Assessing the Neuromechanical Requirements for Efficient Early Stone Tool Use and Their Evolutionary Implications through an Experimental Approach

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Table of Contents

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ABSTRACT

Tool use, in the context of hominin evolution, is arguably one of the most important behavioral traits to define our species. Tool use is observed in many other animals, including our closest living relatives; however, the complexity of human tool use and our reliance on it today distinguish us from other animals. Understanding the origins, development, and requirements of such complex behavior, which has become an integral human skill, requires a multifaceted approach. As such, it has been studied by many research fields since the initial discovery of stone tools. Research has been conducted on fossil hominins to examine how and why the human hand may have evolved, on the stone tools themselves, to determine how they were produced and whether remnants of material culture remain via microwear analysis. Over the last 20 years, the biomechanical and neural requirements for performing such tool tasks have also been investigated through experiments using various neuroimaging and biomechanical measurement techniques. This dissertation contributes to the growing number of studies that are using these interdisciplinary methodologies within the context of experimental analysis to capture both the cognitive and biomechanical complexities involved in early stone tool activities. This dissertation presents three cumulative experimental studies, each building on our novel and integrative protocol designed to simultaneously record electroencephalography (EEG) and surface electromyography (sEMG) during experimental stone tool tasks. These studies collectively validate this new methodological approach and apply it to investigate how efficiency and expertise influence the neural and muscular demands of two fundamental early stone tool behaviors: Oldowan-style flake cutting and hammerstone nut-cracking.

The first study introduces and validates the combined EEG/sEMG methodology within experimental archaeology through a step-by-step protocol. Participants performed an Oldowan-style flake cutting task divided into three temporally distinct stages: Hold, Aim, and Execute. Neural activation was most pronounced in the frontal and premotor cortices during the Aim stage, regions known to be involved in action planning, decision-making, and problem-solving processes. Muscular activation peaked during the Execute stage, reflecting physical task performance in both the dominant and non-dominant (stabilizing) hand. Notably, a sharp decrease of beta power in the motor cortex was observed during the Execute stage, potentially displaying beta event-related desynchronization, which likely suggests enhanced neural engagement within the motor region, as is the case in many studies monitoring cued voluntary movement. These findings closely aligned with expectations and demonstrate the validity of the outlined methodological protocol. In addition, we segmented the tool use task into distinct action stages (initial grasping of the tool, preparatory, and execution). These stages also highlighted the role of the non-dominant hand in stabilization throughout the task. This allowed us to establish a clear, but often overlooked, aspect of stone tool use behavior, offering additional insights into the importance of analyzing the neural and muscular requirements during task preparation, not just execution, whilst also emphasizing the importance of monitoring the stabilizing hand.

Building on this validation study, the second paper investigates how extensive practical knapping experience impacts efficiency during two early stone tool use tasks (Oldowan-style flake cutting and hammerstone nut-cracking). A two-fold assessment of efficiency was used here, based upon muscular activation levels and task success. Participants were categorized as Novices (lack of relevant experience), Intermediates (theoretical knowledge only), or Experts (extensive theoretical and practical knapping experience) based on their tool-related experience. Results showed that Experts performed the Oldowan-style flake cutting task with significantly higher success rates and lower muscular activation than less experienced participants. In contrast, no significant difference in success rates was observed between experience groups during the hammerstone nut-cracking task. However, over the course of repeated trials, Experts showed a more rapid improvement curve, suggesting a capacity for skill transfer and adaptation derived from their expansive knapping repertoire. This study supports the view that cumulative tool-use experience is not only beneficial for specific tool tasks but may foster generalizable motor strategies likely critical to the adaptive flexibility of early hominins.

The final study explores how expertise shapes neuro-biomechanical interactions during the preparatory stage (Aim) for both tool tasks. Combined analysis of EEG and sEMG data revealed clear differences between Experts and Novices. Experts engaged the left frontal and premotor/motor cortices more than Novices. This was especially true during the more cognitively demanding flake task. The increased cortical engagement was accompanied by reduced muscular activation in both hands. These findings suggest a more efficient, top-down neural control of motor output in Experts. By contrast, Novices showed increased activation in the parietal cortex, indicating greater reliance on visuospatial processing and mechanical knowledge (the ability to understand the physical properties of an object), and relatively increased activation in all muscles during both tasks. Additionally, when analyzing the tasks together, we found that the flake cutting task elicited greater overall cognitive activation in the left frontal and motor regions, likely due to the cutting task requiring more fine motor coordination than the hammerstone task, particularly in Experts. This aligns with previous findings that flake production represents a more cognitively demanding behavior when directly compared to hammerstone pounding behaviors. Interestingly, the non-dominant stabilizing hand was also shown to be relatively more active during the flake cutting task in Experts, reinforcing the critical role of the non-dominant hand in stabilization during precise tool use. These results demonstrate task-specific neuromechanical recruitment strategies that counter the proposed neural-efficiency hypothesis. Instead, we propose that Experts' neural engagement may be better characterized by functional specialization and adaptive flexibility, rather than always simply reflecting a reduction in cognitive load.

Together, these studies provide the first experimentally validated protocol that evidences cumulative, hands-on experience leads to more efficient, targeted engagement of neural and muscular systems during early stone tool use. By segmenting tool behavior into discrete stages and adopting a combined EEG/sEMG approach, this research uncovers nuanced patterns of brain-hand interaction that would be obscured by only assessing one aspect of tool use in

isolation, or by simply capturing the execution of such a task. These findings suggest that stone tool-related expertise is not merely a product of repetition but is underpinned by refined motor planning and executive functions. Furthermore, this work provides direct empirical support for the fundamental theory that the gradual expansion of the human brain likely facilitated the emergence and increasing sophistication of stone tool technologies throughout hominin evolution, either through adaptation or exaptation. This thesis thus represents a significant methodological and theoretical advancement in experimental archaeology and contributes to broader discussions within paleoanthropology about the origins of tool use and hominin evolution.

ZUSAMMENFASSUNG

Die Verwendung von Werkzeugen ist im Zusammenhang mit der Evolution der Homininen eines der wichtigsten Verhaltensmerkmale unserer Spezies. Die Verwendung von Werkzeugen kann bei vielen anderen Tieren observiert werden, darunter auch bei unseren nächsten lebenden Verwandten; die Komplexität des menschlichen Werkzeugeinsatzes und die Tatsache, dass wir heute darauf angewiesen sind, unterscheiden uns jedoch von anderen Tieren. Um die Ursprünge, die Entwicklung und die Voraussetzungen eines solch komplexen Verhaltens, das zu einer wesentlichen menschlichen Fähigkeit geworden ist, zu verstehen, ist ein vielseitiger Ansatz erforderlich. Seit der Entdeckung von Steinwerkzeugen wurde es von vielen Forschungsbereichen untersucht. So wurde an fossilen Homininen untersucht, wie und warum sich die menschliche Hand entwickelt haben könnte. An Steinwerkzeugen wurde erforscht, wie sie hergestellt wurden und mit der Hilfe von Microwareanalysis wurde analysiert, ob Reste der materiellen Kultur erhalten geblieben sind. In den letzten 20 Jahren wurden auch die biomechanischen und neuronalen Vorrausetzungen für die Ausführung von Werkzeugnutzung durch Experimente mit verschiedenen Neuroimaging- und biomechanischen Messverfahren untersucht. Diese Dissertation trägt zu der wachsenden Zahl von Studien bei, die diese interdisziplinären Methoden im Rahmen einer experimentellen Analyse einsetzen, um sowohl die kognitiven als auch die biomechanischen Komplexitäten zu erfassen, die mit frühen Steinwerkzeugaktivitäten verbunden sind. In dieser Dissertation werden drei kumulative experimentelle Studien vorgestellt, die jeweils auf unserem neuartigen und integrativen Protokoll zur gleichzeitigen Aufzeichnung von Elektroenzephalographie (EEG) und Oberflächen-Elektromyographie (sEMG) während experimenteller Steinwerkzeugaufgaben aufbauen. Diese Studien validieren gemeinsam diesen neuen methodischen Ansatz und wenden ihn an, um zu untersuchen, wie Effizienz und Fachwissen die neuronalen und muskulären Anforderungen von zwei grundlegenden frühen Steinwerkzeug-Verhaltensweisen beeinflussen: Schneiden mit Flakes im Oldowan-Stil und Knacken von Nüssen mit Hilfe eines Hammersteines.

In der ersten Studie wird die kombinierte EEG/SEMG-Methode in der experimentellen Archäologie anhand eines Schritt-für-Schritt-Protokolls vorgestellt und validiert. Die Teilnehmer führten eine Aufgabe zum Schneiden von künstlichem Leder im Oldowan-Stil mit Flakes durch. Die Aufgabe war in drei zeitlich getrennte Phasen unterteilt: Halten, Anvisieren und Ausführen. Die neuronale Aktivierung war während der Zielphase im frontalen und prämotorischen Kortex am stärksten ausgeprägt, also in Hirnarealen, die bekanntermaßen an Handlungsplanung, Entscheidungsfindung und Problemlösungsprozessen beteiligt sind. Die muskuläre Aktivierung erreichte während der Ausführungsphase ihren Höhepunkt und spiegelte die körperliche Leistung sowohl in der dominanten als auch in der nicht-dominanten (stabilisierenden) Hand wider. Bemerkenswert ist, dass während der Ausführungsphase eine starke Abnahme der Beta-Leistung im motorischen Kortex zu beobachten war, was möglicherweise auf eine ereigniskorrelierte Desynchronisation hindeutet. Diese deutet wahrscheinlich auf ein verstärktes neuronales Engagement in der motorischen Region hin, wie es in vielen Studien zur Beobachtung willkürlicher Bewegungen auch der Fall ist. Diese Ergebnisse stimmten mit den

Thesen überein und belegen die Gültigkeit des skizzierten methodischen Protokolls. Des Weiteren wurde die Aufgabe der Werkzeugbenutzung in verschiedene Handlungsphasen unterteilt (anfängliches Greifen des Werkzeugs, Vorbereitung und Ausführung). In diesen Phasen wurde zusätzlich die Rolle der nicht-dominanten Hand bei der Stabilisierung während der Aufgabe hervorgehoben. Dies ermöglichte es uns, einen wichtigen, aber oft übersehenen Aspekt des Verhaltens bei der Verwendung von Steinwerkzeugen festzustellen. Darüber hinaus konnten zusätzliche Einblicke in die Bedeutung der Analyse der neuronalen und muskulären Voraussetzungen während der Aufgabenvorbereitung und nicht nur während der Ausführung erreicht werden, wobei auch die Bedeutung der stabilisierenden Hand betrachtet wurde.

Aufbauend auf dieser Validierungsstudie wird in der zweiten Studie untersucht, wie sich umfangreiche praktische „knapping" Erfahrungen auf die Effizienz bei den zwei zuvor erläuterten Steinwerkzeugaufgaben auswirkt (Schneiden von Kunstleder im Oldowan-Stil mit Flakes und Knacken von Nüssen mit Hammerstein). Die Effizienz wurde hier anhand der Muskelaktivierung und des Aufgabenerfolgs auf zwei Ebenen bewertet. Die Teilnehmer wurden je nach ihrer Erfahrung im Umgang mit Werkzeugen in Neulinge (ohne einschlägige Erfahrung), Fortgeschrittene (nur theoretische Kenntnisse) oder Experten (umfangreiche theoretische und praktische Erfahrung) eingeteilt. Die Ergebnisse zeigten, dass die Experten die Aufgabe zum Schneiden des Kunstleders mit signifikant höheren Erfolgsquoten und geringerer Muskelaktivierung ausführten als die weniger erfahrenen Teilnehmer. Im Gegensatz dazu wurde beim Knacken der Nuss mit dem Hammerstein kein signifikanter Unterschied in den Erfolgsraten zwischen den Erfahrungsgruppen festgestellt. Mit zunehmenden Wiederholungen zeigten die Experten jedoch eine schnellere Verbesserungskurve, was auf eine Fähigkeit zur Übertragung und Anpassung von Fertigkeiten schließen lässt, die sich aus ihrem umfangreichen „knapping" Repertoire ergibt. Diese Studie bestätigt die Ansicht, dass kumulative Erfahrung im Umgang mit Werkzeugen nicht nur für spezifische Werkzeugaufgaben von Vorteil ist, sondern auch verallgemeinerbare motorische Strategien fördern kann, die für die adaptive Flexibilität der frühen Homininen entscheidend sind.

In der letzten Studie wird untersucht, wie die Expertise die neurobiomechanischen Interaktionen während der Vorbereitungsphase (Aim) für beide Werkzeugaufgaben beeinflusst. Die kombinierte Analyse von EEG- und sEMG-Daten ergab deutliche Unterschiede zwischen Experten und Anfängern. Experten beanspruchten die linken frontalen und prämotorischen/motorischen Kortexe stärker als Anfänger. Dies galt insbesondere für die kognitiv anspruchsvollere Schneideaufgabe. Die erhöhte kortikale Aktivität ging mit einer geringeren Muskelaktivierung in beiden Händen einher. Diese Ergebnisse deuten auf eine effizientere neuronale Top-down-Kontrolle der motorischen Leistung bei Experten hin. Im Gegensatz dazu zeigten Anfänger eine erhöhte Aktivierung im parietalen Kortex, was auf eine stärkere Abhängigkeit von visuell-räumlicher Verarbeitung und mechanischem Wissen (die Fähigkeit, die physikalischen Eigenschaften eines Objekts zu verstehen) hinweist. Bei Anfänger wurde ebenfalls eine relativ erhöhte Aktivierung aller Muskeln während beider Aufgaben festgestellt. Bei der kombinierten Analyse der Aufgaben stellten wir außerdem fest, dass das

Schneiden von Kunstleder eine größere kognitive Gesamtaktivierung im linken frontalen und motorischen Bereich auslöste, was wahrscheinlich darauf zurückzuführen ist, dass das Schneiden mehr feinmotorische Koordination erfordert als das Schlagen der Steine, insbesondere bei Experten. Dies deckt sich mit früheren Befunden, wonach die Schneiden von Materialien ein kognitiv anspruchsvolleres Verhalten darstellt, wenn man es direkt mit dem Schlagen von Hammersteinen vergleicht. Interessanterweise zeigte sich auch, dass die nicht-dominante, stabilisierende Hand bei den Experten während des Schneidens mit Flakes relativ aktiver war, was die kritische Rolle der nicht-dominanten Hand bei der Stabilisierung während des präzisen Werkzeuggebrauchs unterstreicht. Diese Ergebnisse zeigen aufgabenspezifische neuromechanische Voraussetzungen, die die vorgeschlagene Hypothese der neuronalen Effizienz widerlegen. Stattdessen legen unsere Ergebnisse nahe, dass das neuronale Engagement von Experten besser durch funktionelle Spezialisierung und adaptive Flexibilität charakterisiert werden kann und es nicht nur eine Verringerung der kognitiven Belastung widerspiegelt.

Zusammengenommen liefern diese Studien das erste experimentell validierte Protokoll, das belegt, dass kumulative, praktische Erfahrung zu einer effizienteren, gezielten Beanspruchung der neuronalen und muskulären Systeme während des frühen Gebrauchs von Steinwerkzeugen führt. Durch die Unterteilung des Werkzeugverhaltens in einzelne Phasen und die Anwendung eines kombinierten EEG/SEMG-Ansatzes zeigt diese Forschung nuancierte Muster der Interaktion zwischen Gehirn und Hand, die durch die isolierte Bewertung nur eines Aspekts der Werkzeugnutzung oder durch die Kombination von EEG und REMG nicht ermittelbar gewesen wären. Diese Ergebnisse deuten darauf hin, dass steinwerkzeugbezogenes Fachwissen nicht nur ein Resultat von Wiederholung ist, sondern durch verfeinerte motorische Planung und exekutive Funktionen verstärkt wird. Darüber hinaus bietet diese Arbeit direkte empirische Unterstützung für die grundlegende Theorie, dass die allmähliche Expansion des menschlichen Gehirns die Entstehung und zunehmende Verfeinerung von Steinwerkzeugtechnologien im Laufe der Homininen-Evolution entweder durch Anpassung oder Exaptation erleichtert hat. Diese Arbeit stellt somit einen bedeutenden methodischen und theoretischen Fortschritt in der experimentellen Archäologie dar und trägt zu einer breiteren Diskussion innerhalb der Paläoanthropologie über die Ursprünge des Werkzeuggebrauchs und der Evolution der Homininen bei.

ABBREVIATIONS

cm – centimeter

DI1 – first dorsal *interosseus*

EEG – electroencephalography

FCR – *flexor carpi radialis*

FCU – *flexor carpi ulnaris*

fMRI – functional magnetic resonance imaging

fNIRS – functional near infrared spectroscopy

FPL – *flexor pollicis longus*

HTE – hypothenar eminence (*abductor digiti minimi*, *flexor digiti minimi*, and *opponens digit minimi)*

µV – microvolts

MYA – million years ago

PC – principal component/s

PCA – principal component analysis/es

PET – positron emission tomography

sEMG – surface electromyography

TE – thenar eminence (*abductor pollicis brevis*, *flexor pollicis brevis*, and *opponens pollicis)*

PUBLICATIONS

Within the following cumulative dissertation, a total of three manuscripts are included in fulfillment of the requirements: two accepted and one manuscript under submission.

Accepted articles:

Study I

This first study includes a separately published peer-reviewed technical protocol; the protocol DOI is referenced below.

Eteson, B., Affinito, S., & Karakostis, F. A., 2025. The mind & muscles: Introducing a validated EEG/EMG protocol for recording cognitive/muscular interactions in experimental archaeology. *PLoS One*. 20 (5). https://doi.org/10.1371/journal.pone.0324103.

Eteson, B., Affinito, S., & Karakostis, F. A., 2024. The Mind & Muscles: A Protocol for the simultaneous measuring of cognitive and muscular activation during stone tool tasks using surface Electromyography and Electroencephalography. protocols.io https://dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1

DOI: https://doi.org/10.1371/journal.pone.032410

Study II

Eteson, B., Affinito, S., Moos, E. T., & Karakostis, F. A., 2024. "How Handy was early hominin 'know-how'?" An experimental approach exploring efficient early stone tool use. *AJBA*, 185 (3), 1–21. https://doi.org/10.1002/ajpa.25019

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Submitted manuscripts:

Study III

Eteson, B., Affinito, S., & Karakostis, F.A., Mind Over Muscle: Neural and Biomechanical Signatures of Expertise in Early Stone Tool Use.

Status: under submission

PERSONAL CONTRIBUTION

I hereby declare that the research presented in this cumulative dissertation is my own original work and that my personal contributions to the publications included herein are substantial.

This dissertation comprises two peer-reviewed publications and one under submission, to which I contributed as the first author in all cases.

Specific contributions for conception of scientific ideas, data generation, analysis and interpretation, and writing of the paper are listed in percentages below each included manuscript.

Study I: Eteson, B., Affinito, S., & Karakostis, F. A., 2025. The mind & muscles: Introducing a validated EEG/EMG protocol for recording cognitive/muscular interactions in experimental archaeology. *PLoS One*. 20 (5). https://doi.org/10.1371/journal.pone.0324103.

60% | 70% | 80% | 80%

Study II: Eteson, B., Affinito, S., Moos, E. T., & Karakostis, F. A., 2024. "How Handy was early hominin 'know-how'?" An experimental approach exploring efficient early stone tool use. *AJBA*, 185 (3), 1–21. https://doi.org/10.1002/ajpa.25019

70% | 90% | 90% | 90%

Study III: Eteson, B., Affinito, S., & Karakostis, F.A., Mind Over Muscle: Neural and Biomechanical Signatures of Expertise in Early Stone Tool Use.

70% | 80% | 90% | 90%

In all three studies, my role as first author involved the integration of interdisciplinary methods, including the design, validation, and application of a novel combined EEG/sEMG protocol, and the execution of statistical and comparative analyses that underpin the primary conclusions.

I confirm that the above statement accurately reflects my contributions to the collaborative works forming the basis of this dissertation.

1 INTRODUCTION

1.1 THE ORIGIN OF STONE TOOLS

Tool use is arguably one of the most important behavioral activities to define hominin evolution over the last 3 million years (Biro, Haslam, and Rutz, 2013; Harmand et al., 2015; Osiurak, Jarry, and Le Gall, 2010), with the oldest tools dating to over 3.3 MYA at the Lomekwi 3 site in Kenya (Harmand et al., 2015) and even predating the genus *Homo*, marking a critical behavioral transition in our lineage. Whilst tool use is far from unique to humans (Boesch and Boesch, 1990; 1993; Fragaszy et al., 2004; Goodall et al., 1964; Haslam, 2013; Ottoni and Mannu, 2001; Proffitt et al., 2016, 2023; Whiten et al., 1999), the complexity, diversity, and intentionality of hominins' tool use far surpass that of any other species. In addition, modern humans' dependence on tools in everyday life spans across culture, geography, and historical periods, as tool use remains a fundamental aspect of all human life (Biro, Haslam, and Rutz, 2013; Osiurak, Jarry, and Le Gall, 2010). Stone tools marked a shift in the diet for hominins, enabling them to access nutrient-dense resources, such as nuts, tubers, marrow, and animal protein (Linares-Matás and Clark, 2022; Plummer, 2004; Plummer et al., 2023; Semaw, 2000), and to exploit a wider range of resources during periods of ecological instability (Clark and Linares-Matás, 2024; Linares-Matás and Clark, 2022; Sanz and Morgan, 2013). This dietary flexibility and shift would likely have had significant implications for hominins, potentially supporting the evolution of a larger brain (Aiello and Wheeler, 1995; Ferraro et al., 2013; Foley, 2001), and a reduction in the size of powerful jaw muscles (Raia et al., 2018; Wrangham et al., 1999), amongst other evolutionary changes, which in turn may have led to further technological innovations.

Our reliance on tools dates back to the oldest proposed archaeological finding of the Lomekwian tools (Harmand et al., 2015), described as being larger and thicker flakes and cores than the subsequent Oldowan technology (Harmand et al., 2015). The Oldowan industry then emerges as the earliest temporally persistent lithic technology from ~3 MYA (Plummer et al., 2023), providing evidence of habitual and intentional production of flakes (Braun et al., 2019; Semaw, 2000; Plummer et al., 2023). This industry, comprising predominantly of flakes removed by striking a hammerstone against a core, (typically made from basalt, quartzite, or chert; Hay, 1976), was what laid the foundations for later hominin technological complexity and likely reflects the onset of cognitive and biomechanical transformations (Karakostis et al., 2021; Marzke, 2013; Toth and Schick, 2018; Williams-Hatala et al., 2018; Wynn and Coolidge, 2016). For this reason, stone tools form a foundational topic within much archaeological and paleoanthropological research. As we will explore in this dissertation, critical aspects of evolutionary research on lithic industries include the origin and intentionality of early stone tool production and use, biomechanical and cognitive studies on their requirements, associated hominin skeletal morphology, and the cognitive implications of stone tool cumulative experience (“know-how”).

The focus of this dissertation is on both the biomechanical and cognitive requirements of efficient early stone tool use, predominantly the Oldowan tool industry and its theorized predecessor, hammerstone pounding (Bril et al., 2012), which is also part of the repertoire of non-human primate stone tool use (Arroyo et al., 2016; Bril et al., 2012; Gumert and Malaivijitnond, 2012; Proffitt et al., 2016, 2023; Wynn and McGrew, 1989). Specifically, we examine how muscular and neural activity changes during two fundamental early stone tool tasks (Oldowan-style flake cutting and hammerstone nut-cracking). Participants were grouped based on their varying levels of expertise to determine how experience and efficiency affect neuromechanical requirements during these tasks. This research relies on the development and validation of a new integrated protocol for the combined use of electroencephalography (EEG) and surface electromyography (sEMG) within the context of experimental archaeology and hominin evolution.

1.2 HOMININ MORPHOLOGY AND STONE TOOLS

The discovery of the proposed Lomekwian lithic industry, dating back to approximately 3.3 million years in the late Pliocene epoch (Harmand et al., 2015), considerably changed our understanding of hominin tool use, as these large flakes predate the genus *Homo* by several hundred thousand years (Harmand et al., 2015). This forced researchers to reconsider who the earliest stone tool makers were, with the most likely candidates being either *Kenyanthropus platyops*, found in the West Turkana region (Leakey et al., 2016), or *Australopithecus afarensis* in the Lower Awash Valley (Alemseged et al., 2006; McPherron et al., 2010). Despite *K. platyops*' lack of post-cranial remains, *A. afarensis*' hand morphology has been studied thoroughly to determine it as a likely candidate for stone tool production and use (Alba, Moyà-Solà and Köhler, 2003; Almécija and Alba, 2014; Domalain, Bertin and Daver, 2017; Kivell, 2015; Marzke and Shackley, 1986). Due to few bones definitively being associated with one individual, studies have varying conclusions on their candidacy as a tool maker (Alba, Moyà-Solà and Köhler, 2003; Almécija and Alba, 2014; Domalain, Bertin and Daver, 2017; Kivell, 2015; Marzke and Shackley, 1986). However, without soft tissue, fossils can only portray part of the story.

