Homo naledi* using the reverse engineering method.

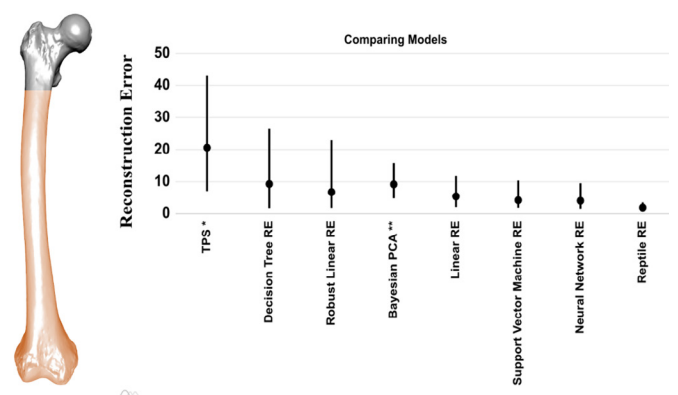
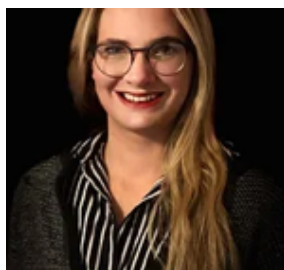


Figure 3. Performance accuracy across various reconstruction models. The meta-learning reverse engineering method (Reptile RE) generates the smallest reconstruction errors in comparison to other methodologies tested in this study when estimating large bone portions (depicted in orange).

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The Evolution of Deception in Great Apes



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Introduction

Humans have often been characterised as ‘cognitively superior’ to other animals, including non-human primates (Tomasello & Rakoczy, 2003). More recently, comparative studies reveal that some of these ‘unique’ cognitive features in humans are, in fact, present in other animals (Laland & Seed, 2021; Read, Manrique, & Walker, 2022). For example, one of the most intriguing parts of primate cognition is non-human primate’s ability to *intentionally* deceive (Laland & Seed, 2021). There is a particular interest in examining the evolutionary origins of deception in the primate lineage and the level of complexity involved, as this would inform the evolution of these abilities in humans.

Byrne and Whiten (1988, 1990) argue that deception can be divided into two categories amongst non-human primates and humans. The simplest form, found in certain species of ceboids (e.g., Capuchin monkeys) and cercopithecoids (e.g., Rhesus monkeys), is a learnt response, developed through trial-and-error and observational learning (Hatchett, 2001). Here, the subject seeks to attain a particular goal, and stumbles upon a particular deceptive strategy that assists with reaching a specific goal, which is then repeated in similar circumstances (Hatchett, 2001). For example, primates learn to avoid rival mating partners, and they will only attempt mating when the rival is out-of-sight,

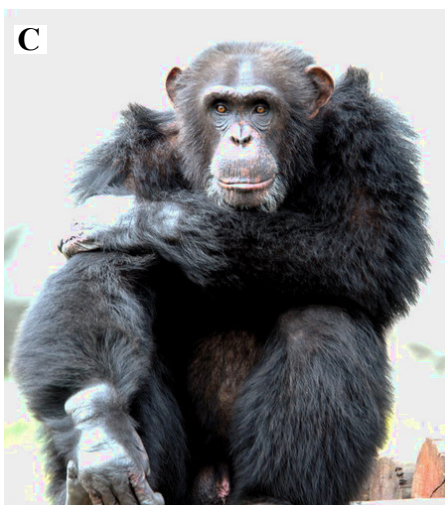
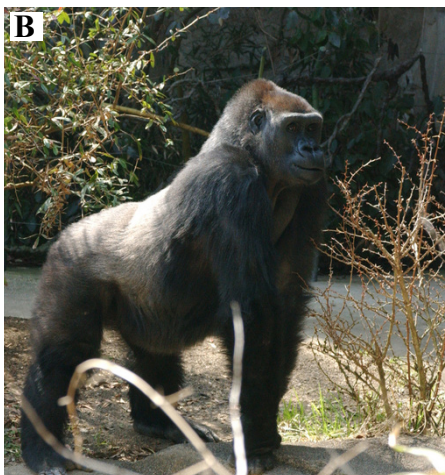


Figure 1. Great Apes are a group of primates that includes gorillas, orangutans, bonobos, chimpanzees, and humans. They are known for their complex social structures and advanced cognitive abilities. (A) Bonobo (B) Gorilla (C) Chimpanzee
Sources: <https://animaldiversity.org/> and <https://commons.wikimedia.org/>

or when the rival's sight is obscured (Tomasello & Call, 1997). Mitchell (1986) describes this type of deception as 'open plan', as the animal has a series of learnt responses that they can refine or customise. In this instance, the deceptive act can be considered intentional, but not *intentionally deceptive* (Ureña Gómez-Moreno, 2019). The animal acts in a way to elicit a desired response or outcome through deception. Nonetheless, they are not consciously aware that they are 'deceiving' another individual, and consequently, they do not actively manipulate the mental state of the deceived (Mitchell, 1986).