This controversy continues to play a role in the later, more geographically and temporally persistent Oldowan technology (Stout et al., 2019), with many hominin species being considered as the potential makers of these tools (Leakey, Tobias, and Napier, 1964; Susman, 1991; Williams et al., 2025). The most commonly discussed hominin candidates (*A. afarensis, Australopithecus africanus, Australopithecus sediba, Homo habilis,* and *Paranthropus boisei*) all display a mosaic of primitive and derived features in the hand (Dunmore et al., 2023; Kivell, 2015; Kivell et al., 2023; Marzke, 2013; Richmond et al., 2020), such as a shorter, more robust thumb (derived), forceful precision grasping necessary for prolonged stabilization of objects between the thumb and fingertips (derived), and long, curved phalanges for arboreal locomotion (primitive) (Kivell, 2015; Marzke, 2013). However, despite certain primitive traits found in these fossil remains, which may have limited efficiency for human-like tool use (Karakostis et al., 2021), recent research on early hominin entheseal patterns (muscle or ligament attachment sites on bone surfaces) has further proposed that habitual human-like tool use may indeed have preceded certain morphological adaptations for increased human-like dexterity (Kunze et al., 2022, 2024). This suggests that the evolution of hominin anatomy and interspecies morphological variation may not always correspond directly to the habitual lifetime behaviors of individuals, which are themselves shaped by a number of complex environmental factors. This is why diverse methodologies are considered necessary for addressing both habitual behavior and evolutionary adaptation in the fossil record. In this context, experimental insights into the exact biomechanical requirements of specific manual behaviors are fundamental for guiding the hypotheses and interpretations of such paleoanthropological approaches (Karakostis et al., 2023).

1.3 NON-HUMAN PRIMATE STONE TOOL USE

The process of hard-hammerstone percussive knapping used to create flaked tools, such as those seen in the Oldowan technology (Bril, Parry, and Dietrich, 2015; Nonaka, Bril, and Rein, 2010), is often compared to hammerstone pounding activities we observe in non-human primate species (Arroyo et al., 2016; Bril et al., 2012; Gumert and Malaivijitnond, 2012; Proffitt et al., 2016, 2023; Wynn and McGrew, 1989). On this basis, hammerstone pounding has been labeled a potential precursor to stone tool knapping (Bril, Parry, and Dietrich, 2015) due to similarities drawn between the two manual activities (Boesch and Boesch, 1993; Davidson and McGrew, 2005; Marchant and McGrew, 2005; Sugiyama and Koman, 1979; Wynn and McGrew, 1989). It has also been theorized that hammerstone pounding was likely part of the behavioral repertoire of the last common ancestor to humans and other great apes (Kahrs, Jung, and Lockman, 2014; Panger et al., 2002), as the behavior is associated with several non-human primate species (Arroyo et al., 2016; Bril et al., 2012; Gumert and Malaivijitnond, 2012; Proffitt et al., 2016, 2023; Wynn and McGrew, 1989) and early hominins (Bril, Parry, and Dietrich, 2015; Goren-Inbar et al., 2002). This is assumed based on the principle of maximum parsimony, which suggests that a trait existing in related species was potentially present prior to divergence (Panger et al., 2002). In contrast, intentional flake cutting behavior is not observed in extant non-human primates in the wild, suggesting that it may be unique to hominins (Bandini and Tennie, 2023; Plummer, 2004; Roux and Bril, 2005; Wynn and McGrew, 1989).

Within the last decade, Proffitt and colleagues (2016, 2023) have reported the production of flaked tools, “almost indistinguishable” from Oldowan tools (Proffitt et al., 2023), through tool-assisted foraging via percussive stone-on-stone activities in non-human primate species. However, unlike the persistent appearance of Oldowan technology for almost 2 million years (Kimura, 2002; Plummer et al., 2023), these conchoidal, sharp-edged flakes are seemingly produced unintentionally as a byproduct of their foraging activities (Proffitt et al., 2023). This recent groundbreaking research has called into question some of the earliest examples of Lomekwian and Oldowan stone tool industries, previously assumed to have been intentionally produced by hominins, and instead proposes that original stone tool knapping may have started as a byproduct. It could have originated as an anvil for stabilization during intentional hammerstone pounding activity, which in turn became the core used in flaking (Proffitt et al., 2023). Intentionality in tool production/use implies a conscious understanding of the desired outcome and the steps required to achieve it, such as the selection of appropriate material and the application of controlled, planned action. In contrast, non-intentional production might involve incidental breakage or shaping that resulted in useful, albeit accidental, cutting edges.

Despite these studies challenging the original intentionality of the production of some sharp-edged flakes, substantial direct evidence of associated hominin tool-using activities remains. We observe this in cutmarks on animal bones (Bunn, 1981; Domínguez-Rodrigo et al., 2005; Potts and Shipman, 1981), evidence of raw material selection (Braun et al., 2009; Stout et al., 2005), tool transport (Braun et al., 2008), and re-touching of stone tools (Stollhofen et al., 2021; Toth, 1985). Additionally, studies have shown that intentional and repetitive production of Oldowan flakes requires extensive knowledge and comprehension of fracture mechanics, angle of blow, ideal raw material, the correct size of hammerstones, planning and coordination control, and visuospatial awareness (Hovers, 2009; Roche et al., 1999), which is not typically observed in non-human primate studies (Bandini et al., 2021; Bandini and Tennie, 2023; Proffitt et al., 2022, 2023). The current debate thus centers on whether the first hominins recognized and then replicated incidental flakes, eventually and gradually evolving into intentional knappers (Gürbüz and Lycett, 2021; Luncz and Arroyo, 2022).

Despite the ambiguity surrounding the initial intentionality of stone tool knapping, a plethora of previous studies have specifically placed a focus on exploring the cognitive and biomechanical requirements of stone tool production as opposed to use (Moore and Perston, 2016; Putt et al., 2017; Stout et al., 2000, 2015; Macchi et al., 2021; Marzke et al., 1998). In contrast to lithic production (knapping), much less experimental research has been conducted on the use of stone tools, including tasks that are considered exclusive to hominins, such as cutting, which have significant evolutionary implications. In this context, this dissertation focuses on two contrasting tool-use behaviors: hammerstone pounding and Oldowan flake cutting. Oldowan tools are especially significant as they represent the earliest evidence of human-like reliance on forceful precision grasping (Susman, 1991) and exhibit one of the first instances of cutting behavior (Plummer et al., 2023; Toth, 1985). These tools would have enabled hominins to substantially expand their diets and allowed for access to greater resources (Linares-Matás and Clark, 2022; Plummer, 2004; Plummer et al., 2023; Semaw, 2000). In contrast, hammerstone pounding primarily recruits a power grip, observed in several extant non-human primates (Arroyo et al., 2016; Bril et al., 2012; Gumert and Malaivijitnond, 2012; Proffitt et al., 2016, 2023; Wynn and McGrew, 1989). Analyzing the differing requirements of these two tool technologies is particularly interesting when considering that previous studies have associated hammerstone pounding activities as likely preceding Oldowan knapping (Bril et al., 2012). Therefore, the comparison between these two tasks is critical for understanding the emergence of human-specific manual and cognitive abilities, and for distinguishing tool-use behaviors that are unique to hominins.

1.4 BIOMECHANICAL EXPERIMENTAL STUDIES

Techniques such as EMG and pressure sensor systems have been extensively employed in the sports sciences to quantify muscle activity, grip force, and pressure distribution in the hand (Clarys and Cabri, 1993). Within the field of kinesiology, these techniques are applied to analyze muscle function and coordination, to optimize athletic performance and rehabilitation, and to evaluate movement techniques, skill execution, and training methodologies (Clarys and Cabri 1993). EMG is also widely used in medicine (Garcia and Vieira, 2011) for diagnostic procedures to determine nerve and muscular function and health (Hodes, Larrabee, and German, 1948; Ramani, Lui, and Arya, 2025). More recently, these methods have also been increasingly utilized in archaeological sciences.

Over the past two decades, several archaeological studies have garnered insights into stone tool production and use through sEMG experiments (Hamrick et al., 1998; Key et al., 2020; Marzke et al., 1998). EMG is a method used to measure the electrical activity of muscles at rest and during contraction. Within medicine, needle EMG is often performed by inserting needle electrodes directly into the muscle belly to ensure more accurate monitoring of the muscle. However, this invasive technique restricts the movement of the patient (Al-Ayyad et al., 2023; Reaz, Hussain, and Mohd-Yasin, 2006). Therefore, previous experimental studies within archaeology have used sEMG (surface electromyography (Hamrick et al., 1998; Key et al., 2020; Marzke et al., 1998). sEMG is performed by attaching small electrodes to the surface of cleaned skin, directly over the muscle belly, in line with the muscle fibers (Garcia and Vieira, 2011; Steele, 2012). These electrodes are connected to an amplifier. The amplified electrical potentials are then filtered and passed to an adapter component. This adapter facilitates the connection between the sEMG electrodes or sensors and the computer. The computer then enables the transmission of electrical signals from the muscles, allowing the signals to be captured and analyzed in microvolts (μV) (Garcia and Vieira, 2011; Steele, 2012). This methodology allows researchers to identify the specific muscular activation during different stages of experimental tasks. Additionally, methodologies such as pressure sensor systems (Key and Dunmore, 2015; Williams, Gordon, and Richmond, 2012; Williams-Hatala et al., 2018), manufactured instrumentation measuring reaction forces (Rolian, Lieberman, and Zermeno, 2011), and kinematics of hand bones (Bardo, et al., 2024) during lithic production, have also been crucial to advancing the field in understanding hominin lithic behavior. These biomechanical empirical studies have established a firm basis of knowledge for the physical demands of stone tool production and use, including important muscles and digits that are engaged during specific stone tool activities (Hamrick et al., 1998; Key and Dunmore, 2015; Key, Dunmore, and Marzke, 2019; Key, Merritt, and Kivell, 2018; Key et al., 2020; Marzke, 1998), grasping patterns necessary to efficiently use such tools (Kivell, 2015; Marzke, 1997, 2013; Napier, 1962), and the distinct forces applied across different types of stone tool use (Key et al., 2020; Rolian, Lieberman, and Zermeno, 2011; Williams-Hatala et al., 2018).

In the context of this dissertation, one of these studies found that hammerstone nut-cracking placed higher manual pressure on all recorded digits when compared to flake use (Williams-Hatala et al., 2018). Whilst recent sEMG research reportedly found that stone tools with a larger mass and size, such as Acheulean handaxes, recruited the *abductor digiti minimi* in the fifth digit to a higher degree than smaller lithics, such as Oldowan flakes (Key et al., 2020). This paper also highlighted the importance of the following thenar and second digit muscles during early stone tool use (Hamrick et al., 1998; Key et al., 2020): first dorsal *interosseous*, *flexor pollicis brevis*, and *flexor pollicis longus*. Despite the fundamental groundwork these previous studies have laid, this dissertation compiles the first published studies that directly compare the biomechanical requirements of two of the earliest lithic activities, hammerstone pounding and Oldowan-style flake cutting. Importantly, whilst most studies have simply focused on the action stage, or moment of execution (Hamrick, 1998; Key, Dunmore, and Marzke, 2019, 2020), the approach of this thesis is to examine all stages of the tool-using process. Analysis begins at the initial stage of picking up the tool, the preparatory "aiming" stage, and the execution of the intended action (either nut-cracking or flake cutting), thereby capturing important insights into the functions and movements that occur prior to task execution.

1.5 NEUROARCHAEOLOGICAL EXPERIMENTAL STUDIES

In addition to the insights that biomechanical analyses of stone tool use can provide, another crucial factor of lithic behavior is essential to fully understanding the behaviors of the hominin stone tool repertoire: cognitive engagement. Cognitive aspects of stone tool production have previously been explored using neuroimaging techniques, such as functional magnetic resonance imaging (fMRI) (Stout et al., 2015), positron emission tomography (PET) (Stout et al., 2000, 2008), and functional near-infrared spectroscopy (fNIRS) (Putt et al., 2017; Putt, Wijeakumar, and Spencer, 2019), significantly advancing our understanding of the cognitive demands of early stone tool making. These methods have enabled researchers to determine the brain regions most activated during stone tool-related tasks.

In particular, these cognitive studies found that increased activity in the dorsolateral prefrontal cortex, the inferior parietal lobe, and the temporal cortex was observed during stone tool knapping tasks. These areas are known to be crucial in understanding tool mechanics and function, problem solving, and integrating sensory and semantic information (Putt et al., 2019; Stout, 2011; Stout et al., 2008, 2015). Experimental modern tool-use studies have also demonstrated that regions in the frontal, temporal, and parietal cortices are activated, in action-observation, preparation, and execution tasks (Aydin et al., 2022; Berchicci et al., 2012, 2015; Di Russo et al., 2017; Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Osiurak and Badets, 2017; Osiurak et al., 2021). The particular regions of the brain that have displayed increased activation are known to be related to problem solving, action planning, goal-directed actions, mechanical knowledge, fine motor control, and visuospatial processing (Aydin et al., 2022; Berchicci et al., 2012, 2015; Carius et al., 2023; Di Russo et al., 2017; Ehrsson et al., 2000; Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Iturrate et al., 2018; Lu, Kim, and

Kim, 2023; Osiurak and Badets, 2017; Osiurak et al., 2021). This extensive body of research has established a foundation for future studies. It has pinpointed the precise regions of the brain that are activated during tool tasks. With their high spatial resolution, these studies have also enabled us to understand how these specific regions interact with one another. They have further allowed us to accurately identify the neural requirements for tool production and use. (Sturzbecher and de Araujo, 2012; Brain Products, 2024).

However, as with most of these neural mapping methods, there are several technical limitations in their use. fMRI and PET, in particular, despite offering high spatial resolution, have low temporal resolution, are non-portable and relatively expensive compared to other neuroimaging techniques, and limit participants' ability to move naturally during the experiments (Stout et al., 2000, 2015). This makes it harder to accurately measure neural activation during real-time tool production or use (Stout et al., 2000, 2015). In this context, temporal resolution refers to how precisely a method can measure activity changes over time, whereas spatial resolution refers to how precisely each technique can locate where those changes occur within the brain. EEG, contrary to other neuroimaging techniques, has a very high temporal resolution (within the millisecond range), but relatively low spatial resolution, is less costly, and allows relatively greater movement of participants during monitoring (Bulea et al., 2013; Dal Maso et al., 2018; Enders and Nigg, 2016; Klimesch, 1999; Pfurtscheller and Lopes da Silva, 1999; Qidwai, Ajimsha, and Shakir, 2019; Sarhan, Al-Faiz, and Takhakh, 2023). Despite numerous advantages, EEG's applications remain scarce in the field of neuroarchaeology.

In addition, as previous studies within the medical and sport science fields have demonstrated (Bulea et al., 2013; Dal Maso et al., 2018; Enders and Nigg, 2016; Qidwai, Ajimsha, and Shakir, 2019; Sarhan, Al-Faiz, and Takhakh, 2023), neuroimaging techniques like EEG are often combined with sEMG to determine dynamic interactions between cognition and muscle recruitment for diagnosis of neurological conditions, rehabilitation, and motor memory control (Bulea et al., 2013; Dal Maso et al., 2018; Enders and Nigg, 2016; Qidwai, Ajimsha, and Shakir, 2019; Sarhan, Al-Faiz, and Takhakh, 2023). In archaeological sciences, investigating this interplay can allow for a deeper understanding of a tool's task neuromechanical requirements, taking into consideration the brain-body relationship and when specific brain regions and muscle groups are more highly co-activated, e.g., understanding if certain brain regions are activated before execution, during the preparatory stage. In the future, applying this approach to other key hominin behaviors, such as gestural or vocal communication, could enable neuromechanical comparisons across different behaviors and tasks. This, in turn, would provide a basis for the re-evaluation of fundamental hypotheses surrounding the co-evolution of tool use and communication abilities in hominins (Frey, 2008; Stout et al., 2008; Stout and Chaminade, 2012).

1.6 EARLY HOMININ TOOL-USING EFFICIENCY AND KNOW-HOW

In addition to the methodological advances within our field, research into the biomechanics and cognition processes underlying stone tool use has increasingly emphasized the importance of understanding hominin tool-using efficiency and cumulative know-how. The term efficiency here refers to the effective use of energy and materials in producing functional tools (Böning, Maassen, and Steinach, 2017; Bril, Parry, and Dietrich, 2015; Williams-Hatala et al., 2020), while know-how encompasses the practical knowledge and technical skill required to successfully perform such learned motor tasks/skills (Moore and Perston, 2016; Tennie, Snyder, and Planer, 2025).

Previous experimental studies have shown that individuals experienced in knapping (tool production) consistently outperform novices in both biomechanical efficiency (through more accurate percussion, greater ability to predict and control flake shape, and fine-tuned adjustments to changing conditions such as hammer weight) and task success (displaying higher overall success rates in flake removal), particularly in lithic production and nut-cracking experiments (Bril, Parry, and Dietrich, 2015; Bril et al., 2010, 2012; Nonaka, Bril, and Rein, 2010; Pargeter et al., 2020). Beyond archaeological sciences, neurological studies on modern tool use have identified patterns of increased frontoparietal activation during complex tool-use tasks among experts, including regions associated with decision-making, problem solving, motor planning, and fine motor control (Landau and D'Esposito, 2006; Ehrsson et al., 2000; Vogt et al., 2007; Yang, 2014). These findings collectively highlight the need to consider how skill acquisition influences both neural and muscular dynamics during tool-related activities. Understanding how expertise plays a role in efficient tool-using performance is an essential step towards interpreting the cognitive and motor capabilities of early hominins engaged in stone tool production and use. Such empirical observations can be used to evaluate the fundamental hypothesis that an evolved ability to accumulate practical experience played a fundamental role in shaping both biomechanical and cognitive efficiency during early hominin stone tool use. Consequently, investigating the interaction between tool-related experience, neural engagement, and task-specific biomechanical demands can offer valuable insights into the factors driving early hominin biocultural evolution.

Building on these experimental studies, it is also important that we examine how know-how and cumulative experience shaped some of the earliest stone tool use behaviors, particularly those discussed within this thesis: Oldowan-style flake cutting and hammerstone pounding. These tasks represent the first emergence of human-like tool-related behaviors in the fossil record (Mora and De la Torre, 2005; O'Malley et al., 2025; Plummer et al., 2023), with flake cutting marking the earliest evidence of human-like pad-to-side precision grasping (Plummer et al., 2023; Susman, 1991; Toth, 1985). Experimental investigations into these behaviors can help determine whether the ability to accumulate practical tool-related experience may have provided an evolutionary advantage for efficient tool use (Morgan et al., 2015; Nonaka, Bril, and Rein, 2010; Stout, 2011), even before the appearance of the genus *Homo* (Plummer et al., 2023). Such findings would imply that experience, and as such, expected efficiency formed a crucial foundation for the later gradual development of increasingly sophisticated material culture (Morgan et al., 2015; Muller and Clarkson, 2016; Muller, Clarkson, and Shipton, 2017; Nonaka, Bril, and Rein, 2010; Stout, 2011).

2 OBJECTIVES

This doctoral dissertation aims to provide novel insights into the neuromechanical relationship between expertise and efficiency in early stone tool use tasks. Emphasis is placed on a new integrated methodology introduced through these studies, which includes the combined use of EEG and sEMG to measure the synchronous cognitive and muscular activity of participants during stone tool tasks. More specifically, two early stone tool behaviors were examined: Oldowan-style flake cutting and hammerstone pounding on participants with three levels of expertise: Novices, with no prior knowledge of stone tool production and use; Intermediates, with theoretical knowledge of lithic production and use; and Experts, with extensive theoretical and practical stone tool knapping experience. Additional characteristics and information were provided by each of the participants, including biological sex, age, stature, hand size, and grip strength. The main objectives of this doctoral project were to:

(1) Create and validate a novel integrative methodological protocol in experimental archaeology that simultaneously records and processes EEG and sEMG data, enabling the investigation of brain-hand interactions during stone tool experiments.
(2) Improve understanding of how interindividual variability, including stone tool theoretical and practical expertise in stone tool use, influences biomechanical and cognitive efficiency during the performance of two stone tool tasks of fundamental evolutionary significance (hammerstone pounding and flake cutting).
(3) Evaluate the importance of analyzing all stages of each tool-use process to capture crucial cognitive and biomechanical information prior to task execution, including preparation and planning.

The core research questions for each of the three studies (I–III) comprising this thesis are outlined below:

1. **Study I: "Does the newly introduced integrative EEG/sEMG protocol provide accurate analyses of neurological and muscular activity during experimental stone tool tasks, thereby offering a reliable methodological toolkit for experimental archaeology?"** Building on previous experimental studies into lithic production and use within the broader field of experimental archaeology (e.g., Hamrick et al., 1998; Hecht et al., 2023; Key et al., 2020; Macchi et al., 2021; Marzke et al., 1998; Putt, Wijeakumar, and Spencer, 2019; Putt et al., 2017; Stout et al., 2000, 2008, 2015; Williams-Hatala et al., 2018), the first paper of this cumulative thesis aimed to introduce and validate a novel integrative protocol for quantifying neuromechanical activity across three distinct stages of stone tool use ("Hold", "Aim", and "Execute"), relying on the high temporal precision of EEG and sEMG technologies.

2. **Study II: "Does extensive practical stone tool-related experience impact muscular efficiency (defined as success rate relative to the degree of muscular effort; Böning, Maassen, and Steinach, 2017; Bril, Parry, and Dietrich, 2015; Williams-Hatala et al.,**

2020) during early stone tool use tasks? Additionally, are knapping Experts able to adapt more rapidly to less familiar tool-using tasks than Novices, suggesting increased skill transfer?” Although multiple sEMG studies have previously examined stone tool production and use (e.g., Key et al., 2020; Hamrick et al., 1998; Marzke et al., 1998), no experimental research has directly compared the impact of efficiency-related factors in two of the earliest known hominin stone tool behaviors: hammerstone pounding (also observed in other extant primates) and flake cutting activities (exclusively associated with hominins) (Boesch and Boesch, 1990, 1993; Fragaszy et al., 2004; Haslam, 2013; Ottoni and Mannu, 2001; Plummer et al., 2023; Proffitt et al., 2016, 2023; Whiten et al., 1999).

3. **Study III: “Do knapping experts exhibit, as expected based on the neurological literature (e.g., Aydin et al., 2022; Brandi et al., 2014; Goldenberg and Spatt, 2009; Hecht et al., 2015; Johnson-Frey, 2005; Osiurak et al., 2021; Putt, Wijeakumar, and Spencer, 2019; Stout et al., 2000, 2008), increased neural activity in dominant hemisphere regions (for right-handed individuals, the left-frontal, premotor/motor, and left-parietal cortices) along with decreased muscular activation during the preparatory stage of early stone tool use? Furthermore, do experts display distinct patterns of cognitive and muscular activation during the Oldowan-style flake cutting task compared to the hammerstone nut-cracking task?”** Expanding on the previous sEMG study on muscular efficiency, the third paper of the thesis relied on the introduced EEG/sEMG protocol to investigate how expertise influences neuromechanical activity across these two fundamental stone tool tasks.

3 RESULTS AND DISCUSSION

This section presents the results and interpretations of the three papers comprising this cumulative thesis, each in a separate subsection (3.1-3.3). Subsection 3.4 then synthesizes the main conclusions of the three studies in relation to the overarching aim and objectives outlined in section 2. Among the three studies presented, two are published and one is currently under submission (see Appendix).

Each of the first three subsections (3.1-3.3) outlines the framework and methodology of the corresponding study, followed by a concise summary of the main results and their core interpretation. As all three papers draw on data from the same broader experiment, most of the doctoral project's methodology (including EEG and sEMG preparation, raw data recording, and processing) is outlined in detail within Study I (subsection 3.1; Eteson et al., 2025). Subsequently, each study's statistical analyses and results will be addressed separately. Then, even more detailed descriptions of the methodology and results can be found in each study itself (see Appendix) as well as in our extensively documented, peer-reviewed step-by-step protocol (Eteson et al., 2025; https://dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1).

3.1 STUDY I: A new and validated approach for exploring brain-hand interactions in experimental archaeology

This first paper presents and validates the first combined EEG/sEMG methodological step-by-step protocol for future experimental archaeological studies exploring brain-hand interactions during tool-related tasks (Eteson et al., 2024a, 2025). Relying on this newly proposed approach (Eteson et al., 2024a), its methodological validation analyses focus on investigating cognitive and muscular activation during Oldowan-style flake cutting, typically regarded as the earliest known form of tool use exclusively associated with hominins (Bril et al., 2012; Eteson et al., 2025; Harmand et al., 2015; Proffitt et al., 2016, 2023). Since the aim of the initial study was to develop an unprecedented interdisciplinary methodological toolkit at the intersection of neurology, biomechanics, and archaeology, the following pages provide a complete overview of the developed protocol, which forms the solid foundation for the other parts of this doctoral thesis (other subsections below). This is followed by a concise summary of the validation analyses' results and interpretations.

Participants (*n* = 23) performed an Oldowan-style flake cutting task in three distinct stages: Hold, Aim, and Execute. All experimental sessions were performed in a shielded cabin within the Max Planck Institute for Intelligent Systems in Tübingen (see Acknowledgements). This cabin was used to help reduce electrical noise that would otherwise potentially interfere with the true EEG signal by blocking electromagnetic fields (Suwandi and Khotimah, 2022). This is particularly important for increasing the signal-to-noise ratio in EEG and sEMG, both of which are particularly prone to artifacts (Boyer et al., 2023; Jiang, Bian, and Tian, 2019; Villasana, 2022). Participants were informed 24 hours prior to the experiment of various contraindications for the study (i.e., smoking and caffeine intake), to avoid effects on brain activation levels (Gilbert, 2000).

In addition, participants were shown an instructional video of the tasks they were required to perform.

For the first study of this thesis (Appendix A; Eteson et al., 2024*a*, 2025), only the Oldowan-style flake cutting task was used in the validation analyses. This task, as previously discussed, was split into three stages, Hold, the initial stage of the tool task to pick up the flake tool in the dominant hand; Aim, the preparation stage of the task, in which participants aim the flake tool at the intended object (the faux leather) and prepare for execution of the task; and finally Execute, which is when the participants performed the intended task (cutting entirely through the fibers of the fabric in a pre-marked Z shape on the fabric surface). Participants performed a minimum of 50 repetitions of each task, as EEG guidelines recommend a minimum of 40 repetitions for data quality (Graham, 2021). In addition to the stone tool tasks, a control task was performed to activate the motor cortex. This control task is necessary for identifying and isolating the specific neural activity during tool tasks by comparing the experimental tasks with the control task. This establishes activity (primarily in the motor cortex) that is common in both the control and the tool tasks (Riehle, 2004). In this experiment, the simple motor task consisted of opening and closing the hand into a fist shape, following standard neurological protocols (e.g., Muralidharan and Aron, 2021).

The flaked tools (*n* = 26 Oldowan-style flakes) used within this study were provided by Moos, E. T. (co-author of Study II; Eteson et al., 2024b), following proportions outlined in previous papers (Gladilin and Sitliviy, 1987; Hayden, 2008). Synthetic faux leather was used for the flake cutting task as a substitute for leather or hide, which has previously been used to replicate animal butchery in sEMG and use-wear analysis studies (Hamrick et al., 1998; Ibáñez and Mazzucco, 2021). Faux leather was chosen in place of real leather to control for inconsistencies in thickness, strength, and torque across trials. The faux leather was cut into 6cm x 6cm squares, with a 'Z' pattern formed of 3 x 3cm lines stenciled onto the square to mark where participants should cut. Using sEMG, eight muscles or muscle groups in the dominant and non-dominant hand and forearm were recorded. These muscles were selected based on previous application in stone tool sEMG studies and are widely regarded as being crucial for hominin stone tool use (e.g., see Key, Dunmore, and Marzke, 2019; Key et al., 2020; Kivell et al., 2023; Marzke et al., 1998). They consist of two powerful wrist flexors, *flexor carpi radialis* (FCR), *flexor carpi ulnaris* (FCU), a powerful flexor muscle in the thumb, *flexor pollicis longus* (FPL), the thenar eminence (TE) (consisting of *abductor pollicis brevis*, *flexor pollicis brevis*, and *opponens pollicis*), the first dorsal *interosseus* (DI1), and the hypothenar eminence (HTE) (consisting of *abductor digiti minimi*, *flexor digiti minimi*, and *opponens digiti minimi*). Muscles recorded in the non-dominant hand were: the first dorsal *interosseus* (ndDI1) and the thenar eminence (ndTE) (in Appendix B, see Figure 3 and Table 1; Eteson et al., 2024b), as both the thumb and second digit are known to be important in stabilization during stone tool production and nut-cracking (Key and Dunmore, 2015; Marzke et al., 1998; Marzke and Shackley, 1986). Both tasks undertaken in this study required stabilization of the target object (i.e., faux leather) (in Appendix B, see Figure 1; Eteson et al., 2024b). Additionally, prior to the start of the experiment, participants performed a series of maximum voluntary contraction (MVC) exercises. These were used to record the maximum signal for each muscle, allowing the data to be adjusted for interindividual differences in muscle strength (Zellers et al., 2019). Two different MVCs were recorded for each participant, including a power grip and a pad-to-pad pinch grip, relying on the Baseline BIMS power strength dynamometers (Functional model, Fabrication Enterprises, New York). Each MVC was performed three times and held for five seconds each time. Participants' highest strength measurements (in kg) were recorded for each MVC. After the end of the experiment, all participants' sEMG data were transformed into %MVC values (i.e., muscle "X" displayed 10% of the MVC during the "X" task).

For the recording of neural activity, a standard 32-channel EEG cap, following the 10-20 system configuration, was used (Brain Vision Recorder software, version 1.24.0101, Brain Products GmbH, Gilching, Germany). These EEG channels cover the superficial layers of the cerebral cortex in the frontal, parietal, temporal, and occipital lobes. For the validation study, the areas of focus for analysis were the left frontal and motor regions. These regions were chosen due to their known importance in tool use (Federico et al., 2023; Gallivan et al., 2013; Goldenberg, 2009; Johnson-Frey et al., 2005; Lesourd et al., 2023; Osiurak et al., 2021), including precise fine motor tasks, planning, and decision making. Additionally, previous stone tool knapping studies found prominent activation in these neural regions (Putt, Wijeakumar, and Spencer, 2019; Putt et al., 2017; Stout et al., 2000, 2008; Stout, 2011; Stout et al., 2015). All EEG and sEMG signals were recorded using the Brain Vision Recorder (version 1.24.0101, Brain Products GmbH, Gilching, Germany), with a sampling rate of 2500 Hz. The standard online FCz reference was used for recording and later re-referenced. Before recording, EEG electrodes were filled with electrode gel to improve impedance for better signal transmission and were subject to scrupulous checks to ensure impedance remained below 25 kΩ for all EEG channels, as recommended (Laszlo et al., 2014; Leuchs, Pizzamiglio, and Bellomo, 2022; Mathewson, Harrison, and Kizuk, 2017). Abrasive electrolyte gel was used to improve skin conductivity and prime electrode contact for sEMG muscle sites. BrainAmp amplifiers were used to convert weak electrical signals for the brain (EEG) and muscles (sEMG) to amplify the real signal, enhancing the signal-to-noise ratio, measured in microvolts (μV). For the application and recording of sEMG, the European standards for surface electromyography (SENIAM project; Stegeman and Hermens, 2007) were used. Bipolar electrodes were placed over the muscle belly, in line with the muscle fibers, onto cleaned skin, and then secured with kinesiology tape (in Appendix B, see Figure 5; Eteson et al., 2024b). Placement was then evaluated by performing movements and exercises known to activate the muscles monitored (Eteson et al., 2024b; Key et al., 2020; Standring, 2021). Prior to the start of the experiment, markers for each stage were created (i.e., Hold, Aim, Execute, Rest). These markers were then manually triggered when the stimulus sound was played. One cycle (trial) of a task was performed over a period of 20 seconds, 5 seconds for each task (in Appendix B, see Figure 4; Eteson et al., 2024b). A repeating five-second stimulus sound was recorded within the BrainVision Recorder software (version 1.24.0101, Brain Products GbmH, Gilching, Germany) as an AUX channel to cue participants on when to perform each stage of the task and to enable accurate syncing of the markers to each stage of the task during pre-processing and cleaning of the data, after recording. EEG and sEMG data were preprocessed in the BrainVision Analyzer software (Version 2.2, Brain Products GmbH, Gilching, Germany) post-recording. Based on the differing preprocessing steps necessary, EEG and sEMG data were processed separately after markers were moved to correctly align with the AUX auditory stimulus.

Once all tasks had been recorded, all EEG and sEMG data were imported into the BrainVision Analyzer software (Version 2.2, Brain Products GmbH, Gilching, Germany). All markers were synchronized with the auditory cue to ensure each stage (i.e., Hold, Aim, Execute) was captured accurately and aligned with the participants' auditory cue. To process the sEMG data, all data signals were checked for large artifacts, dead channels, signal loss, or signal clipping (Gage, Signal Quality Monitor), sEMG data was then downsampled to 500 Hz, with a low cutoff of 20 Hz and a high cutoff of 450 Hz to maintain the important frequencies for sEMG (Ives and Wigglesworth, 2003; Merletti, 1999; Potvin and Brown, 2004; Reis et al., 2014; Stegeman and Hermens, 2007). A notch filter was also applied at 50 Hz to filter out power line noise (Kappenman and Luck, 2010). Data was segmented based on the three distinct stages of each stone tool task (Hold, Aim, Execute). Once segmented, rectification was performed to transform sEMG signals into positive values. This technique is typical in sEMG studies as sEMG has a mean close to zero due to the oscillations of the muscles creating both negative and positive values; therefore, rectification creates more meaningful data to export (Negro, Keenan, and Farina, 2015; Neto and Christou, 2010). Repetitions of each segment were then averaged into a single segment, creating mean values of each of the muscles within each stage of a task (after cleaning and removal of noisy segments, all participants had ≥46 repetitions). sEMG data was then exported into an Excel spreadsheet (Excel help and learning, Microsoft Support), into 0.4 ms epochs. These epochs were then averaged again, so each muscle had one mean value for each stage of the tasks. MVCs are also processed in the same way as the other sEMG data. Prior to exporting the data, maximum values (*max markers*) are taken from the MVCs. Maximum values are then imported into an Excel spreadsheet and can be used to create a percentage MVC (%MVC) value, which ensures sEMG data is comparable between participants. The %MVC value is calculated as a basic percentage calculation: $(averaged\ sEMG\ data) \div (MVC\ value) \times 100$.

Similarly to sEMG, EEG data were also downsampled, in this case to 250 Hz, with a low cutoff of 1 Hz and a high cutoff of 40 Hz (Resampling, ILCB Center of Experimental Resources). As with sEMG, a notch filter was also applied at 50 Hz to filter out power line noise (Kappenman and Luck, 2010). After an initial screening for artifact removal and noisy channels, EEG data is re-referenced using the Reference Electrode Standardization Technique (REST) (Yao, 2001). Re-referencing is a crucial step in EEG pre-processing, as electrode voltage is measured relative to the reference electrode. The REST technique has been shown to provide a more accurate representation of brain activity, as it does not rely on specific electrodes, unlike the online reference (FCz), averaged, or mastoids referencing (Leuchs, 2019; Yao et al., 2019), which are all electrically active, but rather uses a mathematical model of the brain, to reconstruct EEG signals as if they had been referenced from a neutral "infinite point" (Leuchs, 2019; Yao, 2001). This has been proven to be particularly useful for event-related potential (ERP) studies and frequency analyses (Yao, 2001; Yao et al., 2019). After referencing, independent component analysis (ICA) and inverse ICA were performed to remove ocular artifacts (eye blinks, side-eye movements) and other persistent muscular artifacts (i.e., neck tension) (Abo-Zeid, Ahmed, and Abbas, 2015; Luck, 2018; Plank, 2013; Subramaniyam, 2018; Villasana, 2022). Channels removed earlier in the process due to noise or signal loss were then interpolated by surrounding channels (Villasana, 2022). The data was then segmented to encompass the entire tool task period, and 200 ms prior to task onset (Hold (5000 ms), Aim (5000 ms), and Execute (5000 ms) + 200 ms prior to stimulus = 15,200 ms). Baseline correction was then performed on the segments from -200 – 0 ms, prior to the start of the task ("Baseline Correction", 2024; Liland et al., 2011). Further segmentation was then additionally performed to separate each stage of the task; this was made possible due to the markers previously positioned within the data and synchronized with the auditory AUX channel. These segments captured the first second of each stage (0 – 1000 ms). This segment was chosen as the P300 component, a positive wave or increase in amplitude, is typically observed around 300 ms after the auditory stimulus and is associated with cognitive processes, such as decision-making (Sur and Sinha, 2009; Zhong et al., 2019). Additionally, after segmenting participants' data into various epochs (from 0 – 300ms to 4000 – 5000ms), we determined that the 0 – 1000 ms epoch provided the highest level of beta power across participants. A final artifact rejection was performed to identify and remove large or sudden increases in voltage and maximum/minimum amplitude not previously removed. A Fast Fourier Transformation (FFT) was then performed on the segmented data, with a 10% Hanning window to reduce spectral leakage and ensure the true frequency and amplitude of the signal was captured. Trials were then averaged (ensuring ≥40 clean trials for each participant; Graham, 2021), as with sEMG, to create one data point for each stage, per participant, per channel. The mean beta activity (μV) (12.5 – 30 Hz) was then exported from the BrainVision Analyzer software (Version 2.2, Brain Products GmbH, Gilching, Germany). Beta activity was selected for EEG analyses, as it is generally associated with increased activity during motor and movement tasks (Athanasiou et al., 2018; Enders and Nigg, 2016; Eoh, Chung, and Kim, 2005; Kirstein, 2008; Stern, 2005; Xavier, Su Ting, and Fauzan, 2020).

Prior to EEG exportation, grand averages were created from all participants' data. Grand averaging is the process of averaging EEG segments across multiple participants to enhance signal-to-noise ratio and represent average neural activity across groups of participants (the entire dataset, or a subset, such as experience groups). Grand averaged mean spectra data were then used to produce FFT topographic maps to visualize neural activity across the major brain regions. All maps were generated in BrainVision Analyzer (Version 2.2, Brain Products GmbH, Gilching, Germany). Data was then exported for further analysis. All EEG and sEMG data were analyzed using PAST (version 4.03, Hammer, Harper, and Ryan, 2001), SPSS (version 29.0.2, Field, 2013), and BrainVision Analyzer (Version 2.2, Brain Products GmbH, Gilching, Germany).

Finally, we report the following statistical analysis in the context of Study I's validation paper's expectations (Eteson et al., 2025). We hypothesized that participants would display peak muscular activation (sEMG) during the Execute stage. This is due to the increased ergonomic demands and sustained pressure required during cutting, which necessitate greater force and manual dexterity (Key, Merritt, and Kivell, 2018; Key and Lycett, 2011; Key et al., 2020; Marzke, 2013; Williams-Hatala et al., 2018). We also expected increased neural activation in the prefrontal and frontal regions during the Aim stage (Jones and Graff-Radford, 2021; Putt, Wijeakumar, and Spencer, 2019; Stout, 2011; Stout et al., 2008; Stout et al., 2015). This stage involves anticipating and planning the sequence of movements required for execution (Aydin et al., 2022; Berchicci et al., 2012, 2015; Di Russo et al., 2017). A correlation-based principal component analysis (PCA) was performed on the sEMG data to determine whether all muscles (in both the dominant and non-dominant hands) were recruited differently at each stage of the Oldowan-style flake cutting task. An additional PCA was also performed, excluding the non-dominant hand muscles, as the Hold stage did not recruit the non-dominant hand for stabilizing, unlike the Aim and Execute stages. After running normality tests on the extracted PC scores to determine whether the muscular activation displayed significant differences across the stages, a repeated-measures analysis of variance (ANOVA) was run, followed by a post-hoc test to determine where the differences lie. To visualize the neural activation in tandem, the EEG data of all participants were averaged (grand average mean spectra) to create one segment of beta mean activity for each stage of the flake task (and control task), depicting an average of all participants throughout their trials. The grand-averaged data were then plotted on a topographic map, indicating areas of the brain that displayed increased or decreased activity at each stage of the task. The topographic maps were then visualized next to the sEMG PCA plots to demonstrate how the combined EEG-sEMG protocol can highlight differences in activation levels during task stages and identify brain-hand interactions throughout the process to be used as a basis for future research of hominin tool use and behavior.

The results broadly aligned with expectations regarding muscular and neural activation, broadly consistent with the conclusions of previous literature (Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Key and Lycett, 2011; Key, Merritt, and Kivell, 2018; Key et al., 2020; Osiurak and Badets, 2017; Osiurak et al., 2021; Marzke, 2013; Stout, 2011; Stout et al., 2008, 2015; Williams-Hatala et al., 2018). In particular, we observed peak muscle engagement across all muscles during the Execute stage of the tasks, including in the non-dominant hand, which was primarily used for stabilization during the experiment. Based on the neurological data and analyses (EEG), beta power was highest during Aim (preparatory stage) in the left frontal brain region (associated with planning, problem-solving, and working memory) and the motor cortex (consistent with Aydin et al., 2022; Berchicci et al., 2012, 2015; Di Russo et al., 2017; Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Osiurak and Badets, 2017; Osiurak et al., 2021). Overall, these findings reflect the expected outcomes of our methodological paper's validation analyses and thereby support the new protocol's efficacy in approaching the biomechanical and cognitive processes required for stone tool use. Moreover, our results additionally highlight the importance of separating experimental tool tasks into distinct stages (e.g., Hold, Aim, Execute). This process revealed valuable insights into the unique demands of each stage of the entire tool using process, thus exploring the differing levels of muscular and cognitive activation that would be missed if only one stage of the task were recorded (as in Hamrick et al., 1998; Key et al., 2020) (Eteson et al., 2024b, 2025; Williams, Gordon, and Richmond, 2014).

Nevertheless, the results also showed that beta power in the frontal and prefrontal regions was higher during the Aim (preparatory) stage than during task execution. Moreover, the motor cortex displayed steadily decreasing hemispheric lateralization throughout the task, due to both the Aim and Execute stages requiring stabilization from the non-dominant hand. Consequently, we observe apparently decreasing levels of beta power in both hemispheres of the motor cortex. However, this pattern in the beta power topographic maps (in Appendix A, see Figure 3; Eteson et al., 2025), despite visually manifesting as lower levels of beta power, probably demonstrates a phenomenon known as beta event-related desynchronization (ERD), which is known to occur in the sensorimotor cortex and is instead associated with increased (rather than decreased) neuro-motor engagement during voluntary movement (Crone et al., 1998; Pfurtscheller and Lopes da Silva, 1999; Zaepffel et al., 2013; Nakavashiki et al., 2014). We identified this ERD pattern throughout the three stages, as well as in the control task (in Appendix A, see Figure 3; Eteson et al., 2025), with a particular intensification during the Execute stage, where motor activation is reasonably expected to be at its highest.

More broadly, the reliability of our approach can also be confirmed by a comparison of our findings to those of multiple neurological studies on modern human tool use. Our study aligns with previous findings that the left-lateralized prefrontal region, along with the parietal region, plays a fundamental role in tool-related activities. The prefrontal cortex, which was particularly active during the preparatory stage, is necessary for action planning, motor imagery, and executive control (enabling goal-directed action), whilst the parietal region is known for its application in tasks requiring problem-solving and visuospatial organization (Aydin et al., 2022; Berchicci et al., 2012, 2015; Di Russo et al., 2017; Federico et al., 2023; Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Osiurak et al., 2021; Putt, Wijeakumar, and Spencer, 2019; Stout, 2011; Stout et al., 2008, 2015). These align with observations witnessed within this study.

In the context of hominin evolution, Oldowan technology, associated with fine precision grasping (Susman, 1991) and the uniquely hominin behavior of intentional cutting (Bandini and Tennie, 2023; Plummer, 2004; Roux and Bril, 2005; Wynn and McGrew, 1989) is known to have emerged alongside hominin encephalization and the gradual expansion of the frontoparietal network (Bruner, Battaglia-Mayer, and Caminiti, 2023; Stout et al., 2008). In particular, the frontal and prefrontal regions of the brain are known to be involved in executive functions, such as action planning, decision-making, and problem solving (Adin et al., 2022; Berchicci et al., 2012; Goldenberg and Spatt, 2009; Jones and Graff-Radford, 2021; Putt, Wijeakumar, and Spencer, 2019; Stout, 2011; Stout et al., 2008, 2015), which may have been advantageous to the evolution of hominins by providing a neural foundation for the gradual emergence of increasingly complex material culture (Bruner, Battaglia-Mayer, and Caminiti, 2023; Putt, Wijeakumar, and Spencer, 2019; Stout, 2011; Stout et al., 2015).

This validation paper also gathered insights into the importance of the stabilization hand (in this case, the non-dominant hand), which was necessary during both the preparatory Aim stage and the Execution stage. This stabilization was essential for task success to provide torque, resistance, and force to the faux leather, to allow for a counter force to be applied to the flake to cut through the material. The coordinated use of both hands, one striking hand that executes the precise cutting action, and one stabilizing hand that provides critical support to the "manipulating hand", is often overlooked in experimental studies, as focus is solely on the dominant hand (Key et al., 2020; Hamrick et al., 1998; Williams-Hatala et al., 2018). However, here we highlight the importance, from an evolutionary perspective, of analyzing the emergence of this bimanual coordination as a potentially key adaptation in early hominins (Bril, Parry, and Dietrich, 2015; Marzke, 2013; Stout et al., 2008). Such bimanual coordination has been argued to underpin the efficiency of early stone tool production, displaying superior manual dexterity to non-human primates (Bril, Parry, and Dietrich, 2015) and neural hemispheric lateralization specializations for both the dominant (striking) hand and non-dominant (stabilizing) hand (Stout et al., 2008). Therefore, we argue that this may also be the case during bimanual early stone tool use. Evolutionary sciences may therefore benefit from future experimental research into the neural and biomechanical mechanisms of bimanual coordination in various other stone tool technologies and hominin behavior. Such research would undoubtedly offer additional valuable insights into the evolution of hominin manual dexterity and may further our understanding of how our unique coordination of the dominant and non-dominant hand during stone tool behaviors (Bril, Parry, and Dietrich, 2015; Marzke, 2013; Stout et al., 2008) may have contributed to the development of complex tool technologies (Morgan et al., 2015; Muller and Clarkson, 2016; Muller, Clarkson, and Shipton, 2017; Nonaka, Bril, and Rein, 2010; Stout, 2011).

3.2 STUDY II: An sEMG Experimental Approach to Exploring Efficiency in Early Hominin Stone Tool Use

The second study of this thesis relied on sEMG to assess the factors influencing participant efficiency in performing the two fundamental early stone tool use tasks addressed in this doctoral project. In this study, efficiency (broadly defined as achieving the desired outcome with minimal waste of resources such as time, effort, or materials; Böning, Maassen, and Steinach, 2017; Bril, Parry, and Dietrich, 2015; Williams-Hatala et al., 2020) was measured by quantifying muscle activation in the dominant and non-dominant hand and forearm, as well as by calculating the number of successful trials performed during the tool-use tasks, including flake cutting and hammerstone pounding (nut-cracking). These two distinct measures of efficiency were monitored in all participants who were categorized into three levels of relevant stone tool knapping expertise. Participants with an absence of any experience were labeled as Novices (*n*

= 16); the next group was defined as participants with theoretical stone tool knowledge, but minimal/lack of practical experience, hereafter known as Intermediates (*n* = 4); finally, the most experienced group, labeled Experts (*n* = 5), were participants with extensive practical stone tool knapping experience.

In addition to the aforementioned Oldowan-style flake cutting task described in Study I, participants also performed a hammerstone nut-cracking task. As explained in the Introduction of this thesis (section 1), hammerstone nut-cracking was chosen as a comparative tool-use task for several reasons. These include its documented prevalence among non-human primate species and hominins (Arroyo et al., 2016; Bril et al., 2012; Bril, Parry, and Dietrich, 2015; Goren-Inbar et al., 2002; Gumert and Malaivijitnond, 2012; Kahrs, Jung, and Lockman, 2014; Panger et al., 2002; Proffitt et al., 2016, 2023; Wynn and McGrew, 1989), its biomechanical similarity with Oldowan knapping techniques (Boesch and Boesch, 1993; Davidson and McGrew, 2005; Marchant and McGrew, 2005; Sugiyama and Koman, 1979; Wynn and McGrew, 1989), and the hypothesis that it might acted as a potential precursor to intentional freehand knapping techniques associated with the Oldowan industry (Bril et al., 2012; also see Proffitt et al., 2023). The hammerstones (*n* = 19) used in our study were sourced by Moos, E. T. (co-author of Study II; Eteson et al., 2024b), following morphological specifications from previously published archaeological findings associated with Oldowan contexts (Titton et al., 2018). For the hammerstone nut-cracking task, macadamia nuts (*Macadamia integrifolia*) were used as a substitute for oil palm tree nuts (*Elaeis guineensis*) (Arroyo et al., 2016; Bril et al., 2015; Hirata et al., 2009), commonly consumed in the wild (Arroyo et al., 2016; Hannah and McGrew, 1987; Proffitt et al., 2018).

As with the first paper (Study I), both tasks are separated into three stages: Hold, Aim, and Execute. Data from the Execute stage was also used to assess the success of each task for each participant trial. Success for each participant trial was determined using a binary scoring approach, with "1" indicating success and "0" indicating failure. The criteria for success in each task were as follows: for the hammerstone nut-cracking task, the macadamia nut must be retrievable from its hard outer shell after initial contact with the hammerstone and without the use of any additional tool. For the flake cutting task, fabric fibers of the faux leather were to be entirely cut through along the stenciled Z-pattern. Materials (macadamia nuts and faux leather) were collected after each task, and video footage was monitored after the experiment to determine participants' success rate. Success rates were then calculated into a percentage of success for each participant based on all trials (≥50).

In this study, we tested three hypotheses regarding the role of experience and biomechanics in early stone tool use (for further details, see Study II in the Appendix). First, we predicted that participants with greater knapping experience and higher grip strength would perform both tool-using tasks more efficiently, defined as higher success rates and lower muscular activation, across all task stages. This was based on several previous experimental studies that found this to be the case (Bril et al., 2010, 2012; Key and Lycett, 2011). Second, we expected that flake cutting, an exclusively hominin behavior (Bril et al., 2012; Harmand et al., 2015; Proffitt et al., 2016, 2023), would benefit more from accumulated practical experience, whereas hammerstone nut-cracking would rely more heavily on biomechanical factors such as grip strength. Finally, we hypothesized that cumulative experience in stone tool behaviors may increase participants' adaptability to transfer their skills to less familiar tool-using tasks. This would enable more experienced participants to master both tool-using tasks more quickly than less experienced individuals, as previous studies have demonstrated that skill transfer can effectively improve success in stone tool production (Heyes, 2018; Seifert et al., 2013).

Overall, our results showed that participants with extensive practical stone tool experience (Experts) displayed significantly improved efficiency (defined as higher success rates and lower muscular activation) during the Oldowan-style flake-cutting task. However, this pattern was not observed during the hammerstone nut-cracking task. Although Expert participants consistently exhibited lower muscular activation than Novice and Intermediate participants in both tasks, differences in success rates were not significant. Despite this, the reduced muscular activation highlights the biomechanical advantages conferred by expert know-how. Moreover, across the 50 hammerstone task trials, Experts demonstrated a faster rate of improvement. These findings suggest that cumulative practical experience may have been crucial for the development of energy-efficient tool use in early hominins and for supporting the cognitive and behavioral flexibility necessary for the emergence of intentional tool production.