The second type of deception requires awareness of self and other and is thus more cognitively demanding, as a subject must intentionally deceive or manipulate someone else to gain an advantage (commonly referred to as 'tactical deception'). In this instance, different types of tactical deception require different cognitive skills, which vary in complexity, but there is some overlap in terms of the cognitive processes involved. Tactical deception, for example, requires perspective taking and theory of mind to understand the mental states (e.g., the beliefs, knowledge, desires, intentions) of others. It also relies on executive functions (e.g., a set of complex cognitive abilities), such as response inhibition and working memory.

In the current study, we review the literature on tactical deception in Great Apes, including bonobos (*Pan paniscus*) (Figure 1A), gorillas (*Gorilla gorilla*) (Figure 1B), chimpanzees (*Pan troglodytes*) (Figure 1C), and humans (*Homo sapiens*). More specifically, we focus on the extent to which similarities and differences are observed between species. Given the close phylogenetic relationship between chimpanzees and humans, we examine the extent to which chimpanzees engage more readily in acts of deception. In addition, we look for potential differences in terms of complexity between bonobos, gorillas, chimpanzees, and humans. For the purposes of this study, the term 'deceptive behaviours' is classified according to the functional categories of tactical deception outlined in Byrne & Whiten (1988), which are then assessed according to the level of complexity involved.

Evidence for tactical deception in non-human apes

There are a range of deceptive behaviours (e.g., teasing, concealing, pretending, and distraction) observed in non-human great apes, which implies that they engage in different types of tactical deception, which vary in cognitive complexity. For the purposes of this study, two of these behaviours are briefly discussed in non-human great apes. The first type of deception is ‘pretending’, which occurs during play, and many examples of this type of deception have been observed in non-human apes (e.g., Byrne, 1995; Parker & McKinney, 1999; Savage-Rumbaugh & Talbot, 1998). From a cognitive perspective, it requires executive functions, such as sustained attention and response inhibition, as the player needs to hold simultaneous representations of two conflicting sets of knowledge or beliefs in mind and understand when to withhold responding to events. It has been observed in bonobos (e.g., Savage-Rumbaugh & Talbot, 1998), gorillas (e.g., Byrne, 1995), and chimpanzees (e.g., Byrne, 1995; Parker & McKinney, 1999).

The second type of tactical deception is ‘concealment’. In this instance, information is withheld without ‘saying anything untrue’ (e.g., lies of omission), and it requires the ape to infer the perspectives of others (‘theory of mind’). The strongest evidence for this type of deception is found in chimpanzees, i.e., observed with food competition (e.g., Hare, Call & Tomasello (2006). Studies such as this show that chimpanzees have the mental ability to intentionally manipulate the psychological states of others through deception. This is currently the strongest evidence for intentional deception in non-human great apes, a cognitive capability once believed to be unique to humans.

Based on the above studies, there are many behaviours in non-human apes that meet the requirements of Whiten and Byrne (1988) so-called definition of ‘tactical deception’, but it remains elusive whether they are examples of intentional deception. In comparison to orangutans and bonobos, intentional acts of decep-

tion are most common in chimpanzees. For example, studies, such as Hare et al. (2006), reveal that chimpanzees are capable of actively manipulating what an individual experiences, cognitively.

Evidence for tactical deception in humans

There are certain types of deception that are also observed in children, and as the child’s brain develops, their ability to deceive progresses in cognitive complexity. Interestingly, evidence for deception is found as early as infancy. For example, certain types of deception, such as pretending, teasing and concealment, are apparent in the first year of life (e.g., Reddy & Mireault, 2015).