Contrary to the expectations outlined in our first hypothesis, no correlations were found between participants' grip strength (via dynamometer strength tests, see subsection 3.1) and success rates in either task, despite a previous study having observed this pattern (Key and Lycett, 2011). This indicates that strength was not a significant factor in either task, potentially due to the relatively small mass of both tools (particularly the Oldowan-style flakes), and the tasks relying much more on experience using the stone tools, rather than overall strength. Despite this, Expert participants with relevant and extensive practical stone tool experience were clearly distinguishable from their less experienced counterparts, displaying significantly lower levels of activation across all muscles, observable in all six PCAs conducted. The PCAs were conducted on each of the stages of the tool tasks (Hold, Aim, Execute). In each PCA, a clear separation between the Experts and the two less experienced groups was visible along PC1. Experts consistently presented mostly negative scores against all loadings (muscles) (in Appendix B, see Figure 8 and Table 2; Eteson et al., 2024b). These visual trends in the PCA plots, highlighting overall lower muscle recruitment in Experts, were further confirmed by statistical probability tests and illustrated using box plots and radar plots (in Appendix B, see Figure 9 and 10, Table 3; Eteson et al., 2024b).

This confirmed that, as hypothesized, Experts recruited their muscles relatively less than those without related experience, demonstrating consistently lower effort across the Aim and Execute stages of the tasks. However, unlike most of the muscles recorded, two muscles known for their critical role in human-like tool use (Karakostis et al., 2018; Key, Dunmore, and

Marzke, 2019; Kivell, 2015; Kivell et al., 2023; Kunze et al., 2022; Marzke, 1997; Marzke et al., 1998) did not demonstrate the lowest activation levels in Experts (particularly during the hammerstone task). These muscles (the hypothenar eminence and thumb flexor FPL), which display recruitment similar to that of the less experienced participants, may highlight their particular importance within the context of evolution and their essentiality for human manipulation. This is particularly interesting considering the absence of the FPL in non-human primates and its appearance in early, potentially tool-using hominins (Dunmore et al., 2023; Karakostis et al., 2021; Kunze et al., 2022). During tool use, the FPL crucially functions to flex the distal phalanx of the thumb against objects, such as tools, in the hand (Key et al., 2020; Kivell, 2015; Standring, 2021), enabling the control and fine manipulation necessary to perform fundamental human-like precision grasping patterns (Hamrick et al., 1998; Marzke, 1997; Marzke et al., 1998; Susman, 1991). Activation of the FPL has also been shown to increase during increased resistance to the thumb (Hamrick et al., 1998). In this study, its consistent recruitment in both Expert and Novice participants suggests that the FPL is heavily relied upon regardless of experience level, underscoring its central role in enabling fine motor control for human-like tool-related behaviors (Susman, 1991). From an evolutionary perspective, the emergence of the FPL may have therefore been a key adaptation that enabled early hominins to more efficiently perform precision tasks, such as intentional flake cutting, that are not observed in other primates (Karakostis, 2023; Kunze et al., 2022; Marzke, 1997; Marzke et al., 1998).

The additional efficiency measured within this study was proposed in the second hypothesis and is based on the success rates of participants. In contrast to the first hypothesis, which was only partially sustained, the second hypothesis was largely confirmed. Based on ANOVAs, success rates in the flake cutting task differed significantly between Expert and Novice participants. This significance was maintained, even after controlling for grip strength. As expected, however, this effect was not significant in the hammerstone task. These results, aligned with expectations, suggest that successful hammerstone nut-cracking relies less on accumulated experience than precision grasping activities, such as flake cutting. This suggests that all individuals, regardless of their experience, display similar levels of efficiency. However, based on our first hypothesis, we know this is not the case. Unlike the less experienced participants, Experts maintained significantly lower muscular activation levels even in the hammerstone nut-cracking task. Importantly, this suggests that despite one measure of efficiency displaying no difference between experience groups, Experts still display an improved understanding of the biomechanical requirements for the hammerstone task, a trend that is not observed in either Novices or Intermediates. This suggests that the increased ability of hominins to acquire practical know-how through “trial and error” may have been fundamental for achieving energetic efficiency during early stone tool use.

Evaluating the third hypothesis of this study provided deeper insights into the impact of expertise on tool-using efficiency and skill transfer. Despite no correlation between hammerstone nut-cracking success rates and expertise when success rates were calculated across all ≥50 trials, we explored whether success rates improved throughout the trials, as hammerstone nut-cracking has previously been theorized to show similarities to stone tool knapping (Boesch and Boesch, 1993; Bril et al., 2012; Bril, Parry, and Dietrich, 2015; Davidson and McGrew, 2005; Sugiyama and Koman, 1979), a behavior in which our Expert participants had extensive experience. Therefore, we conducted two statistical analyses to establish whether any of the three experience groups displayed increased rates of improvement. First, we sectioned the first 50 trials of each participant into 5 segments (10 trials in each section) and statistically evaluated their correlation with knapping experience using Kendall's tau tests (Kendall, 1938; Khamis, 2008). From this, we garnered that, after around the 30th repetition of the hammerstone task, Experts' success was visually consistently higher than the other experience groups, while the last 10 repetitions were found to be significantly correlated with the level of experience. By contrast, in the cutting task, four out of five trial segments (including also the initial 10 trials) were significantly positively correlated with experience, without signs of changes in success rates throughout the experiment. These findings were further confirmed using three repeated-measures binary logistic regression models to determine the predicted probabilities of success for each experience group across all 50 trials (Eteson et al., 2024b; Hosmer Jr, Lemeshow, and Sturdivant, 2013; Iddrisu et al., 2023). The model for Experts found a substantial decrease in error ("failure") rates when compared to the Novice and Intermediate groups, both of which only showed minimal changes in performance throughout the tasks.

Altogether, these results support the study's third hypothesis, suggesting that Experts' extensive knapping experience allowed them to improve their hammerstone nut-cracking skills more rapidly than less experienced individuals. Similar findings have been reported in previous stone tool studies, where experienced knappers achieved higher success during nut-cracking and flake knapping tasks (Bril, Parry, and Dietrich, 2015). This pattern suggests that perhaps an evolved capacity for cumulative experience likely facilitated skill transfer in early hominin evolution, directly promoting behavioral flexibility in response to novel challenges and eventually contributing to the gradual later development of more sophisticated lithic industries. Furthermore, it could be argued that the capacity for cumulative experience in tool use may have preceded the ability for intentional tool production, as effectively creating a tool (e.g., a cutting flake) likely required prior knowledge of its function and necessary form, which could only be acquired through repeated use.

3.3 STUDY III: Combined EEG and sEMG Experimental Study on the Neuromechanical Signatures of Expertise in Early Stone Tool Use

Building on the sEMG-based analyses of muscle efficiency from Study II, the final paper incorporates EEG data to examine how experience influences neural activity during stone tool use, highlighting the cognitive mechanisms supporting skilled and efficient performance. The study focused on the preparatory (Aim) stage, motivated by prior research on skilled manual behaviors (e.g., pianists, guitarists), which demonstrated that experienced individuals show greater activation in prefrontal, sensorimotor, and parietal regions during action observation and preparation (Bangert and Altenmüller, 2003; Landau and D'Esposito, 2006; Hluštík et al., 2004;

Vogt et al., 2007). These findings suggest that motor training and experience shape task-related neural patterns; however, this relationship has not yet been explored in the context of early stone tool use within neuroarchaeology. Accordingly, we analyzed EEG and sEMG data recorded simultaneously (see subsection 3.1; Eteson et al., 2025) to assess brain-hand interactions during the preparatory stage of both Oldowan-style flake cutting and hammerstone nut-cracking, comparing participants across the three previously defined experience groups.

Building on our findings that experienced knappers show reduced muscular activation without compromising task success (Eteson et al., 2024b), and previous cognitive studies that practical tool-related expertise is linked to increased neural activity in key cognitive regions (Bangert and Altenmüller, 2003; Hluštík et al., 2004; Landau and D'Esposito, 2006), we briefly outline the hypothesis posed in this study. Our first hypothesis is based on the expectation that cumulative experience in early hominin tool-use tasks enhances both muscular efficiency and cognitive engagement. Specifically, we predict that Experts will display lower overall sEMG muscular activation, alongside distinct neural signatures in the premotor/motor, left-frontal, and left-parietal cortices, reflecting enhanced motor planning, executive control, and more efficient neuromuscular coordination (Adin et al., 2022; Berchicci et al., 2012; Goldenberg and Spatt, 2009; Jones and Graff-Radford, 2021; Putt, Wijeakumar, and Spencer, 2019; Stout, 2011; Stout et al., 2008, 2015). Moreover, given that Oldowan flake knapping has been shown to be more cognitively more demanding than hammerstone nut-cracking, due to its greater planning complexity (Bril, Parry, and Dietrich, 2015; Toth and Schick, 2018), reliance on various precision grips (Ehrsson et al., 2000; Iturrate et al., 2018; Marzke, 2013; Susman, 1991), and exclusive association with hominins (Bril et al., 2012; Harmand et al., 2015), we expect more pronounced frontoparietal activation in Experts during the Oldowan-style flake-cutting task. This neural engagement is anticipated to coincide with reduced muscular effort, in contrast to hammerstone nut-cracking, which should elicit greater muscular activation due to its heavier mass and reliance on power grips, recruiting all five digits (Bril et al., 2015; Domalain Bertin, and Daver, 2017; Eteson et al., 2024b; Marzke et al., 1998). Novices are also analyzed separately within this second hypothesis to serve as a basis for comparison. By analyzing Novice participants, we can determine whether the neuromechanical patterns observed here are specific to the Experts or rather reflect a broader trend of cognitive and muscular requirements that can be observed in all participants, regardless of their experience.

The results of this study support our first hypothesis, revealing that Experts displayed distinct neural patterns, as demonstrated by relatively increased neural activation in the regions of interest (ROIs), including the left frontal, premotor/motor, and left parietal regions. By contrast, in the hammerstone task, Experts demonstrated less neural engagement in the premotor/motor regions, exhibited by relatively increased beta power (assumed to be due to beta ERD; Crone et al., 1998; Pfurtscheller and Lopes da Silva, 1999; Zaepffel et al., 2013; Nakavashiki et al., 2014). However, Experts showed similar neural distinction among Novices and Intermediates in the left-frontal and left-parietal regions during the hammerstone task. At the same time, Experts also showed reduced muscular effort during both tasks, consistent with the findings of Study II.

The less experienced groups displayed more variable patterns, with Novice and Intermediate participants spreading widely across the PCA plot; some showed similarities to the Experts, while others did not. This was the case for both the flake and hammerstone tasks.

These findings broadly align with those of previous neurological research on modern manual tasks, reporting that increased engagement of the prefrontal and premotor circuits is expected with expertise during the planning and execution of manual tasks, particularly as these regions are important in high-level executive functions, i.e., motor planning, decision making, and problem solving (Adin et al., 2022; Berchicci et al., 2012; Goldenberg and Spatt, 2009; Jones and Graff-Radford, 2021; Putt, Wijeakumar, and Spencer, 2019; Stout, 2011; Stout et al., 2008, 2015). However, contrary to expectations, in our study, Experts did not show overall increased activation in the left parietal region in the EEG topographic maps. Though previous studies have linked this area to tool conceptualization and spatial processing, differences in task complexity, as well as recording methodology (e.g., EEG vs. fMRI) may explain these discrepancies, as EEG limitations in spatial resolution prevent the localization of specific lobules of the parietal cortex or deeper cortical structures of the brain (Boudewyn et al., 2018; Boyer et al., 2023; Gevins et al., 1994; Jiang, Bian, and Tian, 2019; Muthukumaraswamy, 2013). Additionally, unlike the complex behaviors examined in previous studies (e.g., playing an instrument or professional sports), the relatively simple stone tool tasks in our study did not require extensive specialized training and were largely based on broadly familiar actions. In this context, our results likely suggest that Novices, who exhibited higher overall beta power in the left parietal region, probably relied more heavily on visuospatial and sensory processing to perform the cutting task (Carius et al., 2023). In contrast, Experts likely drew on well-established motor patterns developed through extensive practical experience (Meister et al., 2005; Olsson and Lundström, 2013).

For addressing the second hypothesis of the study, Experts and Novices were analyzed separately. As predicted, during the flake Aim stage, Experts exhibited significantly higher beta power levels in the left frontal and premotor/motor regions, and reduced activation in the dominant hand, compared to the hammerstone task. A likely explanation for this increased frontal activity may be due to the flake cutting task requiring fine motor control (thumb-index precision grasping patterns), which has been broadly associated with activation of the frontoparietal regions (Ehrsson et al., 2000; Iturrate et al., 2018). These patterns tend to align with those reported in previous experimental studies on stone tool knapping, which require a higher degree of planning and manual dexterity than hammerstone nut-cracking (Bril, Parry, and Dietrich, 2015), and as such display increased activation in frontoparietal networks compared to simpler stone tool-use behaviors (Putt, Wijeakumar, and Spencer, 2019; Stout et al., 2008, 2015). In contrast, the hammerstone's heavier mass and size likely resulted in the task recruiting the dominant muscles relatively more than the flake task, as hypothesized. Interestingly, while dominant hand activation was expected to be higher during the hammerstone task, Experts instead showed relatively increased non-dominant hand muscle activation in the flake cutting task, reflecting the importance of stabilization forces during more complex precision-grasping tool use (rather than focusing solely on the dominant hand). Novices also demonstrate a similar but less distinct pattern than Experts. They display relatively increased activation of all dominant hand muscles in the hammerstone task, whilst in the non-dominant hand, the thenar eminence was shown to be relatively more recruited in the flake task. This increased activation of the non-dominant thumb is likely due to the need to stabilize the faux leather in preparation for the cutting task, as witnessed in the Expert participants. Overall, Experts display the expected neuromechanical patterns in both tool tasks, as proposed in our hypothesis. Additionally, whilst Novices do demonstrate similar muscular activation in both the dominant and non-dominant hand, they display relatively less distinct neural activation patterns. This result confirms that Experts demonstrate a specific pattern of neural activity, which is not observed in less experienced participants.

Contrary to this second hypothesis, however, the left-parietal region in Experts showed a different pattern, with the P3 (EEG channel located in the left-parietal region) channel showing relatively more activation (beta power) during flake Aim, while P7 (EEG channel located in the left-parietal region) displayed more beta power during hammerstone Aim, indicating subtle task-specific specialization within the parietal cortex. However, due to the limited spatial resolution of EEG, we cannot confidently localize these activations to specific parietal subregions, and therefore, their precise functional significance remains uncertain. Comparatively, the left parietal EEG channels in Novices showed relatively higher activation during hammerstone Aim, the opposite of the expected pattern, suggesting a heavier reliance on visuospatial processing during the nut-cracking task. This contrasts with Experts, who appeared to recruit parietal subregions more selectively based on each task. Moreover, Novices displayed relatively higher levels of activation in the motor cortex during flake Aim (beta desynchronization), and higher activation in the premotor region in hammerstone Aim. Finally, the left frontal region (in this case, the F3 channel) displayed higher beta power in the flake task, whilst F7 (EEG channel located in the left-frontal region) displayed slightly increased beta power in the hammerstone task. Despite the complicated patterns found in these analyses that cannot be definitively determined due to the relatively poor spatial resolution of EEG, these findings broadly emphasize the more distinctive pattern observed in Experts, potentially displaying task specialization and targeted neural organization (Milton et al., 2007), not witnessed in the less experienced participants. This study also highlights the importance of the integration of neural and biomechanical activation when analyzing early stone tool use, as opposed to analyzing EEG and sEMG separately, where these patterns potentially would have been missed.

Taken together, the two hypotheses proposed in this study were broadly supported, as Experts displayed clear task-specific cognitive and biomechanical patterns, particularly during the more complex flake cutting task. Increased activation in the left-frontal and premotor/motor regions suggests a greater demand for motor planning and goal-directed action during precision-based cutting. This is consistent with prior research comparing flake production to nut-cracking, which has been proposed as being cognitively less demanding (Bril, Parry, and Dietrich, 2015). These findings challenge the proposed “neural efficiency” hypothesis, which suggests that individuals with extensive experience in a related field require less neural activation or engagement when performing the same tasks as those without prior experience. Instead, it supports the view that skilled flake tool use involves increased cortical engagement in areas tied to executive function and motor preparation (Kami et al., 1995; Landau and D'Esposito, 2006; Nakata et al., 2010).

From an evolutionary perspective, the ROIs highlighted in the results of this experimental study, particularly the frontoparietal network (Bruner, Battaglia-Mayer, and Caminiti, 2023; Stout et al., 2008), correspond to brain regions that expanded significantly during hominin evolution. This enlargement may have provided hominins with an advantage in the increasingly sophisticated production and use of stone tool industries (Bruner, Battaglia-Mayer, and Caminiti, 2023; Hecht et al., 2015). While not necessarily implying a direct causal link between brain evolution and efficient tool use, these experimental results support the notion that such expansion would have been advantageous for meeting the cognitive and motor demands of increasingly complex manual behaviors. This could have occurred as a direct adaptation to tool-related tasks or as an exaptation, where brain regions originally evolved for other functions were later co-opted to support tool use (Bruner, Battaglia-Mayer, and Caminiti, 2023; Hecht et al., 2015). Furthermore, our Experts' reduced dominant-hand muscle activation, paired with increased non-dominant-hand engagement during flake cutting, further underscores the importance of improved bimanual coordination during skilled tool tasks (also see subsection 3.1 on Study I). This pattern may likely reflect a crucial adaptation for bimanual coordination in early hominins (Bril, Parry, and Dietrich, 2015; Marzke, 2013; Stout et al., 2008). All together, these findings indicate that early stone tool-related expertise seems to be reflected both in precise, fine motor bimanual control, as well as targeted recruitment of specific brain networks that facilitate the planning of flexible and goal-directed actions.

3.4 SYNTHESIS AND CONCLUDING REMARKS

This doctoral project aimed to address a central question in hominin evolution: whether and how cumulative tool-related experience influenced the efficiency of early stone tool use. Using a rigorous experimental approach, it examined two manual behaviors of major evolutionary significance: Oldowan-style flake cutting and hammerstone nut-cracking. These were chosen as the former represents the earliest tool-using behavior unique to hominins (Bandini and Tennie, 2023; Plummer, 2004; Roux and Bril, 2005; Wynn and McGrew, 1989) (directly linked to the emergence of a modern human-like forceful pad-to-side precision grip; e.g., Susman, 1991), whilst the latter is likely a precursor behavior, still observed in several extant non-human primates, and typically requires a spherical power grip stabilized by the palm and fifth digit (e.g., Bril, Parry, and Dietrich, 2015; Domalain, Bertin, and Daver, 2017). To investigate these behaviors, the project introduced and validated a novel interdisciplinary methodological framework that integrated biomechanical (sEMG) and neurological (EEG) electrophysiological techniques to assess their neuromechanical demands, situating the results within the broader context of the archaeological record and the origins of human-like tool use.

Considering the findings of all three studies together, the novelty of this approach led to original insights into the complex interplay observed between cognitive and biomechanical systems in the context of early stone tool use. Its results demonstrated that, in the flake cutting task, human participants with extensive practical experience in stone tool production (the knapping “Experts” of our studies) displayed more neuromechanical efficiency than their less experienced counterparts (Meister et al., 2005; Milton et al., 2007; Olsson and Lundström, 2013). Specifically, Experts exhibited significantly increased rates of success, lower muscular effort, and heightened neural engagement in the left-frontal and premotor/motor regions during the preparatory flake Aim stage. These patterns were markedly less pronounced in our Novice participants, who instead seemed to rely on greater muscle recruitment (effort) and increased parietal activation, likely indicative of a greater requirement for visuospatial processing and mechanical problem-solving when faced with unfamiliar tool use (Carius et al., 2023). Experts also demonstrated neural signatures associated with high-level executive functions, such as advanced motor planning, decision making, and problem solving (see Adin et al., 2022; Berchicci et al., 2012; Goldenberg and Spatt, 2009; Jones and Graff-Radford, 2021; Putt, Wijeakumar, and Spencer, 2019; Stout, 2011; Stout et al., 2008, 2015), coupled with reduced physical effort (i.e., lower overall muscle activation).

From an evolutionary perspective, these results highlight that the ability to accumulate practical skill through repeated experience would have likely provided a major adaptive advantage, enabling early hominins to use tools more efficiently while conserving energy. In addition, the growing demands of increasingly complex tool use likely benefited from the known expansion of the frontoparietal lobes observed in the hominin fossil record (Bruner, Battaglia-Mayer, and Caminiti, 2023; Hecht et al., 2015; Stout et al., 2015), due to their known importance in executive functions such as action planning, decision-making, visuospatial processing, sensorimotor integration, and mechanical knowledge (Adin et al., 2022; Berchicci et al., 2012; Carius et al., 2023; Goldenberg and Spatt, 2009; Jones and Graff-Radford, 2021; Meister et al., 2005; Olsson and Lundström, 2013; Putt et al., 2019; Stout, 2011; Stout et al., 2008, 2015). Furthermore, the observed neural activation patterns provide direct experimental support that human-like precision grasping, particularly the coordinated interaction of the thumb and index finger, is tightly linked to enhanced cognitive complexity (Ehrsson et al., 2000; Iturrate et al., 2018).

Importantly, these findings on flake use largely contrast with those from the more generalized hammerstone nut-cracking task, where expertise yielded only modest gains in muscle economy and produced less pronounced neural differentiation between experience groups. This divergence may stem from differences in cognitive demands and the degree of fine motor precision required by each task (Bril, Parry, and Dietrich, 2015; Ehrsson et al., 2000; Iturrate et al., 2018). Nut-cracking is not an exclusively hominin behavior, as it is also observed in extant non-human primates (Arroyo et al., 2016; Bril et al., 2012; Gumert and Malaivijitnond, 2012; Proffitt et al., 2016, 2023; Wynn and McGrew, 1989). Accordingly, when compared to flake cutting, hammerstone nut-cracking shows a comparatively reduced reliance on cumulative experience (Eteson et al., 2024b), coupled with lower levels of activation in brain regions that underwent substantial evolutionary expansion in hominins (Holloway, 2015). Unlike nut-cracking, intentional flake cutting is considered to be an exclusively hominin behavior (Bril et al., 2012; Harmand et al., 2015; Proffitt et al., 2016, 2023) and depends on human-like precision grasping and fine manipulation (Susman, 1991). In this context, it is intriguing that efficient flake cutting appears to be more directly influenced by the observed interplay of manual dexterity, ergonomic efficiency (Eteson et al., 2024b), cumulative skill acquisition (Eteson et al., 2024b), and neural specialization (Appendix C; Bangert and Altenmüller, 2003; Hluštík et al., 2004; Landau and D'Esposito, 2006; Vogt et al., 2007).

Nevertheless, the distinct neural signatures observed in Experts across both tasks, along with their demonstrated capacity to self-improve in novel hammerstone pounding tasks via skill transfer (subsection 3.2; Eteson et al., 2024b), indicate that their general proficiency is not simply the result of rote repetition. Rather, it reflects a flexible, experience-based cognitive adaptability that supports the efficient planning and execution of unfamiliar yet conceptually related tool-use behaviors. In this context, it could be argued that an evolved hominin ability for skill transfer associated with the expansion of the frontoparietal network (Bruner, Battaglia-Mayer, and Caminiti, 2023; Holloway, 2015; Stout et al., 2008) may have facilitated the development of increasingly variable and sophisticated tool production and use (Bruner, Battaglia-Mayer, and Caminiti, 2023; Heyes, 2018; Putt, Wijeakumar, and Spencer, 2019; Seifert et al., 2013; Stout, 2011; Stout et al., 2015).

More broadly, from a methodological standpoint, this doctoral thesis overall underscores the value of developing interdisciplinary, integrative approaches in experimental archaeology, exemplified by the combined EEG-sEMG framework established in this project. While both modalities have been widely used in fields such as rehabilitation and sports science (Bulea et al., 2013; Dal Maso et al., 2018; Enders and Nigg, 2016; Qidwai, Ajimsha, and Shakir, 2019; Sarhan, Al-Faiz, and Takhakh, 2023), their integration remains underutilized in the study of early hominin tool-using behavior. By segmenting tool tasks into discrete stages and measuring concurrent neural and muscular dynamics, we offer a replicable and standardized framework that can advance the field's understanding of hominin technological performance.

As with all experimental approaches, the collection of studies presented here is also subject to several limitations, which will be briefly mentioned below. First, although we present a relatively large sample size for an experimental analysis of this kind, it must be noted that the sample sizes, particularly of participants with extensive knapping expertise and theoretical knowledge of stone tools, were relatively small (*n* = 5 and *n* = 4, respectively). This inevitably constrains statistical power and consequently limits our interpretations. However, it should still be observed that recruiting participants locally with such an extensive and specific skillset is rare. Another limitation is in relation to the methodologies used. sEMG, whilst it reliably captures muscular activation, it can only do so with surface muscles and therefore limits the full repertoire of muscles that can be monitored during experimentation. Additionally, both sEMG and EEG have high noise-to-signal ratios, meaning that they are susceptible to external (electrical noise or pressure on electrode sites) and internal artifacts (muscular or cardiac activity). Whilst this can be combated through proper setup, repetition of tasks (≥50 trials; Amin et al., 2023; Boudewyn et al., 2018), and thorough preprocessing of the data, the complete removal of all artifacts is currently not possible, without compromising on losing real EEG/sEMG data (Radüntz et al., 2015, 2017; Villasana, 2022). EEG, while providing excellent temporal resolution, has limited spatial resolution to accurately pinpoint activation within specific neural regions or deep cortical structures (Boudewyn et al., 2018; Boyer et al., 2023; Gevins et al., 1994; Jiang, Bian, and Tian, 2019; Muthukumaraswamy, 2013). Furthermore, as with most experimental settings, the environment, methodologies used, and reliance on standardized materials such as faux leather and roasted macadamia nuts, whilst they ensure experimental control, cannot fully replicate the natural environments and variable biomechanical properties of natural raw materials likely used by early hominins (Eteson et al., 2024b). Additionally, it should be highlighted that our study uses modern human participants as a proxy for the early hominins that would have used these tools. Whilst fossil hominins undoubtedly share many fundamental similarities in their anatomy with modern humans, there are important distinctions in their ergonomic and morphological attributes (i.e., Karakostis et al., 2021; Key et al., 2020; Kivell, 2015; Kunze et al., 2022; Marzke, 2013; Ricklan, 1987). However, humans remain the best possible alternative for these experimental tasks.

Nevertheless, future research could address some of the aforementioned limitations. Analysis of sEMG and EEG with complementary neuroimaging techniques such as fNIRS or fMRI could provide improved spatial resolution of neural activity during tool use, whilst maintaining the temporal resolution provided by EEG. This combined approach would enable more precise mapping of the interplay between muscular and neural processes in real time. Expanding the experimental framework to include additional lithic industries and tools of major evolutionary importance, such as Acheulean handaxes or Mousterian scrapers, or shifting the focus to tool production techniques, could further illuminate the combined biomechanical and cognitive demands that shaped hominin behavioral evolution. In such studies, expanding on our findings that reaffirmed the importance of the stabilizing hand in early hominin stone tool use (Kivell, 2015; Williams, Gordon, and Richmond, 2012; Williams-Hatala et al., 2018), future research could also explore the differences between the striking and stabilizing hand during different variations of bimanual knapping, especially considering that even the earlier Lomekwian flake production is assumed to have involved bimanual wielding (Harmand et al., 2015), and that extant non-human primates use bimanual coordination when engaging in hammerstone pounding activities (Falótico and Ottoni, 2016; Fragaszy et al., 2020). Beyond lithics, comparative experiments focusing on gestural and/or vocal communication tasks could also shed light on possible neuromechanical correlations between hominin tool use and language evolution, contributing to the ongoing debate on their potential co-evolution (Kulik, Reyes, and Sherwood, 2022; Stout and Chaminade, 2012; Stout et al., 2008; Thibault et al., 2021). Ultimately, the EEG-sEMG methodology developed and presented in this doctoral project provides a novel and reliable toolkit for the growing field of experimental archaeology. By integrating cognitive and biomechanical perspectives, this approach provides a promising foundation for building a more comprehensive framework to investigate the evolutionary foundations and implications of hominin behaviors, thereby enriching broader hypotheses and interpretations on human bio-cultural evolution.

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5 APPENDIX

APPENDIX A

The mind & muscles: Introducing a validated EEG/EMG protocol for recording cognitive-muscular interactions in experimental archaeology

Combined use of electroencephalography and electromyography in experimental stone tool task

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LAB PROTOCOL

The mind & muscles: Introducing a validated EEG/EMG protocol for recording cognitive-muscular interactions in experimental archaeology

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Abstract

Despite extensive research into the biomechanical and cognitive dimensions of early hominin material culture, no study has explored these aspects together in the context of stone tool production and use. In contrast to fields like rehabilitation and sports science, where electroencephalography (EEG) and surface electromyography (sEMG) are often integrated, experimental archaeology lacks such a combined approach. This paper introduces and validates a new protocol that integrates EEG and sEMG to measure neuromechanical activity during a classic stone tool task: cutting leather with a flake. Our experimental design divides the task into three phases: Hold, Aim, and Execute. Consistent with our expectations, results show that all eight muscles are most active during task execution, with the non-dominant hand playing a key role in stabilization during both the Aim and Execute phases. In the preparatory Aim stage, we observed increased beta power in the left frontal region (linked to planning, problem-solving, and working memory) as well as heightened motor activity associated with using the non-dominant hand, which contributes to the stabilization of the target material during this stage. During the Execute phase, beta power in these cortical areas decreased, with peak muscle activation occurring alongside suspected beta desynchronization in the motor region, reflecting intensified movement activity. Overall, these findings closely align with our expectations, validating our combined EEG-sEMG protocol and highlighting the importance of segmenting tool-using tasks into distinct phases, which allows for the identification of dynamic brain-hand interactions throughout the process. The proposed step-by-step protocol offers a new methodological basis for future research into the complexities of hominin behaviors and tool use.

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Introduction

Elucidating the physiological and cognitive implications of hominin tool-using behaviors represents one of the main goals of evolutionary sciences. Many studies have previously reported on the various requirements to perform stone tool tasks (i.e., knapping [1–7], cutting [8–11], and pounding activities [1,11–14]). However, there is yet to be a study that combines the use of multiple methodologies within the same analytical framework, to simultaneously assess both the biomechanical and cognitive requirements of stone tool production and use. More broadly, there appears to be a significant scarcity of detailed step-by-step experimental protocols in the archaeological sciences. This gap often results in a lack of methodological consistency across studies that use similar recording methods, making it difficult for new researchers to learn, replicate, and advance work in this important field.

The functional demands necessary for early hominin stone tool production and use have been a major focus of archaeological sciences for over 20 years [6,8,10,15]. In fact, experimental archaeology as a field has grown in response to an increasing range of archeological material being discovered, including proposed stone tools dating from ~3 MYA [16,17]. Tool use is not only undoubtedly essential to human life, but also a crucial part of many other primate societies [18–20]. This behavior, previously thought to be unique to humans [21], has continually intrigued anthropologists, leading to many experimental studies exploring the foundations of early stone tool production and use, from focus on the biomechanical requirements and grasping patterns required to wield such tools [6,8,10,15,22], to the cognitive activation necessary to perform these tasks [3–5,7,23]. However, despite the various modes of tool use witnessed within the primate order, there is a specific early stone tool task that seems exclusive among hominins (at least in the wild): stone flake-cutting. The earliest use of cutting is reported to date back to ~3 MYA, reflected in the presence of archaeological material such as cut marks on bone [17,24,25] and the emergence of intentionally produced Oldowan flakes [17]. The Oldowan succeeds the proposed Lomekwian industry (dated ~3.3 MYA [16]) and is often referred to as the oldest persistent stone tool industry, both temporally and spatially [17]. Given the critical importance of this tool task for exploring the origins of hominin behavior and considering the need to develop protocols that address both the cognitive and biomechanical demands of stone tool use, this paper aims to introduce a new combined methodology using surface electromyography (sEMG) and electroencephalography (EEG) at the same time, to simultaneously analyze both muscular and cognitive activity during the widely studied Oldowan flake-cutting task.

Previous sEMG studies on the biomechanical requirements of early stone tool use have provided key insights into the grasping patterns and necessary muscular activation [6,8–10,15] to perform such tasks. Additionally, multiple studies have found certain grips are repeatedly recruited during stone tool tasks [9,26–30], which have laid the groundwork for understanding some of the key muscles, grips, and digits most often recruited during lithic production and use. Additionally, over the past 20 years, several studies have worked on another physiological aspect of stone tool experience, by analyzing the cognitive activity in modern humans during and after performing various tasks, such as knapping stone tools [3–5,23]. These various works have yielded particularly insightful results. By analyzing different tool technologies these studies have explored the underlying cognitive processes and activation of brain regions during these tasks [3–5,7,23]. Additionally, some studies have attested that the areas of the brain activated after performing such tasks are linked to regions associated with communication and language processing [31]. However, despite these promising results, there is yet to be a study that analyzes both aspects, muscular and cognitive activation, within the evolutionary sciences. This leaves a major gap within this field, despite other fields of study, such as biomedical rehabilitation [32–34] and the sports sciences [35–38], regularly using this combined methodology within their research.

Previous neuroimaging techniques used in experimental archaeology, including fMRI, PET, and fNIRS [3–5,23], have been instrumental in advancing our understanding of the cognitive demands of stone tool production. These methods offer high spatial resolution, allowing researchers to pinpoint specific brain regions activated during tool-related tasks, thus establishing a foundation of brain areas relevant to these activities [39,40]. However, some of these techniques come with practical challenges, i.e. fMRI and PET have a low temporal resolution, require expensive, non-portable equipment, and often limit participant movement, making it difficult to observe the distinct, structured phases of human-like tool use in real-time [5,23]. Furthermore, the combined use of these neuroimaging methodologies with muscle-recording approaches (e.g., sEMG) within a single experimental design remains rare, resulting in gaps in capturing the dynamic interplay between cognitive and motor demands during actual tool use [3–5,23]. By analyzing the neuro-mechanical processes involved in tool use in real-time, we can gain deeper insights into the requirements for each stage within a tool-using task. For example, understanding the role of brain regions associated with the use of specific muscles for specific stone tool tasks can enhance our comprehension of the energetic demands (ergonomics) associated with each tool-producing or using activity [6,8,11]. Moreover, previous analyses of modern tool use (e.g., [41–44]) have provided valuable insights into the dynamic cognitive patterns required during specific phases or segmentation (such as a preparatory or planning stage and a preview stage).

To bridge the current gap between cognitive and biomechanical studies on stone tool use, we developed a new protocol for the combined use of EEG and sEMG. This protocol was already successfully used in two recent studies that focused on the results of each technique separately [11,45]. These recording methods were chosen for their high temporal resolution (millisecond-level), which allows for accurate, simultaneous recordings of both EEG and sEMG signals [32–38]. Their portability also enables recording during active movement. Drawing on successful applications in other fields [32–38], we developed a protocol that ensures appropriate preprocessing (including cleaning), and analysis of the data resulting from the two combined methods utilized here. In this study, we validate the use of this integrative protocol by focusing on the widely-studied task of Oldowan flake-cutting, which is divided here into three distinct phases (also see [11,45]); the first stage, Hold, involves picking up the tool with the dominant hand; the second stage, Aim, entails positioning the tool at the target object (faux leather) in preparation, whilst stabilizing the fabric using the non-dominant hand; and the final stage, Execute, focuses on cutting through the faux leather using the flake (which is still stabilized by the non-dominant hand). These separate phases allow us to explore the intricate demands of each part of the task.

Focusing on this data, we predict that muscular activation will steadily increase throughout the task in all muscles recorded, with a peak activation occurring in the Execute stage. This is due to an expected increased ergonomic demand during cutting, due to sustained pressure, necessary manipulation of the tool cutting edge, and resistance applied against the cutting object (i.e., hide) [9,10,26,46,47], which requires greater force and dexterity than the previous phases. We also expect this pattern to be reflected in the motor cortex, with increased activation occurring during the Execute stage. Cognitive tool use studies typically demonstrate engagement in specialized regions within the frontal, temporal, and parietal cortices during preparation and execution, due to their role in problem-solving, action planning, understanding of tool functions, sequenced motor skills, and planning of goal-directed movements [48–55]. Previous cognitive studies on stone tool production have demonstrated increased activity in the dorsolateral prefrontal cortex (PFC), and higher-level executive functions are associated with the ventral prefrontal cortex [3,23,31,56,57], whilst the left inferior parietal lobe (IPL) is crucially involved in understanding tool function, mechanical knowledge, and problem-solving [52,53,55]. Additionally, the temporal cortex is known to be critical for tool-related tasks, as it integrates sensory and semantic information [58,59]. While all these regions play a vital role in the planning and execution of tool use tasks, this protocol validation paper will focus its analyses on the frontal region, to demonstrate the utility of the combined EEG/EMG methodology outlined below. This was decided based on the inclusion of EMG, which enables direct links with the motor cortex, as well as the consideration of several other EEG studies reporting increased prefrontal activation during the preparational phases for voluntary motor tasks (including generalized tool use [48–51]). Additionally, the widely discussed role of increased PFC activity as a crucial aspect of modern human brain reorganization further justifies an explicit focus on this brain region [23,60]. More particularly, in this study, we primarily expect increased activation in the frontal (FC) and prefrontal (PFC) cortex during the Aim stage, as we expect participants at this point to be planning the necessary sequence of movements (i.e., motor planning), deciding in the order in which to make the necessary cuts within the time limit, and eventually initiating fine-motor control actions.

Materials and methods

The protocol described in this peer-reviewed article is published on protocols.io (dx.doi.org/10.17504/protocols.io.36wgq-nxbygk5/v1 [61]) and is included for printing purposes as S1 File. To validate this protocol, we conducted a re-analysis of data from two recent studies of ours that employed this protocol and yielded meaningful results on sEMG [11] and EEG [45] separately. However, the present lab protocol paper is the first to present a combined EEG and sEMG study on the same task concurrently, demonstrating the unique advantages of this integrative approach.

In summary, as described in two previous studies [11,45], we recruited twenty-five volunteer participants across two recruitment periods (May 1–31, 2022, and January 10–April 30, 2023), in accordance with the guidelines of Tübingen University's Ethics Committee for Psychological Research (in line with the Declaration of Helsinki, 1964, revised in 2013), which have approved the experiments presented in this study. All individuals were adults and provided informed written consent. Using the Edinburgh Handedness Inventory [62], two participants were identified as being left-handed, and these participants were removed from the study to create a homogeneous sample, due to the known relationship between handedness and brain lateralization [63,64]. Therefore, the final number of participants was 23 (14 biological females and 9 biological males), between the ages of 22–55. All participants declared no physical injury that would prevent natural tool use and no history of neurological disorders. Stone tools were knapped ($n = 26$ Oldowan-style flakes) by an expert tool knapper (ETM; see Acknowledgments) in accordance with documented proportions [65–67]. A synthetic faux leather material was used as the object to cut, in place of hide or leather [15,68], to avoid potential variance in consistency (i.e., thickness, torque, strength). The fabric was also marked by three stenciled 3 cm straight lines forming a Z pattern to ensure consistency across all participants. During the processing stages of the recorded EEG and sEMG data, they were subjected to scrupulous cleaning and processing (see the detailed protocol and our previous research [11,45] for more), to ensure the data displayed true muscular and brain signals while reducing noise as much as possible [69–72]. However, in tool-using experiments involving EEG, the presence of artifacts in some channels is often inevitable [71,73–75] (for more information, see the Discussion). These may consist of internal artifacts; ocular (blinks and side eye movements), motion/muscular (excessive movement of the body or tension in the neck), and external noise (electrical equipment, electrode pops, cable movement, or bad channel connection) [71]. There is yet to be a processing technique that guarantees the complete removal of high frequency artifacts, particularly in tasks requiring movement [72], that ensures the real EEG signal is not lost [76,77].

EEG and SEMG channel selection

The EEG aspect of the experiment relied on a 32-channel EEG cap, following the 10–20 system configuration, using Brain Vision Recorder software (version 1.24.0101, Brain Products GbmH, Gilching, Germany) [78]. The areas of particular interest in this paper are, the motor area, due to the nature of the task, requiring precisely executed voluntary movement; and the frontal region due to its previously researched importance in motor tasks and association in regards to planning, problem-solving, and working memory [3,48–51,79]. Muscle selection was guided by previous stone tool experiments and studies on hominin skeletal remains, highlighting the established importance of specific muscles for achieving key grasping patterns during stone tool use (in this case, cutting) [8,15,80–82]. These muscles are also crucial for the stabilization of the target object provided by the non-dominant hand and for the force exerted in manual tool engagement [6,8,15,28,30,80,83,84]. Therefore, the following muscles and muscle groups were selected for sEMG recording from the dominant hand; *flexor carpi radialis* (FCR), *flexor carpi ulnaris* (FCU), *flexor pollicis longus* (FPL), the thenar eminence (TE) (consisting of *abductor pollicis brevis*, *flexor pollicis brevis*, and *opponens pollicis*), first dorsal *interosseus* (DI1), and the hypothenar eminence (HTE) (consisting of *abductor digiti minimi*, *flexor digiti minimi*, and *opponens digit minimi*), and two muscles/muscle groups from the non-dominant hand; first dorsal *interosseus* (ndDI1) and the thenar eminence (ndTE). All anatomical placements were based on descriptions provided in standard anatomical textbooks [83]. Some muscles were grouped because the overlaying skin (onto which the electrode attached) corresponded to more than one muscle underneath (i.e., the thenar and the hypothenar eminence muscles; (for more, see [11]). For a detailed breakdown of the forearm and hand muscles selected for sEMG recording and analysis, and the channels and configuration used in EEG recordings, see dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61] and [45]. Once cleaned and exported, all sEMG muscular signals were transformed into a percentage maximum voluntary contraction (%MVC) [8,11,85,86]. These allowed participants to be directly comparable with one another despite interindividual differences in body size and muscle strength [8,11,85,86]. For a detailed breakdown of the MVC-obtaining process, see dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61].

Experimental design

The experiment took place in a shielded cabin at the Max Planck Institute for Intelligent Systems in Tübingen (see Acknowledgements). Participants first watched an instructional video detailing the experimental design, EEG and sEMG application, and experiment contraindications (see dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61]). Each participant completed an Oldowan-style flake-cutting task, consisting of three phases: picking up the tool (Hold), aiming the tool at the target while stabilizing the faux leather (Aim), and cutting through and stabilizing the faux leather (Execute). Participants were informed that their trials would be assessed for success and were instructed that a successful trial entailed cutting through the fibers of the faux leather entirely (following the indicated Z-pattern), within the provided period of 5 seconds. Participants were not instructed to cut through the marked lines on the fabric in a specific order or to hold the tool in any specific grasp. Therefore, they needed to employ a certain degree of planning and working memory prior to executing the cutting sequence, at the Aim stage. A looped "beep" stimulus is played every 5 seconds to signal and mark the start of each stage (Hold, Aim, Execute). Based on recommendations for EEG signal-to-noise optimization, each participant completed a minimum of 50 trials per task to ensure robust data quality (e.g., see [87–90]). In addition to the stone tool task, a control task was performed. The latter involved a simple motor action (opening and closing the hand) without the use of a tool, which was expected to primarily involve distinctive activation in the motor region. Comparing tool-using tasks and the control condition is crucial because it allows us to distinguish between generic hand use and stone tool usage per se [90]. The European standards for sEMG analyses (SENIAM project) were followed [91]. For a more detailed breakdown of the recording and processing of EEG and sEMG data, see dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61], Eteson and colleagues [11] and Affinito and colleagues [45].

Data visualization and analyses

To analyze the EEG and sEMG data, several visualization techniques and statistical tests were performed. Data visualization was performed in BrainVision Analyzer (version 2.2.1, Brain Products GbmH, Gilching, Germany) [72] and the software package PAST version 4.03. [92]. All statistical analyses were performed in the open-access software PAST version 4.03. [92]. Plots and band maps were produced in the same software [72,92] and modified in Inkscape vector graphics editor version 1.3. [93].

To investigate sEMG muscle synergies, a principal component analysis (PCA) was performed, using all eight muscle recordings (%MVCs) as variables and including all three phases of the tool-using process (Hold, Aim, and Execute) [11]. This approach was chosen to efficiently analyze the interaction among different muscles within the same analytical framework and therefore address our expectation that muscle co-recruitment will gradually increase between the phases of Hold, Aim, and Execute. An additional PCA was performed excluding the two non-dominant hand muscles/muscle groups (ndDI1 and ndTE), to ensure results were not skewed, as only the Aim and Execute phases recruited the non-dominant muscles during the task (for stabilization of the faux leather). The PCAs were performed based on a correlation matrix (Table 1 and S2 Table). The PCAs did not assume groups *a priori*, and the three phases were simply color-labeled to differentiate between them. Statistical comparisons were then performed on relevant principal component (PC) scores, with the broken-stick model used to determine the number of PCs to extract [94]. In particular, prior to further statistical analysis, a Shapiro-Wilk normality test was run on the PC scores of each axis, to ensure that the extracted values followed an approximately normal distribution. Additionally, outliers were detected using the interquartile range approach [95]. Subsequently, repeated-measures ANOVAs were performed on the extracted PC scores of the task phases (Hold, Aim, and Execute), to assess if the muscular activation significantly varies across phases [8,11,95,96], effectively addressing our predictions outlined in the Introduction. Furthermore, Tukey's post hoc pairwise tests were run to determine which phases exactly differ between them. In addition, to visualize the differences in muscular activation across the three phases within each participant, stem graphs were generated.

In this lab protocol validation study, to visualize the EEG data recorded in the same individuals in tandem with sEMG, standard analytical processes were followed. A Fast Fourier Transformation (FFT) was applied with a 10% Hanning window, to compute the power spectrum of the segmented EEG data in the Brain Vision Analyzer (version 2.2.1) software [72]. All trials were then averaged to create a mean power spectrum for each participant. For a detailed breakdown of all pre-processing steps, see dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61] and Affinito and colleagues [45]. Grand average FFT band maps were exported from Brain Vision Analyzer (version 2.2.1) [72] in the relevant frequency bands. This study focuses on the beta (12.5–30 Hz) [97] frequency band, due to its known association with increased alertness during task performance [36,98–102]. All band maps were scaled between $0.1\ \mu\text{V}^2$ and $0.6\ \mu\text{V}^2$. These band maps visually depict the squared amplitude of EEG in the beta frequency during each stage of the task as well as the control task. They are used to compare levels of beta power in the frontal and central regions of the brain, which have been associated with fine motor control, planning, decision-making, and working memory [3,48–51,79]. Finally, band maps were then imported

Table 1. List of eigenvalues, percentages of variance, and factor loadings for the first two principal components of the PCA.

				Factor loadings							
Task	**Principal Component**	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**
Flake-Cutting	PC 1	5.14	64.29	0.39	0.33	0.37	0.39	0.38	0.32	0.32	0.32
	PC 2	0.75	9.39	−0.09	0.42	−0.23	−0.26	−0.45	0.56	0.40	−0.16

Muscle abbreviations are as follows: FCR, *flexor carpi radialis*; FCU, *flexor carpi ulnari*s; FPL, *flexor pollicis longus*; TE, thenar eminence (consisting of *abductor pollicis brevis*, *flexor pollicis brevis*, and *opponens pollicis*); DI1, first dorsal *interosseus*; HTE, hypothenar eminence (consisting of *abductor digiti minimi*, *flexor digiti minimi*, and *opponens digit minimi*)*; ndDI1,* non-dominant first dorsal *interosseus*; ndTE, non-dominant thenar eminence.

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into Inkscape [93], alongside the sEMG PCA plot, to facilitate the visualization of the two integrated methodologies jointly. At the same time, individual phases were initially compared against the control task, allowing us to determine common brain region activation during both the stone flake-cutting task and the control task.

Expected results

All plots, graphs, and tables mentioned in Materials and Methods that do not appear in the results section are available in the linked protocol (see dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61]) or in the supporting information. For all statistical tests, an alpha level of 0.05 was used. According to the Shapiro-Wilk tests, all %MVC values and PC scores showed an approximately normal distribution ($p > 0.05$). Moreover, no extreme outliers were detected. Therefore, parametric tests were conducted when analyzing the sEMG data.

Predictions of muscle use (sEMG)

To observe variation in relative muscle recruitment across the three phases of the cutting task, a PCA was performed on sEMG data. PC 1 (64.29% of variance) showed most of the variance explained, with all variables (muscles) loading positively, indicating that variation on PC1 reflects overall muscle recruitment (across variables; also see the Discussion subsection below for further interpretations of the observed patterns). Following the indication of the broken-stick technique, only the first principal component (PC 1) was extracted. The PCA plot clearly distinguishes between the phases, with flake Execute showing increased activation in all muscles (both dominant and non-dominant hand) in all participants, compared to Hold and Aim (see Table 1, Figs 1 and 2), and the Hold stage demonstrating the lowest overall muscular activation, as hypothesized. Descriptive statistics (Table 2) further supported the results shown in the %MVC sEMG PCA plot (Fig 1). The relevant PC1 scores were then analyzed using repeated measures ANOVA, which displayed significant differences across phases (df = 2 $F = 196.2$, $p < 0.001$). Furthermore, a Tukey's Pairwise test indicated that both Hold ($p < 0.001$) and Aim ($p < 0.001$) are significantly different from Execute, however, Hold and Aim are not significantly different from each other ($p = 0.24$). A stem graph (Fig 2) displays the variation in muscular activation across PC 1 scores of each stage. This stem graph further confirms our prediction that the Execute stage involves significantly higher muscular activation in all eight muscles, compared to both the Hold and Aim phases. Muscular activation is also marginally higher in all participants during the Aim stage, when compared to Hold, as predicted. Results remained significant (d.f. = 2, $F = 80.52$, $p < 0.001$) when the non-dominant hand muscles were removed from the analysis (see S3 Fig. for PCA plot). Tukey's pairwise tests again confirmed that significance was maintained between the Execute phase and both Hold ($p < 0.001$) and Aim ($p < 0.001$), even when the non-dominant hand variables were excluded (see S2 Table for PCA statistics).

Predictions of brain activation (EEG)

Initially, all phases' band maps were compared against the control task (Fig 3). In all cases, beta power displays increased levels across the frontal brain region, when compared to the control task, as expected. Nevertheless, increased power in the frontal region displays minimal differences between the control task and the Execute stage. One reasonable explanation for this may be that the necessary planning process occurs prior to this final stage of the task, during the preparatory phases Hold and Aim (see Discussion for more in-depth detail).