In contrast to non-human apes, humans can engage in more advanced forms of tactical deception. For example, ‘prosocial lies’ (e.g., false statements made to deceive others with the intention of protecting or helping others) are believed to be unique to humans (Talwar & Lee, 2008). This is unsurprising, as it is cognitively demanding, and consequently, it is interesting to explore the cognitive mechanisms involved in prosocial lying. The latter, for example, requires advanced theory of mind to understand the mental states of self and others. It also involves a range of executive functions, such as: (1) ‘response inhibition’, i.e., to conceal the transgression, the deceiver must inhibit interfering thoughts while focusing on the lie and withhold responding inappropriately, (2) ‘cognitive flexibility’, as liars must shift between ‘what actually happened’ and the false information proposed, so as not to give anything away, and (3) ‘working memory’ to assist with the control of ‘semantic leakage’, i.e., to prevent revealing the truth.

For most children, prosocial lies are observed from about 4 years of age (Demedardi, Brechet, Gentaz, & Monnier, 2021). Even though prosocial lies appear early in life, the frequency, effectiveness and complexity of prosocial lying continues to develop with age. For example, children, aged 7 and older, are more inclined to tell prosocial ‘white lies’ (e.g., unimportant lies that

intend to avoid hurting another person), despite the potential costs to themselves (for examples see Talwar & Lee, 2008; Lee, 2013). As children grow older, there is increasing concern for the needs of others (e.g., they engage more readily in altruistic behaviour), and as a result, they are more likely to tell both ‘prosocial white lies’ and ‘prosocial blue lies’— e.g., lies that are intended to benefit an in-group collective — (for examples see Talwar & Lee, 2008; Lee, 2013). In this instance, it appears that these lies are often told to conform to social norms and to encourage mutual trust and societal stability.

Implications for understanding modern humans

Given that prosocial deception is not observed in non-human mammals and appears to be unique to humans, there is an interest in theorising ‘how’ and ‘why’ it was selected for in human evolutionary history. Evolutionary theorists, such as Simpson and Beckes (2010, p. 50) argue that it might be the result of many selection pressures and many evolved cognitive mechanisms, all of which have “pushed human evolution in an increasing cooperative and prosocial direction, relative to other species”. Simpson and Beckes (2010, p. 50) state that “multiple forces and selection pressures probably favoured cooperation and caring during human evolution” and that this “runs counter to the common misconception that evolution entails fierce direct competition”. Consequently, our most reproductively successful ancestors might have been the most cooperative and resourceful individuals within their groups (Simpson & Beckes, 2010). Prosocial lying might thus have been socially encouraged. Not only does it enhance collaboration and social cohesion, but it also provides a peaceful, harmonious society, which might have been critical for human survival.

Conclusion

The evolutionary strategy for tactical deception, once believed to be unique to humans, has been observed in non-human apes, including chimpanzees, gorillas, and orangutans, however it varies in frequency and complexity. Despite these findings, tactical deception is most clearly shown in chimpanzees, when compared to other non-human apes. This review also reveals that human deception differs from that of other non-human apes. ‘Prosocial lies’, for example, have only been observed in our species. This is unsurprising, as it requires more complex cognitive mechanisms, when compared to other types of deception. It involves advanced theory of mind and executive functions, such as response inhibition, cognitive flexibility and working memory. Not only does it encourage trust and cooperation within a group, it might also explain how more complex human societies evolved.

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Cognitive abilities and identity of Early Pleistocene (2.6-0.8 million years) stone-tool makers, an overview



Sandrine Prat

Sandrine Prat is a senior researcher at the CNRS HNHP laboratory at the Musée de l'Homme in Paris. Her research focuses on early Homo, Paranthropus and Australopithecus to understand their anatomical and behavioral diversity, phylogeny and dispersal and addresses issues such as the definition of the genus Homo.

Context

To understand the evolution of higher-order cognitive functions, such as the planning involved in tool-making, researchers must draw inferences from contemporary human and non-human primate studies and apply these insights to fossil and archaeological records. This approach, while insightful, faces the challenge of direct evidence. The evolution of the brain and its cognitive functions remain one of the foremost scientific challenges in this field (de Sousa et al., 2023), largely because it is impossible to observe the functional brain activity of extinct hominin species directly.

The evolutionary history of our ancestors and their techniques has become considerably more complex over the last twenty-five years thanks to new methods of analysis and new archaeological and palaeoanthropological discoveries (Figure 1), and therefore, exploring the link between the lithic assemblages and the Early Pleistocene (2.6-0.8 Ma) stone-tool makers could be challenging.

Brain activation processes during Oldowan and Acheulean production: an overview

Various researchers have explored the relationships between stone-tool making and brain function through the analysis of brain activation processes during Oldowan and Acheulean tool production. In this per-

spective, diverse methods of functional brain imaging have been used, for example, fluorodeoxyglucose positron emission tomography (FDG-PET)¹, functional magnetic resonance imaging² and image-based functional near-infrared spectroscopy³. The purpose of this research was to discuss which brain regions are the most active during these stone tool productions using different techniques: free-hand percussion⁴ and bifacial shaping⁵, which are mainly used by Oldowan and Acheulean stone-tool makers, respectively. In these experimental setups, participants with varying levels of expertise (from novices to experts) engage in tool-making tasks or watch videos related to these processes.

In their 2000 study, using FDG-PET with one expert subject, Stout and collaborators (Stout, Toth, Schick, Stout & Hutchins, 2000) discovered that different regions of the cerebral cortex involved in the processing of sensory (visual and somatosensory) and motor information, as well as the cerebellum involved in the integration and control of motor activity were activated (Figure 2). Interestingly, cortical regions associated with high-level planning were not activated during Oldowan debitage.

In a subsequent study by Stout and Chaminade (2007), which involved six right-handed novice subjects during Oldowan production, additional regions were found to be active, i.e., the rostral intraparietal sulcus

¹FDG-PET, with isotope tracer (e.g. Stout et al., 2000; Stout & Chaminade, 2007; Stout et al., 2008).

²fMRI, where the subjects watch videos and are asked to make judgments about predictions of tool-making action outcomes (e.g. Stout et al., 2015).

³fNIRS is a neuroimaging technique that measures changes in oxygenated and deoxygenated haemoglobin in the cortex.

⁴In their protocols, the participants learn to make Oldowan and Acheulean stone tools (e.g. Putt, Wijeakumar, Franciscus & Spencer, 2017).

⁵Debitage with multidirectional flaking, the hammerstone is held by the dominant hand and the core is maintained by the non-dominant hand without the help of an anvil.

⁶Consists of shaping a stone into a handaxe or cleaver and maintaining a sharp edge along the entire piece.

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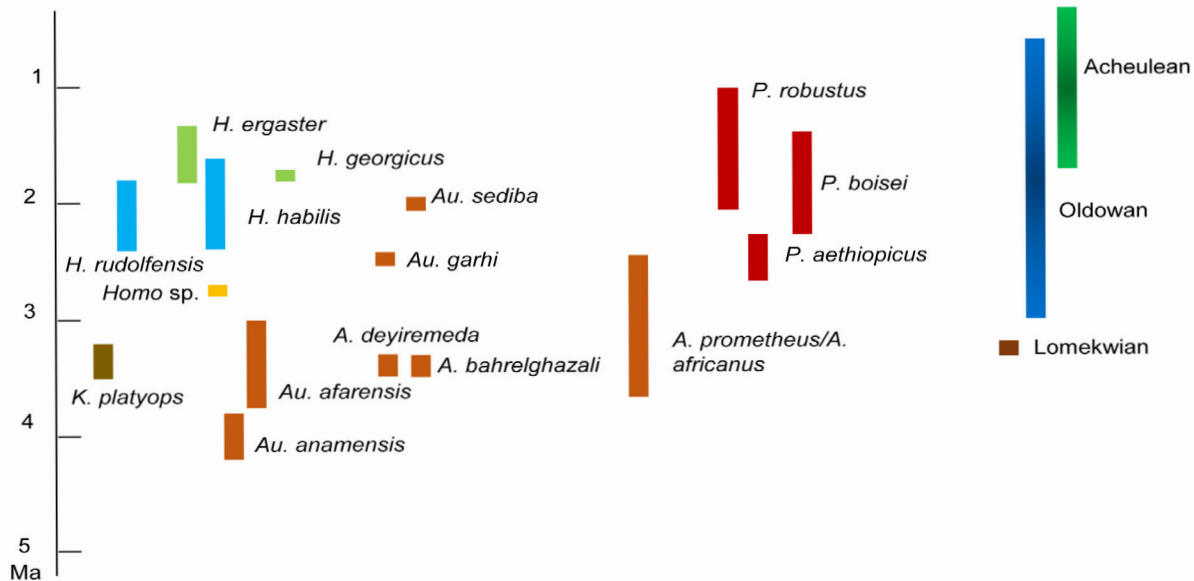