A total of six frequency band maps (two for each stage, focusing on the areas of interest; see Materials and Methods) were produced alongside the muscle recruitment EMG PCA plot (Fig 1). These band maps were comparatively examined to evaluate the expectations of this analysis regarding neural activation patterns in the frontal lobe (for further statistical analyses and results, see Affinito et al. [45]). Based on these (Fig 3), both Hold and Aim can be seen recruiting higher levels of beta power in the left frontal area when compared to the Execute stage. The strongest beta power is observed in the frontal lobe and occurs during the Aim stage, which shows a sharp increase in power (particularly in the left lateral

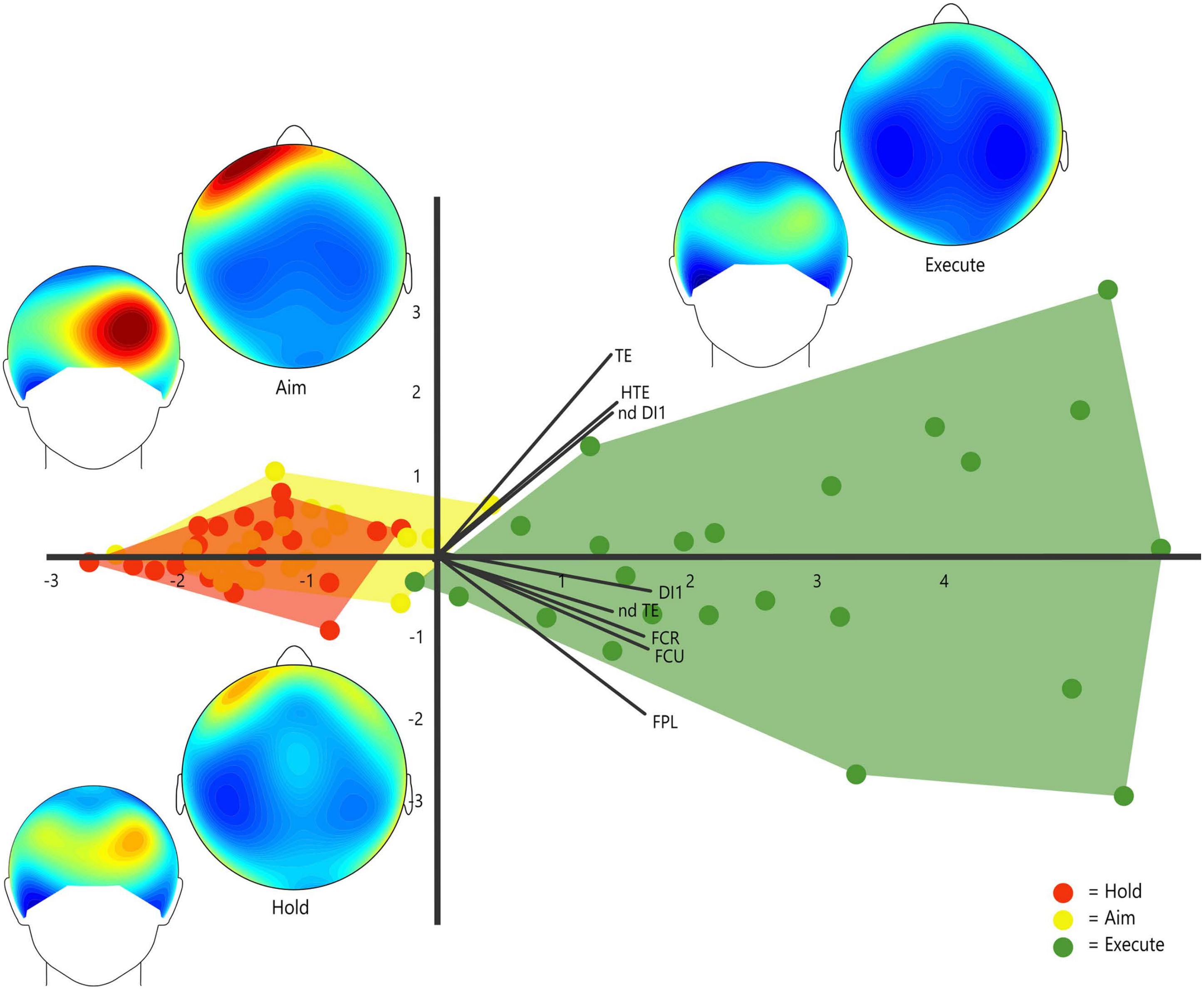

Fig 1. %MVC sEMG PCA plot (PC 1 = 64.29% of variance; PC 2 = 9.39% of variance). PCA plot summarizing overall muscular recruitment, with accompanying EEG bands maps (beta) displaying beta power levels throughout the cutting task (i.e., during Hold, Aim, and Execute). Phases are color-labeled (Red = Hold; Yellow = Aim; Green = Execute). PC 1 (64.29% of variance) reveals a clear contrast between Execute and the other phases of the task (Hold and Aim), with the former displaying increased activation across muscles (factor loadings are listed in Table 1).

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frontal region). This finding clearly aligns with the study's expectations (see Introduction) as the left PFC has been associated with increased focus on the processing of stimuli and fine-motor planning [3,48–51,79] during precise control of tools, including the processes of adjusting grip strength, positioning the hand/tool, and deciding the angle of the first cut. The Hold stage also seems to recruit increased levels of beta power in the frontal region, compared to the control task and the Execute stage.

In addition to the above patterns of higher beta power in the frontal region during Aim, which has been associated with an increased state of alertness [103–105], a phenomenon known as event-related desynchronization (ERD) is also known

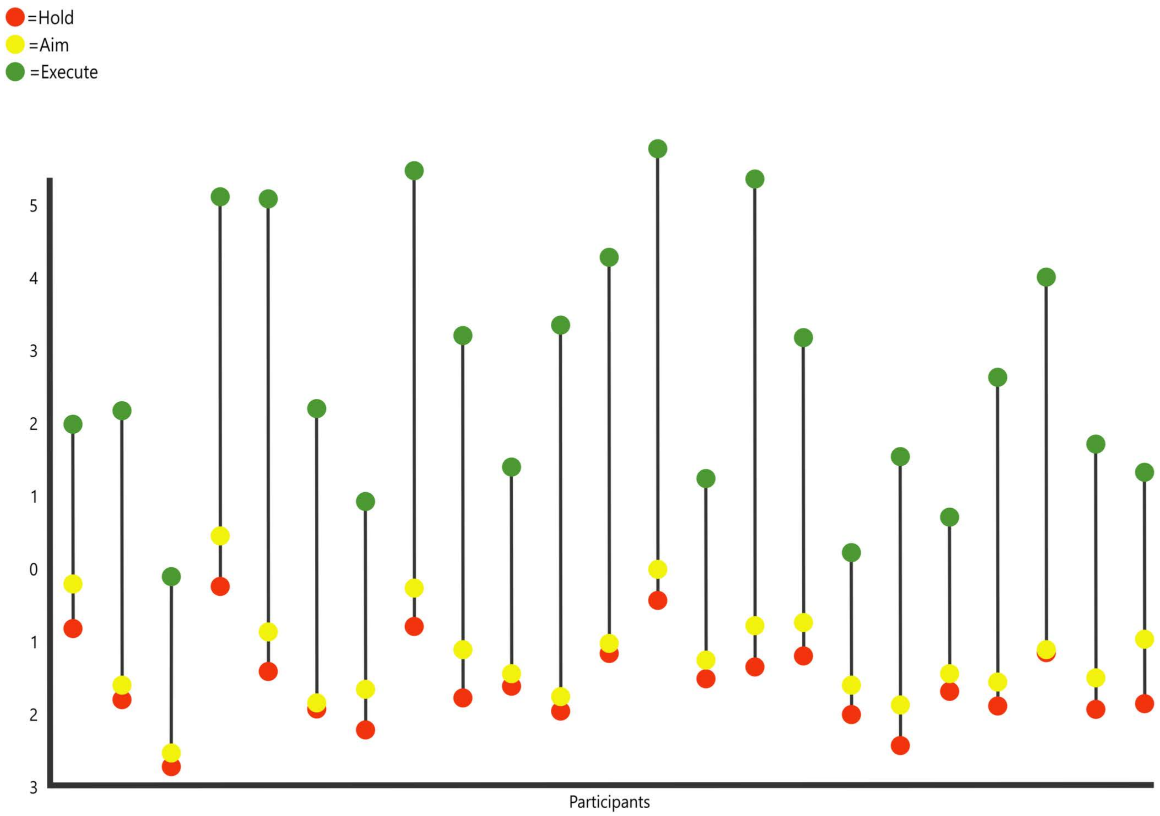

Fig 2. Stem plot of PC 1 scores (vertical axis), representing all three phases within participants Hold (red); Aim (yellow); Execute (green). Each stem represents a participant. All participants' PC1 scores for the Execute stage were larger than their Hold and Aim PC1 scores.

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Table 2. Descriptive statistics of the mean %MVC values for each stage.

Task	Stage	DI1	HTE	FCR	FCU	FPL	TE	ndDI1	ndTE
Flake	**Hold**	1.61	2.97	3.19	1.62	2.43	4.19	0.54	0.96
	Aim	1.95	2.72	2.82	1.81	2.39	3.38	2.87	8.16
	Execute	11.80	6.66	7.11	7.50	9.86	13.52	6.15	17.45

For each muscle, the highest mean value is highlighted in green, and the second highest value is highlighted in amber. Overall, a comparison between phases within the tool-using task shows that the Execute stage consistently recruits more muscular activity across all eight muscles than either Hold or Aim.

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in event-related potential (ERP) studies to occur during voluntary movement [38,105–108] which, despite showing a visible decrease in beta power in sensorimotor brain areas, is linked to a state of motor activation [105,107]. This phenomenon is typically explicit to the sensorimotor areas, known to display a pronounced decrease in the beta frequency band [38]. As this study's cutting task involves voluntary active movements, particularly including shifts from an idle state to an active processing state that involves decision-making, planning, and fine motor control, the ERD phenomenon is a likely explanation for some of our results, particularly in the Execute stage [38,105–109]. We argue that this is to be expected when analyzing such a continuous series of repetitive hand motions (i.e., the consequent cutting motions of the Execute stage and the repetitive finger movements of the control task). At the same time, as previously suggested in Affinito et al.

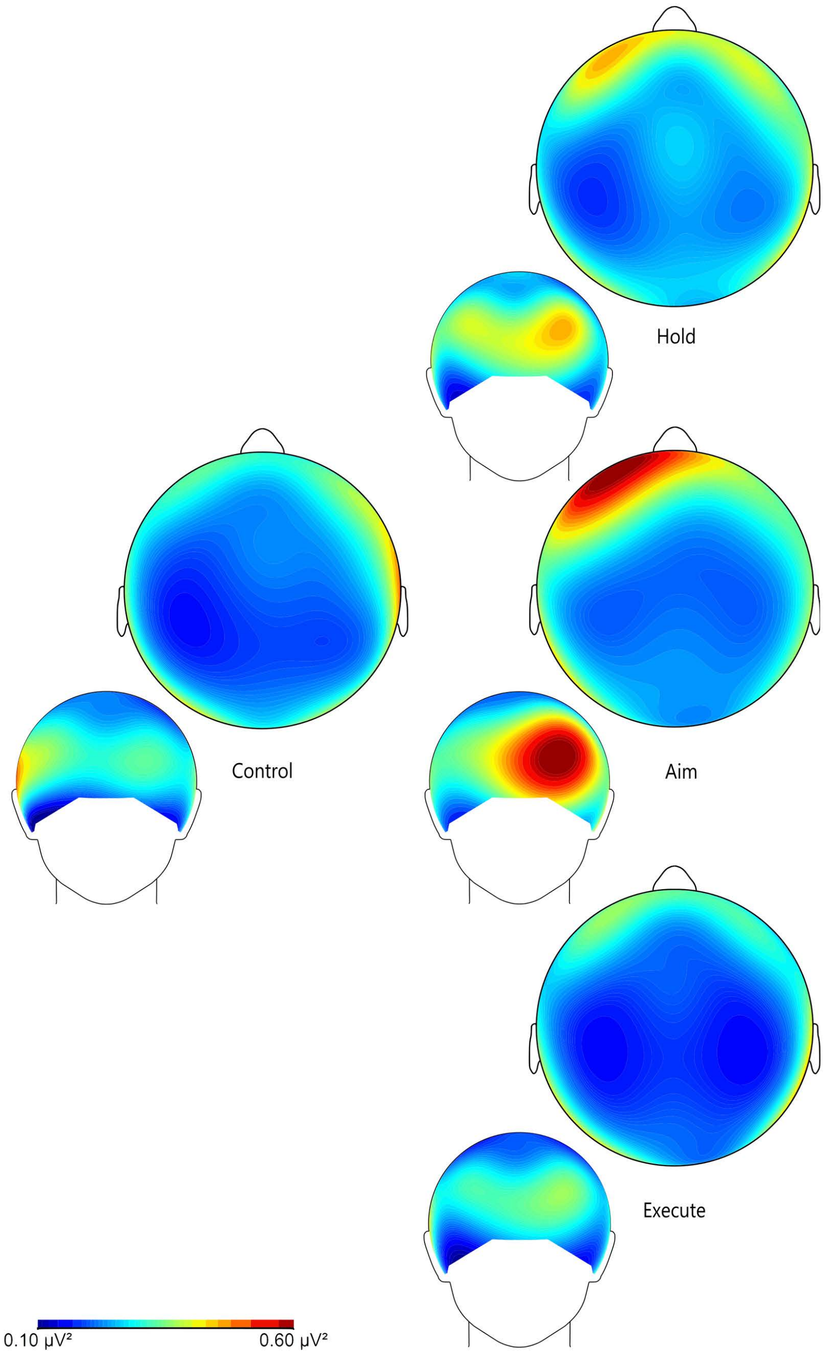

Fig. 3. Beta frequency band maps of all three phases within the Oldowan flake-cutting task and the control task Maps are configured at 0.1–0.6 μV². The scale represents lowest to highest power, from blue to red respectively. Band maps shown are from front and top views, focusing on the brain areas of interest.

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[45], it is also possible that many of the cognitive processes essential for successful task performance occur primarily during the preparatory (Hold and Aim) phases of the overall activity (involving the frontal region), prior to actual "cutting".

The findings also reveal intriguing patterns in bimanual coordination across different phases of the task. In the cutting task, participants used their non-dominant hand (in this case, the left hand) to stabilize the faux leather during both the preparation phase (Aim) and the cutting phase (Execute). Notably, this additional role of the non-dominant hand is reflected in the motor area (see Fig 3). Specifically, during the Hold phase (unimanual stage), only the left hemisphere of the motor region, which controls movements on the dominant (right) side of the body, displays low levels of beta power. This aligns with the expected motion-related desynchronization pattern observed in similar motor tasks [110,111]. However, in the Aim and Execute (bimanual phases) band maps, both the left and right hemispheres of the motor area show this relatively low level of beta power. Moreover, this is further visually confirmed by the control task band map (simple motor task), which predominantly shows low levels of beta power only in the left hemisphere of the motor region, as only the dominant hand was used.

Discussion: Interpretations, limitations, and future possibilities

This paper aimed to introduce and evaluate a novel protocol for studying brain-hand interactions during stone tool use by simultaneously recording EEG and sEMG data during the well-studied task of flake-cutting [8,112–115]. We anticipated gradually increasing patterns of muscular activity across the three task phases: beginning with picking up the tool (Hold), followed by preparing and aiming it for action (Aim), and peaking in activation during the actual cutting of faux leather (Execute). Furthermore, we hypothesized that the Aim stage would show an increase in beta power in the PFC and FC, reflecting the task's preparatory demands, which involve planning, object processing, and precise motor control [3,48–51,79]. Based on the interpretation of the produced beta frequency maps and the sEMG analyses, our core predictions were confirmed (also see previous studies on this data [11,45]), demonstrating that our proposed step-by-step protocol can provide a suitable basis for future experimental research on early stone tool production and use. Furthermore, this validation paper highlights the importance of distinguishing specific phases within each stone tool task during experiments. This segmentation allows for a more precise exploration of the unique biomechanical and cognitive demands required at each stage of the process [11,22,45].

More specifically, we found muscular forces increased during the Execute (cutting) stage, which showed distinctively higher positive PC1 scores. Notably, the muscles/muscle groups with the highest positive PC1 loadings (i.e., *flexor pollicis longus*, the two wrist flexors, and the first dorsal *interosseus*; Table 1) play a central role in performing the pad-to-side precision pinch grips typically required for flake-cutting [27,81,82,116]. Our analyses also successfully identified the increased importance of the non-dominant hand for stabilization of the target object, which was crucial not only during Execute (cutting) but also during the planning stage (Aim). This process (object stabilization) is used to ensure that the correct torque, resistance, and force are applied to the faux leather before pressure is exerted using the dominant hand carrying the flake.

Additionally, our EEG power band maps provided meaningful insights into the observed tool-related patterns of cognitive activation. As expected, these revealed a distinctive increase in beta power in the frontal region (particularly in association with the left PFC) during the Aim phase, compared to all other phases (including the control task). This aligns with findings from a recent human tool use study, which reported that the left frontal region (along with the left parietal region) was primarily activated during the planning phase of novel tool use, indicating that higher-order cognitive processes, such as goal-directed activities, are initiated prior to execution [44]. Other experimental tool use studies also find the frontal cortex critical in the planning and realization of precise motor planning [41,43]. In our study, in contrast to the Aim phase, Execute showed markedly less beta power in the PFC and FC. As we previously suggested in a recent EEG study [45], a likely explanation for this pattern is that the participants processed most of the motor planning, control, and decision-making required for stone tool use prior to the Execute phase onset, thus exhibiting increases in the frontal region during the earlier two phases of the task, but not during the cutting action itself. Alternatively, the decreased levels of beta power in the motor region during the Execute phase could also likely be indicative of increased motion-related brain activity (probably due to the aforementioned effects of desynchronization).

Nevertheless, it is worth noting that the above findings and interpretations regarding the Execute phase diverge from some of the studies mentioned above, which also reported continued frontoparietal involvement during the execution of the task itself [41,43]. In contrast, our analyses found diminished frontal activation once participants began the cutting action, suggesting that key cognitive processes, such as motor action planning, were largely resolved before movement onset (as previously proposed in Affinito et al., 2024 [45]) This discrepancy may stem from the relatively simpler nature of our stone tool task, as more complex or novel tool-using tasks may likely require sustained frontal involvement [41,44]. Another possibility, also proposed in our prior EEG study [45], is that continuous movement during the cutting task's execution led to sustained beta ERD. Regardless, the observed differences between phases further highlight the importance of analyzing tool use across distinct phases (i.e., planning and execution) for acquiring a more complete understanding of the task's cognitive demands. Studies and methods that focus solely on execution (e.g., cutting) or the entire task (without distinguishing between phases) risk overlooking critical neural processes involved in the structured process of goal-directed tool use (e.g., [8,15]).

This study's central objective was to provide a clear validated example of the combined EEG/EMG methodology described in this lab protocol paper. For this purpose, this proof of concept focused on key brain regions (PFC and motor cortex) alongside relevant hand and forearm muscles. More extensive EEG-only data and results on this task have been already provided in a previous study of ours on the same data [45]. Nevertheless, in the context of this methodological work, it would also be relevant to concisely discuss the broader bases of tool use within the complementary fields of neuroscience and biomechanics. As mentioned in the Introduction, there are evidently also other brain regions and muscles involved in human tool use, not covered in this protocol's case study. Prior research highlights the parietal lobe's (particularly the left IPL) crucial involvement in tool-related conceptual (especially for understanding tool function, mechanical knowledge, and problem-solving) and motor planning [52,53,55]. The importance of the parietal region, alongside the frontal cortex, has been underscored by neurological lesion studies demonstrating that frontal damage alone may not necessarily cause major impairments, but when combined with parietal lesions, tool use deficits become more pronounced [52]. This broadly suggests a complementary relationship between planning and decision-making (largely occurring in the PFC) and the mechanical and spatial principles of tool use (largely occurring in the left parietal region). Our previous EEG study broadly confirmed this expectation, as increased engagement of the frontoparietal regions was observed during the structured Aim phase, which required participants to sequentially plan and execute three precise cuts in a Z-pattern [45]. In summary, our findings align with the established literature on the joint activity of the left-lateralized prefrontal and parietal regions during tool use. The PFC, particularly the inferior frontal gyrus, appears crucial for action planning, motor imagery, and executive control, while the parietal cortex underpins the practical application of tool knowledge, including mechanical problem-solving and the spatial organization of actions [3,23,31,48–57]. As for muscular recruitment, previous EMG studies have highlighted the importance of other upper arm muscles (biceps brachii, triceps brachii, anterior deltoid) and intrinsic hand muscles (palmar interossei, extensor digitorum) during stone tool use and especially Oldowan knapping tasks [6,8]. However, the muscle selection in this case study, as well as in our previous EMG research [11], relied on the knowledge that the highest activation during stone tool use occurs in the first, second, and fifth digits [6,8].

Given the complexity of this experimental protocol, which strives to address multiple parameters simultaneously, several inherent limitations should be noted. As with most controlled laboratory experiments, it is challenging to perfectly replicate fully natural conditions for task performance while adhering to methodological constraints and recommended ethical standards. Additionally, EEG and sEMG are highly prone to noise artifacts [71,73,76,77], especially in tasks involving extensive movement, such as the manual activities analyzed here (also discussed in [45]). Despite the rigorous recording strategy and processing steps followed to account for motion artifacts (see dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61] and [45]), certain channels are widely known to be susceptible to noise, i.e., the mastoids (TP9 and TP10), due to muscular tension, and the location of the carotid artery, causing pulse artifacts [72–75,117]. For this purpose, in addition to implementing a careful experimental design combined with a detailed artifact removal process (as outlined in our step-by-step protocol), we recommend excluding EEG channels from subsequent statistical comparisons that show consistent muscular artifacts (as in dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61]).

Additionally, although EEG and sEMG were chosen for their ability to capture cognitive and muscular activity synchronously (due to their high temporal resolution), it should be noted that EEG has limited spatial resolution compared to other neurological methods [118–121]. This can create challenges when the focus is on exact source localization (e.g., when targeting small important areas with major evolutionary implications, such as Broca's or Wernicke's areas). In this regard, future studies may greatly benefit from combining EEG with other neuroimaging techniques, such as fNIRS, with improved spatial resolution (as in [122–124]). Finally, the EEG data in this study was processed in the frequency domain, specifically the beta frequency. This is common practice in EEG research focusing on active movement tasks, including general tool use [99,125–130]. However, future studies may benefit from analyzing EEG activity in both alpha (8–12 Hz) and beta frequency bands, to enable a more comprehensive understanding. Analyzing the alpha frequency (and/or other bands) may provide a fuller perspective on cognitive activity during experimental tool use tasks, particularly since this frequency band is known to be active during relaxed wakefulness [131] and has also been linked to motor preparation and active movement [99,125,130,132].

Overall, this methodological study introduced the first combined approach for simultaneously recording and analyzing EEG and sEMG data in experimental archaeology, promoting the use of our step-by-step protocol for exploring brain-hand interactions during stone tool tasks (dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1) [61]. We believe that this integrative method offers a currently missing foundation for gaining insights into the complex biomechanical and cognitive requirements of human-like stone tool production and use. Additionally, our studies highlight the importance of segmenting the stone tool task into distinct phases (Hold, Aim, Execute, in addition to a control condition), allowing for comprehensive monitoring of the entire process. This segmentation was shown to reveal valuable muscular and cognitive interactions across phases.

Supporting information

S1 File. Step-by-step protocol, also available on protocols.io (dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61]).
(PDF)

S2 Table. List of eigenvalues, percentages of variance, and factor loadings for the first principal components of the %MVC sEMG dominant hand PCA. Muscle abbreviations are as follows: FCR, *flexor carpi radialis*; FCU, *flexor carpi ulnaris*; FPL, *flexor pollicis longus*; TE, thenar eminence (consisting of *abductor pollicis brevis*, *flexor pollicis brevis*, and *opponens pollicis*); DI1, first dorsal *interosseus*; HTE, hypothenar eminence (consisting of *abductor digiti minimi*, *flexor digiti minimi*, and *opponens digit minimi*).
(PDF)

S3 Fig. Dominant hand %MVC sEMG PCA plot (PC 1 = 70.27% of variance; and PC 2 = 11.59% of variance) PCA plot summarizing overall dominant hand muscular recruitment during all three phases of the flake-cutting task. Phases are color-labeled (Red = Hold; Yellow = Aim; Green = Execute). PC 1 (70.27% of variance) maintains a clear distinction between Execute and the other phases of the task (Hold and Aim). The Execute phase displays increased muscular activation across all dominant hand muscles (factor loadings are listed in S2 Table).
(TIF)

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Funding acquisition: Fotios Alexandros Karakostis.

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Visualization: Brienna Eteson.

Writing – original draft: Brienna Eteson.

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Supporting information

S1 File. Step-by-step protocol, also available on protocols.io (dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1 [61]).

https://doi.org/10.1371/journal.pone.0324103.s001

S2 Table. List of eigenvalues, percentages of variance, and factor loadings for the first principal components of the %MVC sEMG dominant hand PCA.

Muscle abbreviations are as follows: FCR, *flexor carpi radialis*; FCU, *flexor carpi ulnaris*; FPL, *flexor pollicis longus*; TE, thenar eminence (consisting of *abductor pollicis brevis*, *flexor pollicis brevis*, and *opponens pollicis*); DI1, first dorsal *interosseus*; HTE, hypothenar eminence (consisting of *abductor digiti minimi*, *flexor digiti minimi*, and *opponens digit minimi*).

https://doi.org/10.1371/journal.pone.0324103.s002

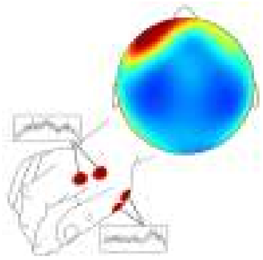
S3 Fig. Dominant hand %MVC sEMG PCA plot (PC 1 = 70.27% of variance; and PC 2 = 11.59% of variance) PCA plot summarizing overall dominant hand muscular recruitment during all three phases of the flake-cutting task.

Phases are color-labeled (Red = Hold; Yellow = Aim; Green = Execute). PC 1 (70.27% of variance) maintains a clear distinction between Execute and the other phases of the task (Hold and Aim). The Execute phase displays increased muscular activation across all dominant hand muscles (factor loadings are listed in S2 Table).

https://doi.org/10.1371/journal.pone.0324103.s003

Dec 02, 2024

The Mind & Muscles: A Protocol for the simultaneous measuring of cognitive and muscular activation during stone tool tasks using surface Electromyography and Electroencephalography



DOI
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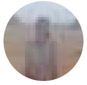

Brienna Eteson
DFG Center for Advanced Studies “Words, Bones, Genes, Tools”...