Figure 1. Chronological framework of hominin species and lithic assemblage during the Pliocene (5.33-2.58 Ma) and early Pleistocene (2.58-0.8 Ma), modified after Prat (2023).

and ventral premotor cortex, which are involved in visuomotor function, as well as the interface between the perceptive and motor systems for controlling arm and eyes movements in motor control. See Figure 2. The brain activation data from these studies indicate that the initial stages of acquiring Oldowan debitage skills primarily focus on perceptual-motor adaptation to task constraints. Since there is no activation of the ventro and dorsolateral cortex, the authors (Stout & Chaminade, 2007) consider that there is no high planification during Oldowan tool production.

Conversely, during the production of Acheulean handaxes with three expert subjects, a specific area of the brain, closely associated with decision-making processes (the right inferior prefrontal cortex, Brodmann Area 45 (BA 45)), shows significant activation (Stout, Toth, Schick & Chaminade, 2008). According to the authors, the activation of the ventrolateral prefrontal cortex, but not of the dorsolateral prefrontal cortex, known for its role in working memory, indicates that Acheulean shaping primarily involves cognitive processes for coordinating hierarchically organized ongoing action sequences.

According to Stout and Chaminade (2012), an overlap between Oldowan and Acheulean is found in several cortical regions of the parietal lobe and the premotor cortex located in the frontal lobe. Regions specifically involved in Acheulean shaping can be found in the frontal cortex, and in particular in the right hemisphere homologue of anterior Broca's area (Stout & Chaminade, 2012) (Figure 2).

Using the fMRI method to identify activation during the observation of tool-making action with videos, Stout et al. (2015) observed that the prefrontal cortex shows greater responses during Acheulean than Oldowan debitage. This finding suggests that Acheulean shaping may involve more complex cognitive processes. According to their earlier work (Stout, Toth, Schick, Stout & Hutchins, 2000), Oldowan tool-making primarily requires coordination of visual attention and motor control, engaging motor and sensorimotor areas of the brain.

On the other hand, research by Putt (Putt, 2016; Putt, Wijekumar, Franciscus & Spencer, 2017), using the fNIRS method where participants learn to make

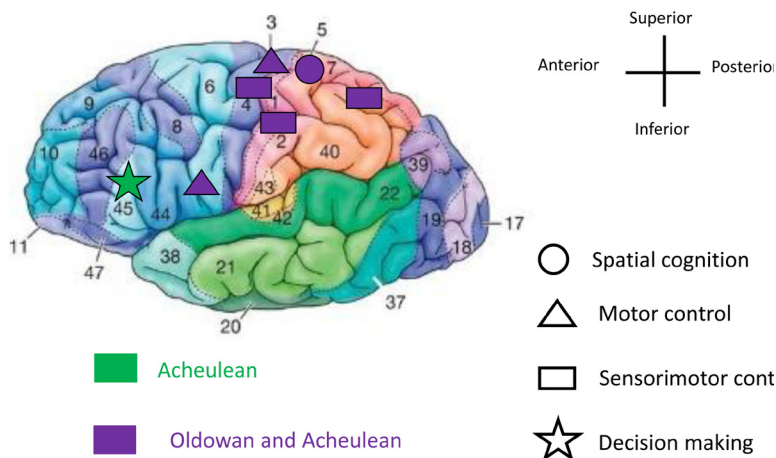


Figure 2. Brain regions activated during Oldowan and Acheulean productions (purple), or more specifically in Acheulean production (green), using FGD-PET (Stout & Chaminade, 2007, 2012; Stout et al., 2000; Stout et al., 2008). Numbers correspond to cortical areas (Brodmann areas) known to be engaged in spatial cognition (circle), motor control (triangle), sensorimotor control (rectangle) or decision-making (star).

Oldowan and Acheulean artefacts in either a verbal or nonverbal training context while carefully controlling the learning context, indicates that Acheulean tool-making involves not just motor control but also integrates higher-order motor planning, working memory, and auditory feedback mechanisms. This distinction between Oldowan and Acheulean tasks points to a possible evolutionary advancement in cognitive abilities and brain functions corresponding to these two different stone tool-making technologies and brain functions corresponding to these two different stone tool-making technologies.

Who could be the stone-tool makers?

Another step in neuroarchaeology is to understand who the stone-tool makers were as well as possible perspectives in palaeoneurology. The conventional belief that *Homo* species only made the Oldowan artefacts is being questioned due to the presence of a temporal and geographical overlap with non-*Homo* species like *Paranthropus boisei*, *P. aethiopicus*, *P. robustus*, and *Australopithecus garhi* (Figure 1). Moreover, the skeleton of *Paranthropus*, exemplified by post-cranial elements, seems compatible with the anatomical features required for stone tool production, as noted by Domínguez-Rodrigo and colleagues

(Domínguez-Rodrigo et al., 2013). Additionally, hand remains, initially allocated to *Homo habilis*, are now considered to belong to *Paranthropus* (Moyà-Solà, Kohler, Alba & Almécija, 2008). Therefore, the anatomical evidence supports the view that *Paranthropus* species were likely users and stone-tool makers. In addition, *Paranthropus* remains have been found together with Oldowan assemblages in some eastern African sites (Prat, 2023). Thus, Oldowan artefacts are associated not only with *Homo* species like *H. habilis* and *H. erectus/ergaster*, but also with *Paranthropus* (Figure 3). *Paranthropus* remains seem clearly more frequently associated than previously thought with lithic assemblages. This observation challenges the long-held view that tool-making is exclusive to the *Homo* genus. In addition, while the presence of *H. erectus* is mainly linked with Acheulean tools after 1.4 Ma, we can highlight evidence of their association with Oldowan tools in Africa and Eurasia (Prat, 2023)

Moreover, the human-like cortical reorganization is not exclusive to the *Homo* genus. It was already evident 3 to 4 million years ago in species like *Australopithecus africanus*, with reorganization in the occipital and prefrontal cortical areas (Holloway & Kimbel, 2004; Beaudet et al., 2018). Such reorganizations are still debated for *Australopithecus afarensis* (e.g. Gunz et al., 2020; Holloway & Kimbel, 1986). Similar

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changes were observed in *Paranthropus robustus* (Holloway, 1972). Recent *Australopithecus* species like *Australopithecus sediba* (1.97 Ma) also show signs of this reorganization, particularly in the prefrontal cortex (Carlson et al., 2011). Additionally, Ponce de León et al. (2021) indicate that early African and Georgian hominins retained a great ape-like frontal lobe structure, but specimens from Africa and Asia younger than 1.5 Ma exhibit a human-like brain organization.

This overview significantly broadens our understanding of early hominin behavior and tool-making skills. It paints a more intricate and nuanced picture of early hominin behavior and cultural evolution, underscoring a more complex narrative of early human evolution.

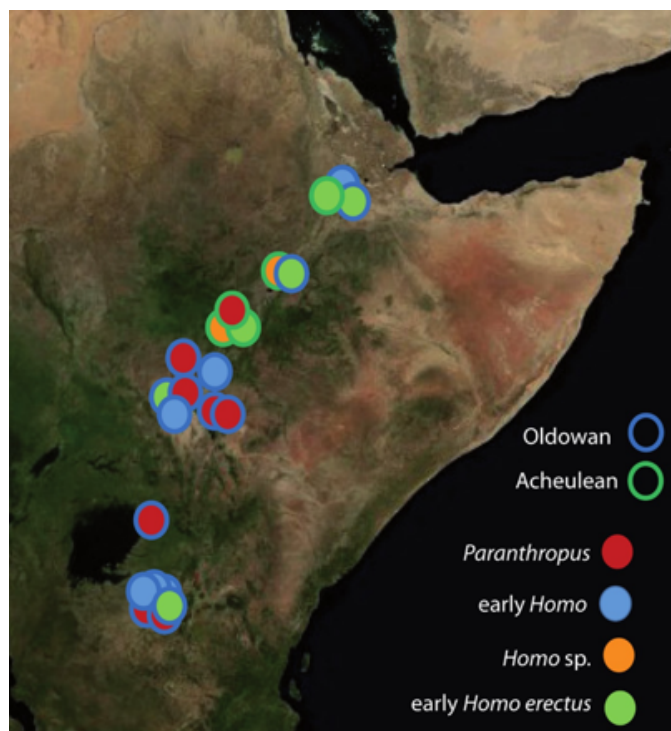


Figure 3. Location of the hominin remains in association with archaeological sites in East Africa (Afar, Lower Omo Valley and Fejej regions in Ethiopia, West and East Turkana and Homa Peninsula in Kenya, Olduvai Gorge in Ethiopia), modified after Prat (2023).

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