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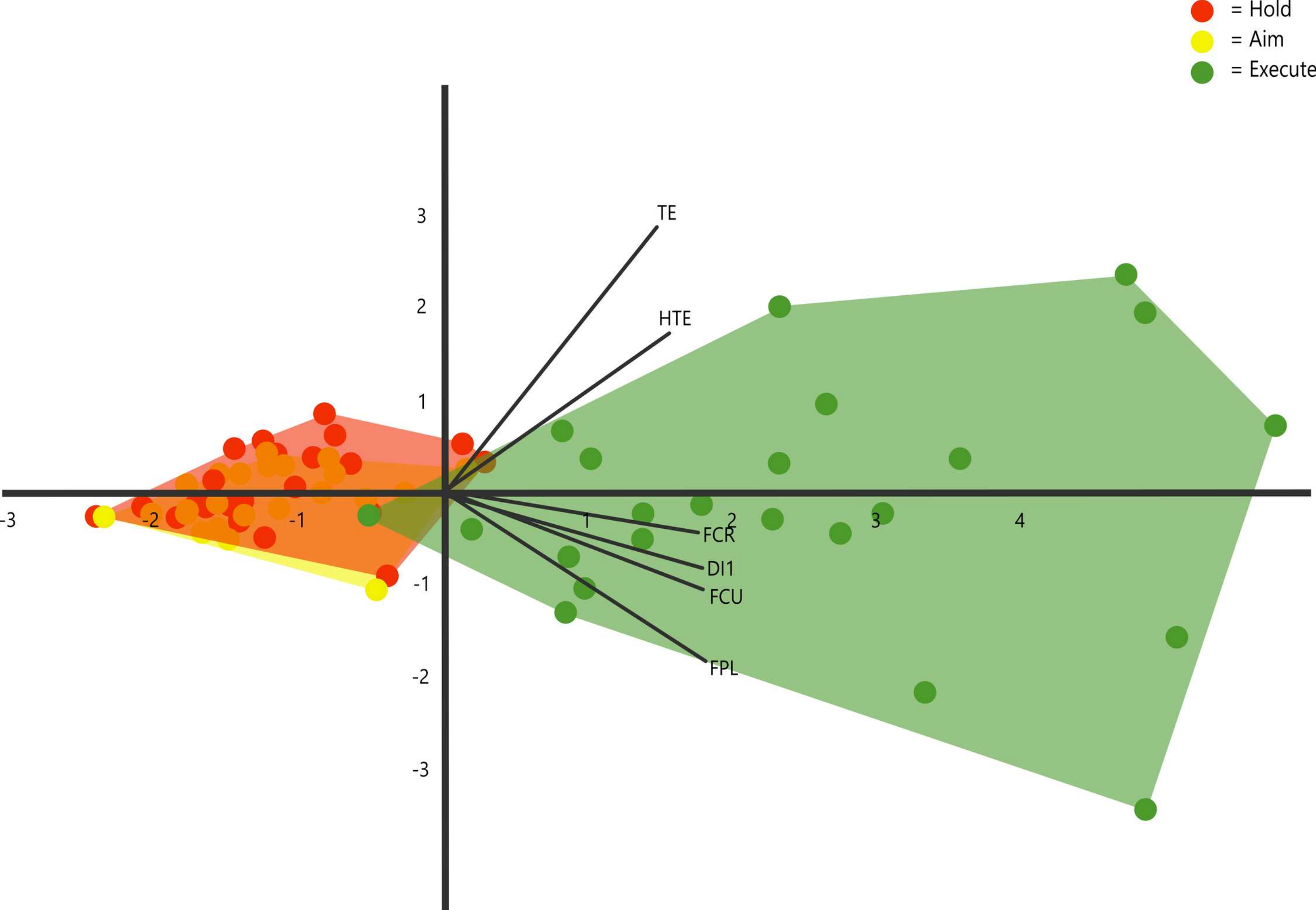
Protocol status: Working
We use this protocol and it's working

Created: October 12, 2024

Last Modified: December 02, 2024

Protocol Integer ID: 109742

				Factor loadings					
Task	**Principal Component**	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**
Flake-Cutting	PC 1	4.22	70.27	0.43	0.37	0.42	0.43	0.43	0.35
	PC 2	0.70	11.59	-0.19	0.43	-0.10	-0.25	-0.44	0.72


= Hold
= Aim
= Execute
TE
HTE
FCR
DI1
FCU
FPL
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-1
-2
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-3
-2
-1
1
2
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4

APPENDIX B

“How Handy was early hominin ‘know-how’?” An experimental approach exploring efficient early stone tool use.

Factors of Early Stone Tool-Using Efficiency

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“How handy was early hominin ‘know-how’?” An experimental approach exploring efficient early stone tool use

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Abstract

Objectives: The appearance of early lithic industries has been associated with the gradual development of unique biomechanical and cognitive abilities in hominins, including human-like precision grasping and basic learning and/or communicating capacities. These include tools used for activities exclusively associated with hominin contexts (cutting flakes) and hammerstones utilized for behaviors shared with non-human primates (e.g., nut-cracking). However, no previous experimental research has focused on comparing the factors affecting efficiency between these two key behavioral patterns and their evolutionary implications.

Materials and Methods: Here, we address this gap with an experimental design involving participants with varying tool-related experience levels (i.e., no experience, theoretical-only experience, and extensive practical knapping expertise) to monitor their success rates, biometrics, and surface electromyography (sEMG) recordings from eight important hand and forearm muscles.

Results: Our results showed that practical experience had a substantial impact on flake-cutting efficiency, allowing participants to achieve greater success rates with substantially less muscle effort. This relationship between success rates and muscle effort was not observed for the nut-cracking task. Moreover, even though practical experience did not significantly benefit nut-cracking success, experts exhibited increased rates of self-improvement in that task.

Discussion: Altogether, these experimental findings suggest that the ability to practice and retain tool-using knowledge played a fundamental role in the subsistence strategies and adaptability of early hominins, potentially providing the cognitive basis for conceptualizing the first intentional tool production strategies.

KEYWORDS

electromyography, ergonomics, Hammerstone, hand use, Oldowan

1 | INTRODUCTION

Tool use is an essential part of human behavior, crossing cultural borders, and spanning the globe (Biro et al., 2013; Osiurak et al., 2010), and has been fundamental to hominin biocultural evolution for over 3 million years (Harmand et al., 2015). Following the Lomekwian industry dated at ~3.3 MYA (Harmand et al., 2015), Oldowan flakes are considered the oldest temporally persistent hominin stone tool industry, at ~3 MYA (Plummer et al., 2023). Oldowan tools have since become recognized as an important characteristic associated with the emergence and gradual diversification of the genus *Homo*, due to their temporal persistence and geographical spread (Stout et al., 2019).

Intentional tool use had long been considered as an exclusively human behavior. However, evidence of chimpanzee (*Pan troglodytes*) tool use was first published in (Goodall et al., 1964) and many other studies have since described wild communities of various great apes, old and new world monkeys frequently engaging in various tool use practices, such as nut-cracking, ant-dipping, and crushed hammers (Boesch & Boesch, 1990, 1993; Fragaszy et al., 2004; Haslam, 2013; Ottoni & Mannu, 2001; Proffitt et al., 2016 and 2023; Whiten et al., 1999). This includes a recent study reporting that macaques (*Macaca fascicularis*) can repeatedly and unintentionally produce conchoidal flakes, comparable to that of Oldowan and Lomekwian stone flake tools (Proffitt et al., 2023). Until recently, such early stone tool industries were assumed to have been intentionally produced by hominins for specific utility. This study, alongside another paper on tool use in wild capuchin monkeys (*Sapajus libidinosus*) (Proffitt et al., 2016), raised questions as to whether original stone tool flaking was initially (and exclusively) an intentional behavior, or whether the prototype of the first Oldowan tool was a byproduct of hammerstone nut-cracking. As suggested by Proffitt et al. (2023), perhaps the anvil, used as a stabilizer in hammerstone pounding[1], became the core used in stone flaking.

While the above research casts doubt on the intentionality behind the earliest conception and production of sharp-edged tools, there remains direct evidence of hominin stone flake-cutting activities. This is demonstrated through cutmarks on animal bones (Bunn, 1981; Domínguez-Rodrigo et al., 2005; Potts & Shipman, 1981), re-touching of flakes that increases their cutting efficiency (Stollhofen et al., 2021; Toth, 1985), and indications of tool transport (Braun et al., 2008). This evidences the intentional production and use of tools in early hominins. In this context, the intentional production of Oldowan flakes via hammerstone knapping requires comprehension of fracture mechanics, knowledge of ideal raw material and size, visuospatial awareness, planning, and sensorimotor control (Hovers, 2009; Roche et al., 1999), traits not typically observed in non-human primate communities. This is primarily due to their observed unintentionality of the produced flakes, unsuitable use of raw materials for producing flakes, and inability to consistently knap flakes (e.g., Bandini et al., 2021; Bandini & Tennie, 2023; Proffitt et al., 2022, 2023; Proffitt, Haslam, et al., 2018). Considering that such purposeful and successful production of a tool requires prior knowledge of its function and utility, exploring the biomechanical and cognitive demands of human-like tool use is crucial to our understanding of the factors affecting early hominin biocultural evolution. Nevertheless, most cognitive evolutionary studies to date have focused on the process of stone tool production rather than use (e.g., Moore & Perston, 2016; Putt et al., 2017; Stout et al., 2000, 2015; for biomechanical EMG studies, see Macchi et al., 2021; Marzke et al., 1998). This is despite previous neurological research in humans showing that aspects of generalized tool use and advanced cognitive processes (gestural communication) share the activation of a similar brain network (Frey, 2008).

The introduction of cutting via sharp-edged stone flakes arguably represents one of the earliest transitions in the hominin archaeological record, proposed as being crucial to human evolution and technological advancement (Bril et al., 2015). Oldowan flakes, alongside cut marks on bones, provide some of the earliest evidence of animal butchery of hominins in the Lower Paleolithic (Plummer et al., 2023; Plummer & Bishop, 2016; Sahnouni et al., 2018). The Oldowan is widely accepted as being a tool industry that enabled the access of carcasses as new food resources (Parkinson et al., 2022; Potts, 1991). More particularly, the use of Oldowan flakes represents the oldest direct indication of hominins relying on a modern human-like forceful pad-to-side precision grip (Susman, 1991; see Figure 1) as well as one of the earliest pieces of evidence of intentional cutting, a behavior that effectively broadened early hominin access to nutrient-rich resources (Linares-Matás & Clark, 2022; Plummer, 2004; Plummer et al., 2023; Semaw, 2000; for disputed 3.3 MYA stone tools[2] see Domínguez-Rodrigo & Alcalá, 2016; Harmand et al., 2015). In contrast, hammerstone pounding activities (e.g., nut-cracking), which are also observable in several non-human primate species (Arroyo et al., 2016; Bril et al., 2012; Gumert & Malaivijitnond, 2012; Proffitt et al., 2016, 2023; Wynn & McGrew, 1989), are suggested as having predated the Oldowan industry (Panger et al., 2002). This is based on the principle of maximum parsimony, which suggests that a trait existing in two related species was present prior to their divergence (Panger et al., 2002). In contrast, flake-cutting behaviors, which only occur in one extant species, may have likely emerged after this divergence.

Importantly, while manipulatory similarities have been identified between hammerstone knapping and pounding activities, particularly with hammerstone pounding being dubbed as a potential precursor to Oldowan tool production (Bril et al., 2012), these two distinct tasks do not recruit identical grasping patterns. Hammerstone pounding primarily involves forceful grasping motions that largely depend on the recruitment of the palm and the fifth digit (Figure 1) (Domalain et al., 2017). Similarly, the grasping patterns used for stabilizing cores during stone tool production (for hard hammer percussion), have also been found to utilize the palm and fifth digit for stabilization (Marzke et al., 1998). However, in contrast to hard hammer percussion during Oldowan stone-tool production, which most often employs a precision pad-to-pad 3-jaw-chuck grasping pattern (Marzke, 1997; Marzke & Shackley, 1986; Williams et al., 2012), hammerstone pounding in humans and chimpanzees typically involves the use of one hand (Falótico & Ottoni, 2016; Fragaszy et al., 2020) and a power grasp (more specifically, a spherical grip; Bril et al., 2015).

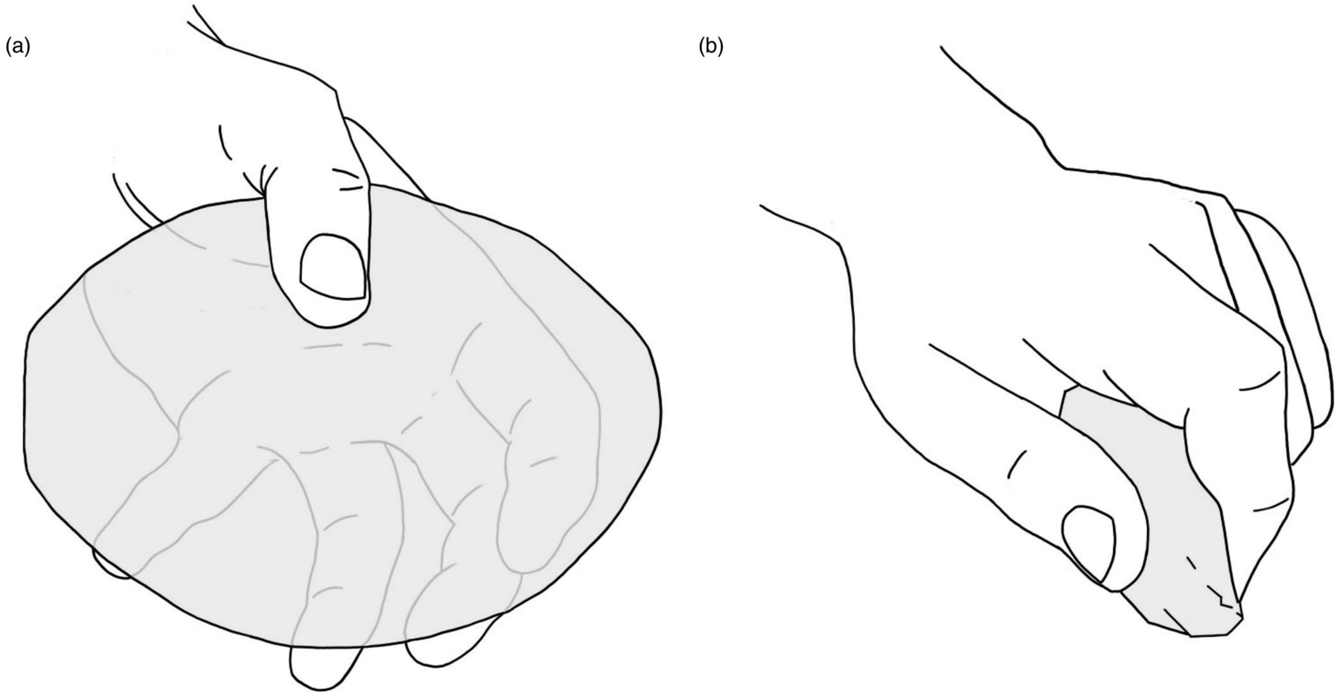

FIGURE 1 Grasping patterns used by the participants during the experiment: (a) "power" (cradle five-jaw) grip used during the hammerstone nut-cracking task, (b) "precision" (pad-to-side) grip used during the flake cutting task. Created using Sketchbook version 6.0.6., based on Rolian et al. (2011).

To address the biomechanical requirements of early stone tool production and use, several previous experimental studies have relied on the use of surface electromyography (sEMG) (Hamrick et al., 1998; Key et al., 2020; Marzke et al., 1998). Williams-Hatala et al. (2018) found that hammerstone pounding and knapping activities resulted in greater loads compared to handaxe or flake use, while Key et al.'s (2018) experimental study found certain grips were repeatedly used during a variety of stone tool tasks. These important works laid the necessary groundwork for further research, effectively pinpointing muscles and digits of the hand of particular importance. However, no previous experimental study so far has focused on directly comparing the biomechanical requirements of hammerstone pounding activities (observable in extant non-human primates) against Oldowan-style flake cutting (apparently exclusive to hominins and not observed in other primates in the wild). Additionally, no EMG study has analyzed the entirety of the tool-using process (i.e., all physical steps required for its completion). More specifically, the tool-using action comprises several phases, involving a variety of intricate and synergized muscle movements. These phases include initial contact (picking up and holding the tool), the grasping pattern required for aiming toward the intended target, and finally the execution of the task itself, employing the force necessary to perform the action. Previous research by Williams et al. (2014) on stone tool production captured successive knapping episodes over five swing phases, to accurately measure force levels. However, previous experimental studies on stone tool use have taken a more specific approach, focusing explicitly on the precise moment of the execution (Hamrick et al., 1998; Key et al., 2019, 2020), which may have led to key insights into the necessary functions for stone tool use being missed.

In this framework, this experimental sEMG study addresses the various factors affecting the successful (efficient) use of hammerstone pounding and cutting stone tools (involving all steps of the process), aiming to explore traits that were evolutionarily advantageous for early hominin tool users. The following three working hypotheses are addressed:

1.1 | Hypothesis A

Based on the definition of efficiency (i.e., the ability to perform a task without wasting materials, energy, and time) and findings from various previous experimental studies (Bril et al., 2010, 2012; Key & Lycett, 2011), we expect participants with more experience and higher maximum grip strength to perform both tool-using tasks more efficiently (i.e., with higher success rates, and lower overall muscular activation) than less experienced knappers, across all steps (stages) of each task ("Hold", "Aim", and "Execute").

1.2 | Hypothesis B

Given that flake cutting appears to be an exclusively hominin manual behavior that likely postdates the earliest hammerstone pounding activities (Bril et al., 2012; Harmand et al., 2015) and relies on the use of tools requiring a production process (when created intentionally), we propose that successful flake cutting may be relatively more benefitted by a human-like ability to accumulate technical experience compared to hammerstone nut-cracking and pounding tasks (observed in several other extant species). In contrast, successful hammerstone pounding (nut-cracking) is expected to be relatively more dependent on biomechanical attributes (i.e., grip strength). For instance, due to the hammerstone's heavier mass and the hardness of the nut's outer shell, we would expect a closer association between nut-cracking efficiency and an individual's overall grip strength.

1.3 | Hypothesis C

Previous studies have shown that individual learning and skill transfer can be effective traits to ensure successful stone tool production (Heyes, 2018; Seifert et al., 2013). However, the impact of skill accumulation and transfer on the use of these early stone tools has not been adequately addressed. Here, we hypothesize that, if accumulated experience in particular aspects of early hominin stone tool behaviors (knapping) can increase an individual's adaptability through skill transfer, we would expect that participants with such tool-related experience will be able to master less familiar tool-using tasks (in this case, successfully cracking hard nuts using a hammerstone or cutting through pieces of faux leather following a specifically indicated pattern) faster than those without.

2 | MATERIALS AND METHODS

To address the above hypotheses, we developed an experimental design relying on sEMG to measure muscular activity during the two aforementioned stone tool types. Hammerstone nut-cracking is the first tool task analyzed for the study, which is a behavior observed in several non-human primate communities to crack hard shells and access the nutrient resources inside (Arroyo et al., 2016; Bril et al., 2012; Gumert & Malaivijitnond, 2012; Proffitt et al., 2016, 2023; Wynn & McGrew, 1989). Oldowan flake cutting is the second tool task, which represents the first direct evidence of habitual human-like pad-to-side powerful precision grasping (Figure 1) (for more details on the importance of this grip for human-like manipulation, see Kivell, 2015; Kivell et al., 2023). Several proposed factors of tool-using efficiency were considered and recorded in this study (see below). Efficiency itself was evaluated based on the success rate of each task, the overall muscle force applied, and the muscular synergies recruited for each participant.

2.1 | Participants and experience level

Twenty-five participants (14 biological females and 11 biological males) originating from 10 different nationalities (seven native languages) took part in the study. All participants provided voluntary and informed consent, while ethics approval was granted by the University of Tübingen's Ethics Committee. Participants were categorized, based on their stone tool experience, into three levels: Novice – absence of related experience ($n = 16$), Intermediate – only theoretical knowledge of stone tool use and production ($n = 4$), and Expert – theoretical knowledge and extensive practical tool knapping experience ($n = 5$). All participants informed us that they never frequently used stone tools for cutting through faux leather (or similar materials), nut-cracking with a hammerstone, or ever attempting to crack macadamia nuts (or any nuts of similar hardness). All data and recordings were anonymized in line with the guidelines of the Ethics Committee.

2.2 | Stone tools and materials

A total of 45 stone tools (26 replica Oldowan flakes and 19 hammerstones) were used in the experiment, all of which were sourced and knapped by an expert knapper (author ETM). All hammerstones were quartzite, and flakes were knapped from Senonian flint with hard hammer percussion. To minimize stone tool size variation, we ensured all utilized hammerstones were between 8 and 14 cm in length (Titton et al., 2018), and flakes were between 5 and 7 cm in length, in line with documented proportions of Oldowan tools (see Figure 2) (Gladilin & Sitliviy, 1987; Hayden, 2008).

For the hammerstone nut-cracking task, macadamia nuts were used because previous studies suggest they provide an adequate substitute for non-human primate nut-cracking activities (Arroyo et al., 2016; Bril et al., 2015; Hirata et al., 2009), due their comparative hardness to nuts commonly consumed in the wild, most notably, oil palm tree (*Elaeis guineensis*) (Arroyo et al., 2016; Hannah & McGrew, 1987; Proffitt et al., 2018). Initially, we used unroasted macadamia nuts during our trial experiments, but all trial participants were consistently unsuccessful in cracking open the hard outer shell due to its hardness, fracture strength, and toughness. Macadamia nuts have been shown to have the same Vickers hardness as annealed aluminum, despite being half as dense (Bril et al., 2012; Jennings & Macmillan, 1986; Sesana et al., 2019). Therefore, to ensure that the nuts could be cracked, while still maintaining high and consistent resistance to breakage across the sample, nuts were roasted using the same heating equipment, temperature, and duration.

Previous studies performing experimental analysis of Oldowan tools have used leather as a substitute for demonstrating animal butchery, to perform use-wear analysis (Ibáñez & Mazzucco, 2021) or assess biomechanical effort during tool use (Hamrick et al., 1998). However, during our experiment, we used faux leather to ensure material consistency across all trials. Faux leather is a synthetic material that is intended to replicate the thickness, strength, and torque of real leather hide. This was preferred over real leather to control for any variability that can occur with natural materials, which could potentially affect the experimental outcomes. Additionally, a pattern was drawn on the faux leather squares to ensure each participant performed the same cutting action (e.g., as in Key et al., 2018). The pattern was three stenciled 3 cm straight lines formed into a Z pattern,

FIGURE 2 Examples of 3-D scans of flake (a) and hammerstone (b) tools used within the experiment (a different set was provided for each participant). The scale is not respected in this figure. Flake dimensions ranged from 5 to 7 cm, while hammerstones were between 8 and 14 cm in length (following dimensions reported for Oldowan industries in Gladilin & Sitliviy, 1987; Hayden, 2008). Stone tools were 3D scanned using an Artec Space Spider scanner (Artec Inc.) and a resolution of 50 microns.

used to ensure participants engaged in specific cognitive and biomechanical processes, which require planning, fine motor control, and hand-eye coordination. To successfully complete the task, participants were instructed to cut through the fibers on the faux leather square entirely, in line with the above-mentioned pattern.

2.3 | Muscle selection

sEMG was used to monitor the participants' muscle activation during the tool using tasks, involving eight muscles (six on the dominant hand, two on the non-dominant hand). All muscles were chosen for their prior application in other EMG studies and widely known importance in human stone tool use (Key et al., 2019, 2020; Kivell et al., 2023; Marzke et al., 1998). The eight muscles (or muscle groups) measured included two powerful muscles of the wrist (*flexor carpi radialis* and *flexor carpi ulnaris*), a powerful flexor muscle in the thumb (*flexor pollicis longus*), the thenar eminence muscle group (consisting of *abductor pollicis brevis*, *flexor pollicis brevis*, and *opponens pollicis*), the first dorsal *interosseus*, and the hypothenar eminence muscle group (consisting of *abductor digiti minimi*, *flexor digiti minimi*, and *opponens digit minimi*) (see Figure 3). The first dorsal *interosseus* and the muscles of the thenar eminence were also measured on the participant's non-dominant hand. These muscles were added because both tasks required stabilization of the target object (nut or faux leather) from the non-dominant hand, predominantly via the use of the thumb and index finger. Both the first and second digits have been shown to play an important role in stabilization during knapping and nut cracking (Key & Dunmore, 2015; Marzke et al., 1998; Marzke & Shackley, 1986). Muscles in the thenar or hypothenar eminences were grouped together due to the small surface area of the skin, which does not enable electrodes to accurately detect singular muscular activation, due to contamination of other muscles close by. Each muscle/muscle group's action and acronym are listed in Table 1.

2.4 | Experimental design

All participant data was recorded in a shielded cabin designed to minimize external electrical noise, at the Max Planck Institute for Intelligent Systems, in Tübingen (see Acknowledgements). Participants were alone in the cabin, with a small table in front of them, a chair to sit on throughout the experiment, and a camera recording all tasks. A small window on the right side (outside the participant's line of sight) allowed for observation of the participant during the experiment. Participants were shown an instructional video containing all the information pertaining to the experiment. The video displayed the experimental design, sEMG application, and any contraindications for the day of the experiment. This was used to ensure that all participants received the same instructions, and the experimental steps were clearly shown to avoid confusion due to potential language barriers.

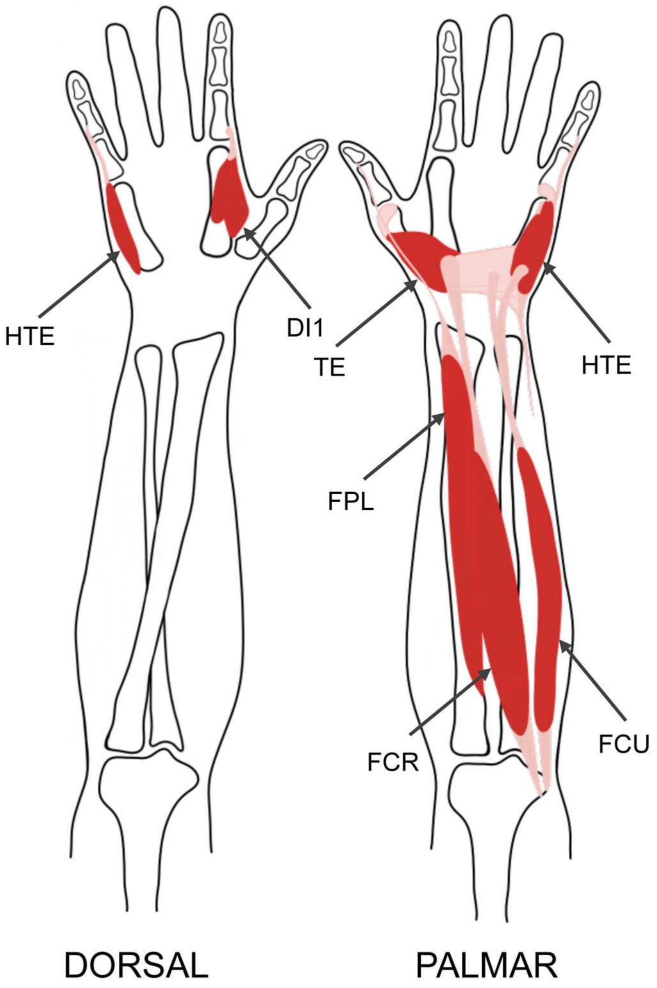

FIGURE 3 Illustration of the muscles monitored during tool tasks using sEMG. Illustrations created in Sketchbook version 6.0.6, based on Standring (2021). L to R: HTE (hypothenar eminence muscle group), DI1 (first dorsal *interosseus*), TE (thenar eminence muscle group), FPL (*flexor pollicis longus*), FCR (*flexor carpi radialis*), FCU (*flexor carpi ulnaris*). The thenar eminence (TE) group and first dorsal *interosseus* (DI1) were also monitored on the non-dominant hand.

The experimental protocol consisted of two parts (two tasks), which were further sectioned into three steps. The two parts consisted of a hammerstone nut-cracking task and a flake cutting task. Each part consisted of three steps: picking up the tool (either hammerstone or flake; referred to as Hold), aiming the tool at the intended target (either the macadamia nut, or z pattern on faux leather fabric; referred to as Aim), and striking the intended target (cracking the macadamia shell, or cutting through the faux leather fabric; referred to as Execute), finally a brief rest period was provided to reset (included removing the nut and shell or faux leather fabric square from the designated tool task area to begin the next repetition; referred to as Rest). Each step was performed over a period of 5 seconds (s), after which a discreet beeping sound notified the participant to begin the next step. Each round consisted of 4 × 5 s intervals of; Hold (5 s), Aim (5 s), Execute (5 s), and Rest (5 s) = total of 20 seconds per round (see Figure 4). Both tasks were performed a minimum of 50 times per participant, which allowed us to observe intra-individual changes in performance and efficiency of the task over time.

TABLE 1 The eight muscles/muscle groups monitored and their movement action.

Muscles/muscle groups	Movement action
First dorsal *interosseous* (DI1)	Abducts and rotates the index finger, assists in adduction of the thumb.
Hypothenar eminence (HTE)	The muscle group contributes to the flexion, abduction, and lateral rotation of the fifth digit.
Flexor *carpi radialis* (FCR)	Flexes and radially abducts the wrist.
Flexor *carpi ulnaris* (FCU)	Adducts and flexes the wrist.
Flexor *pollicis longus* (FPL)	Flexes the thumb and assists in wrist flexion.
Thenar eminence (TE)	The muscle group contributes to the adduction, abduction, flexion, and medial rotation of the thumb.
Non-dominant first dorsal *interosseous* (ndDI1)	Abducts and rotates the index finger, assists in adduction of the thumb.
Non-dominant thenar eminence (ndTE)	The muscle group contributes to the adduction, abduction, flexion, and medial rotation of the thumb.

2.5 | Surface electromyography recordings

The recommended European standards for surface electromyography (SENIAM project) were adhered to in the following protocol (Stegeman & Hermens, 2007). Bipolar surface electrodes were applied to cleaned skin with conductive gel and secured using kinesiology tape over the muscle belly (see Figure 5). Each electrode signal was amplified using a BrainAmp amplifier (Brain Products GmbH, Gilching, Germany), sampled at 2500 Hz (two recordings were originally sampled at 1000 Hz and all recordings were then re-referenced to 500 Hz). All electrode signals were recorded using Brain Vision Recorder (version 1.24.0101, Brain Products GbmH, Gilching, Germany). Electrode placement and signal were tested using exercises known to activate the muscles (based on Key et al., 2020 and Standring, 2021). Maximum Voluntary Contractions (MVC) were then measured to record the individuals' maximum strength outputs for each muscle, which is an essential step for making all participants' data comparable. For this purpose, each participant performed three repetitions of the following power and pinch grip strength tests, using Baseline BIMS power "grip" and "pinch" strength dynamometers (Functional model, Fabrication Enterprises, New York). Both electrode signal (mV) and weight (kg) measurements were recorded. The "grip" dynamometer consisted of a power grasp, with all fingers wrapped around the dynamometer in flexion. The "pinch" dynamometer consisted of a sustained precision pinch, actively engaging the thumb and first finger, on either side of the pinch dynamometer pad. Participants were instructed to perform this task using the maximum strength possible. This maximum measurement was taken over a period of 5 s and

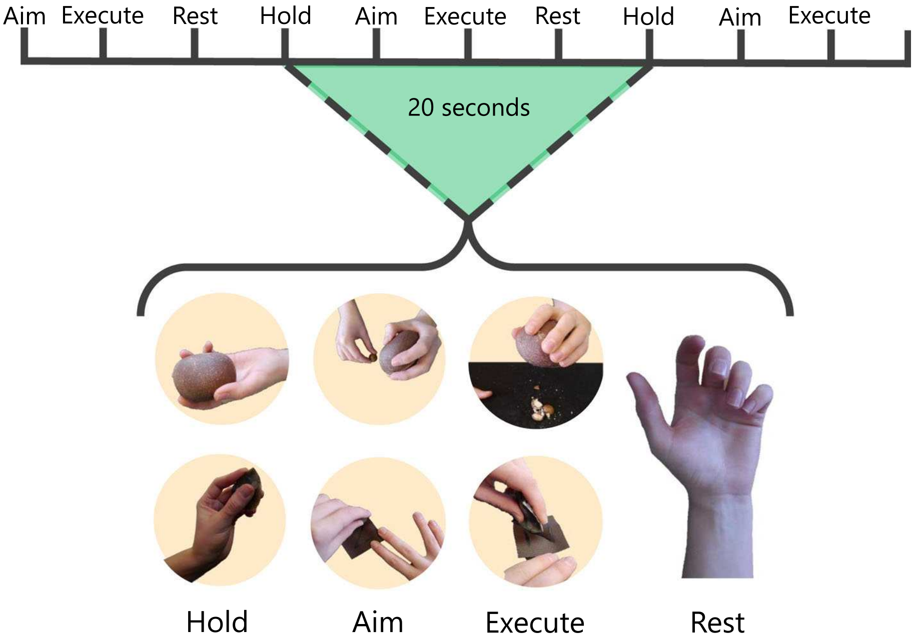

FIGURE 4 Illustration of the experimental steps. This illustration depicts the three steps (Hold, Aim, Execute) recorded in each task, hammerstone nut-cracking task (top), flake cutting task (bottom), and the 5 s *Rest* period. Each step was performed for 5 s. Illustration created in PowerPoint version 2309 (Davenport et al., 2023).

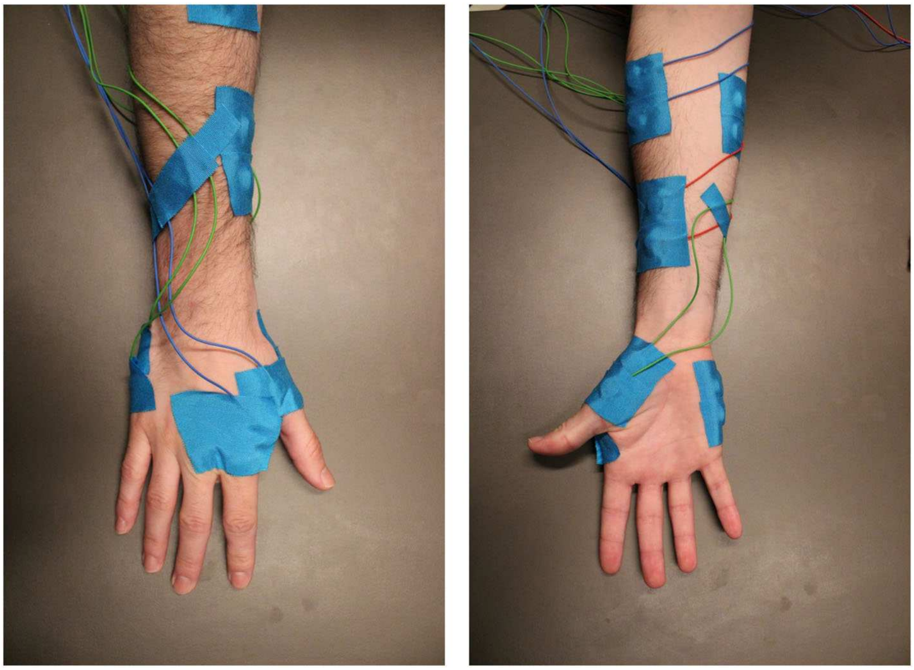

FIGURE 5 Example of the placement of electrodes on the forearm and hand. Bi-polar electrodes were secured using kinesiology tape (True Tape Sports GmbH).

repeated a total of three times for both the dominant and non-dominant hand. The participant's highest measurement from each repetition was recorded.

As described and illustrated in Figure 4, once the experiment began, a looped beep was sounded every 5 s (at each step) throughout the entirety of the experiment. This sound was amplified to notify the participant of when each step began, and was also registered as a signal in the Brain Vision Recorder (version 1.24.0101, Brain Products GbmH, Gilching, Germany) recording software. Each beep sound could then be translated into a step to correctly monitor all steps (within each trial). After successful repetition of at least 50 trials, participants were allocated a 30-min break, before moving on to the next stone tool task, and repeating this procedure.

2.6 | Processing sEMG data

A total of 2680 repetitions were recorded across both tasks (flake cutting = 1294, hammerstone nut-cracking = 1386). Due to sEMG being volatile to internal and external artifacts, (Boyer et al., 2023; Raez et al., 2006) participants whose signal demonstrated a lower signal-to-noise ratio performed more than 50 repetitions, to ensure the recording of a sufficient number of usable repetitions per individual. Following the recordings, all signals were then uploaded into the Brain Vision Analyzer version 2.2. The sEMG signals were then re-referenced at 500 Hz, before cleaning and segmenting the signal to remove all external and internal noise and sectioning each step separately for individual analysis. If the electrode signal was affected by electrode noise, signal loss, or other external noise, these sections were removed from the analysis. In total, there were two participants (both from the novice group) who ended up with less than 50 clean sEMG repetitions (46 and 49 for the hammerstone nut-cracking and 48 and 49 for flake cutting, respectively). Therefore, all participants had a minimum of 46 clean task repetitions with good electrode signals, which were used for our sEMG statistical analyses. It should be clarified that this was not the case for the calculation of success rates, for which all initial 50 repetitions of all participants were considered in the analyses. sEMG signals inherently have a mean close to zero due to the fast oscillations of the muscles swinging the wave on either side of zero, in both positive and negative values. Once smoothed out, the resulting wave would be zero (Negro et al., 2015; Neto & Christou, 2010). Therefore, to be able to analyze the signal, rectification is typically applied to turn negative swings into positive values. Once all data was segmented into the three steps (Hold, Aim, Execute), we further segmented to ensure the analysis only included the period of the action itself, thus reducing each segment's total duration to 4000 ms (except for the hammerstone Execute step, which was performed within 1500 ms). All 5 repetitions were then averaged to create one segment per participant. All signals were then exported into 0.25 s epochs. These were then averaged after exporting into one value per task, per muscle, which represented each step's mean muscular activity.

Maximum Voluntary Contractions (MVC) were taken from the dynamometer recordings and cleaned in the same way as the tasks. Peak activation was then extracted for pinch and power grip dynamometer strength tests. The MVC signals were then used to create individual percentage maximum voluntary contractions (%MVC) for each participant. This was then used as a basis for calculating a participant's relative muscular activation during each task. This enabled all participants to be comparable, despite varying degrees of strength. The %MVC values were then used for statistical analysis.

2.7 | Biometric measurements

Specific biometric data was recorded from each participant. The following variables were recorded: dynamometer power and pinch grip strength (kg) and participant hand preference (right, left, or ambidextrous) based on the Edinburgh Handedness Inventory (Oldfield, 1971). A total of 23 participants identified themselves as right-hand dominant, and two, as left-hand dominant. The left-hand dominant participants were included in the study as no differences in the data were observed (i.e., both individuals presented the expected patterns with regard to the effects of experience and biometric factors, while removing them from the analyses did not alter the observed patterns).

2.8 | Success rate

Successful completion of a task was recorded for each repetition. Success was carefully monitored and recorded for each participant. Successful completion of each task had set criteria from which participants were then assessed. Success of the hammerstone nut-cracking task was quantified by whether the nut was extractable from its hard outer shell without the use of any other tool. Broken shells were collected after each trial and video footage was monitored directly after the experiment to determine the rate at which the participants successfully cracked the macadamia nuts. Success in the Oldowan flake-cutting task required the fabric fibers of the faux leather to be entirely cut through along the indicated Z-pattern. Success was expressed in binary form (1 = successful, 0 = unsuccessful). Percentages of success were calculated based on the relative number of successes and total repetitions performed per participant.

2.9 | Statistical analyses

The exact statistical procedures used to address our three working hypotheses (A-C) are described within the three subsections below. In general, univariate and bivariate analyses were run to statistically evaluate relationships between the biometric data, experience groups, success rates, and muscular activation levels. Multivariate analyses were used to build on the previous analyses to better understand how the different sEMG signals correspond with each other and determine the muscle coordination patterns associated with each task, step, and experience group. All statistical analyses were performed using PAST version 4.03. (Hammer et al., 2001) or R (packages 'lme4' and 'ggplot'). Plots and graphs were produced in the same software and modified in Inkscape vector graphics editor version 1.3. (Rogers, 2023).

2.10 | Hypothesis A

To address hypothesis A, exploring potential associations between participants' biometrics and success rates, several statistical analyses were performed. Before the analyses, four extreme outlier cases in the cutting task's success rates were removed, following the indications of the interquartile range approach (e.g., Field, 2013). As some data (power and pinch grip strength calculations) still showed a non-normal distribution, the non-parametric Kendall's Tau correlation test was preferred for directly comparing all biometric and success rate measurements.

First, we evaluated the strength of association between the success rates of each task (cutting or nut-cracking) and the corresponding maximum grip force (pinch or power grip dynamometer values). The Kendall's Tau correlation test was selected due to its robustness and the experiment's relatively small sample size.

Second, the effect of experience on overall success rates was assessed for each task separately. Initially, all successes were averaged throughout the 50 repetitions of each participant. Then, to compare success rates across experience groups within each task (cutting and nut-cracking), we performed two analyses of variance (ANOVAs), followed by post hoc Tukey's honestly significant difference (HSD) tests to determine where differences between groups are (Field, 2013; Tabachnick and Fidell, 2019). Additionally, we performed two analyses of covariance (ANCOVA), treating strength measurements (either power or pinch grip strength) as a covariate (Field, 2013). All necessary assumptions for these linear models (i.e., absence of outliers in the dependent variable, approximate normality of the dependent variable within each group, homogeneity of variances, homogeneity of regression slopes, within-group linearity between the dependent variable and the covariate, and homoscedasticity) were met, in line with standard recommendations (Field, 2013; Tabachnick and Fidell, 2019).

Third, the relationship between the levels of relative muscle recruitment (i.e., %MVC) and experience was explored using multivariate analyses, looking holistically at overall muscle recruitment (MVC%) and potential muscle coordination patterns (i.e., the combination of different sEMG signal activation levels) that may vary by the level of tool-related experience. A total of six principal component analyses (PCAs) were generated, each focusing on a single step (Hold, Aim, or Execute) of each task (hammerstone nut-cracking and flake cutting). These were performed based on a correlation matrix due to varying ranges among variables. The variables entered in the analysis were the eight sEMG muscular activation signals (see Table 2 for details). In these PCAs, which did not assume any groups a priori, participants were color-labeled based on experience level. Additionally, to exclude any potential bias associated with overall individual grasping strength, before running the PCAs, all values were size adjusted using each participant's grip strength measurement (either the power or pinch grip dynamometer reading, for the nut-cracking or cutting task respectively). The PCAs were also re-run before size adjustment, displaying similar results and patterns. Relevant principal component (PC) scores were then extracted for further analysis based on the indication of the broken-stick model (Jackson, 1993) to appropriately determine the number of PCs to include in our plots and interpretations. In addition to our visual plot observations, Kendall's Tau correlation tests were also run on the extracted PC scores (for each of the six PCAs) to determine whether they significantly correlate with the level of experience.

Finally, to better visualize varying relative muscle forces recruited for each experimental step (as is expected in hypothesis A), radar plots were produced to display overall trends within each step, for each level of knapping experience. These plots combine all participants' (within-group) muscular sEMG (%MVC) data into one figure.

2.11 | Hypothesis B

For testing hypothesis B, which aimed to determine whether the success rate was differentially influenced by experience level for each of the two tasks, we relied on the outputs of the aforementioned ANOVAs, ANCOVAs, and PCAs. In this case, in contrast to hypothesis A, our focus was on comparing the results (in terms of statistical significance and/or PCA patterning) between the two tasks.

2.12 | Hypothesis C

Finally, to address hypothesis C, we wanted to determine whether success rates improved differentially across experience groups throughout the 50 repetitions. Initially, to visualize these potential trends, a line graph was produced. Participants were grouped by experience, and each repetition was averaged per group to create three lines, each represented by 50 data points. Subsequently, to facilitate the statistical evaluation of the average trends observed in that graph, we transformed the 50 nominal (binary) variables into five continuous variables (success rate %), representing each individual's average percentage of success over 5 × 10 repetition segments (from 0 to 50). For each of the five repetition sets, the strength of the correlation between experience level and success rate was assessed using Kendall's Tau correlation test. A three-point moving average was then applied to improve the visualization of variation across the 50 trials.

It should be noted that analyzing this dataset using parametric statistical procedures (e.g., mixed repeated-measures linear models) was not preferred due to consistent violations of key statistical

TABLE 2 List of eigenvalues, factor loadings, and percentages of variance explained per PCA conducted in this study (see Table 1 in Methods and Materials for muscle abbreviations).

				Factor loadings							
Task/Step	Principal Component	Eigenvalue	% of variance	DI1	HTE	FCR	FCU	FPL	TE	ndDI1	ndTE
Nut-cracking											
Hold	PC1	4.00	50.05	0.81	0.69	0.76	0.85	0.75	0.67	0.53	0.52
Aim	PC1	4.37	54.66	0.71	0.75	0.82	0.84	0.78	0.73	0.59	0.67
Execute	PC1	4.48	55.94	0.37	0.34	0.37	0.39	0.38	0.38	0.29	0.28
Cutting											
Hold	PC1	4.49	56.15	0.74	0.70	0.84	0.83	0.81	0.61	0.76	0.68
Aim	PC1	4.77	59.58	0.70	0.84	0.81	0.83	0.79	0.64	0.84	0.71
Execute	PC1	4.36	54.54	0.78	0.74	0.84	0.78	0.77	0.68	0.66	0.64

assumptions (e.g., Field, 2013; Tabachnick and Fidell, 2019). Nevertheless, as an addition to the approach outlined in the paragraph above, we also explored each experience group's change in nut-cracking success over the 50 trials by calculating a repeated-measures binary logistic regression model in R (package 'lme4'), treating individuals as random factors (Hosmer Jr et al., 2013; Iddrisu et al., 2023). Helmert orthogonal contrasts were used to code the categorical variable representing the 50 trials, reducing the risk of multicollinearity by orthogonalizing the contrasts between different factor levels. The average coefficients and associated predictive probabilities of success ("1") for each model/group were calculated across the 50 trials and plotted together for comparison (using 'ggplot2'). The observed trends were further evaluated based on root-mean-square-error (RMSE) comparisons between the first 20 and the last 20 trials. Despite the valuable insights provided by the results of this analysis, which perfectly aligned with the findings of the simpler approach described in the paragraph above, it must be acknowledged that our small sample size does not meet the usual recommendations for binary logistic regression regarding minimum sample size (typically depending on the number of outcome "events" per predictor; e.g., see van Smeden et al., 2019).

3 | RESULTS

The following results are broken down into three subsections (one for each working hypothesis). All results and graphs mentioned in Materials and Methods that do not appear in this section are provided in Supplementary Information (SI) and referenced below. For all statistical tests, an alpha level of 0.05 was used.

3.1 | Hypothesis A

Contrary to predictions stated in hypothesis A, after removing extreme outliers in cutting success rates, no significant correlations were observed between flake cutting success rates and both pinch ($\tau = 0.05$, $p = 0.736$) and power ($\tau = 0.23$, $p = 0.140$) grip dynamometer strength tests. The same was found for the Hammerstone nut-cracking task, for both power ($\tau = 0.19$, $p = 0.174$) and pinch ($\tau = 0.19$, $p = 0.181$) grip strength. Regarding the effects of experience on tool-using success rates, our hypothesis A was only partly supported because a significant effect was only found for the cutting task (more details are provided in the subsection below and in Figures 6-7).

Secondly, in terms of experience-based variation in relative muscle recruitment (i.e., %MVC), similar patterns were found across tasks and steps. Given that the PCA plot focusing on hammerstone nut-cracking execution ("Execute") is rather representative of the consistent group distinctions found across all six PCAs, it was included in the main text of this study as an example (Figure 8). All other PCA plots can be found in the SI (Figures S1–S5). The variation in PC1 (55.94% of variance) of the hammerstone Execute step can be explained by the positive loadings of all eight muscle variables (see Table 2). PC1 clearly distinguishes the most experienced group (experts) from the intermediate and novice groups, as all participants in the expert group plot negatively on PC1 and thus show overall lower levels of muscle activation (for PCA plot, see Figure 8). This closely aligns with hypothesis A, that experienced participants will be more energy-cost-efficient than those with no practical stone tool-using experience. The other five PCAs (in SI) demonstrate similar patterns to hammerstone Execute, with PC1 indicating the differences in muscular activation between experience groups. Additionally, we confirmed that equivalent patterns were present across all steps and tasks when re-running the PCAs without adjusting the values for grip strength. Descriptive statistics (Table 3) further reflect the results of the PCA, with the expert group displaying the lowest %MVC values for most muscles throughout all steps of each task, with a few exceptions, namely for the fifth ray hypothenar muscle group (showing slightly higher values in all tasks except for flake Hold and flake Execute) and the FPL (showing a slightly higher value in hammerstone Hold).

Additionally, as explained in Materials and Methods, PC scores were extracted from the PCA, and Kendall's Tau tests were performed on each step to determine whether PC scores of individuals' eight muscular %MVC values were correlated with the level of experience. Almost all tests showed a negative value of Tau, demonstrating a negative association between experience level and PC1 scores (which represents overall relative muscle recruitment), as expected. More specifically, with the exception of the Hold step in both tasks (hammerstone Hold, $\tau = -0.27$, $p = 0.058$; flake Hold, $\tau = -0.26$, $p = 0.067$), all other steps of both tasks showed a statistically significant correlation (hammerstone Aim, $\tau = -0.31$, $p = 0.032$; hammerstone Execute, $\tau = -0.34$, $p = 0.016$; flake Aim, $\tau = -0.34$, $p = 0.016$; flake Execute, $\tau = -0.39$, $p = 0.007$). Box plots (Figure 9) depict the steps that display significant variation between experience groups (flake Aim, flake Execute, hammerstone Aim, and hammerstone Execute), demonstrating lower overall PC1 scores in experts compared to the other experience groups (as also shown in the PCA plots of Figure 8). The novice and intermediate groups consistently show higher PC scores, and a broader spreading across their group, than the experts. Finally, radar plots (Figure 10) of %MVC values (grouped by experience) were produced for all steps of both tool tasks, to further visually demonstrate what is observed in the PCA plots and the Kendall's Tau correlation tests. These plots further confirm and support the above assessments, clearly showing that most %MVC values of the expert group were consistently lower throughout all tasks, with the few exceptions described in the paragraph above.

3.2 | Hypothesis B

Based on the results of the ANOVAs, success rates were significantly different across experience groups in the flake-cutting task ($F = 4.67$, $p = 0.02$). In contrast, the nut-cracking task had no significant differences between experience groups ($F = 0.21$, $p = 0.81$). The post hoc pairwise Tukey tests showed that the expert and novice groups differed significantly, at $p = 0.035$. The subsequent ANCOVA reported the same results as above: a significant effect of experience was

TABLE 3 Descriptive statistics of the mean %MVC values and their standard deviation for each experience group, across all steps/tasks. For each step and muscle, the lowest mean value is highlighted in green. Overall, experts show consistently lower values in all muscles except the hypothenar muscle group (HTE) and the FPL (only in hammerstone Hold).

Experience level	Task/step		DI1	HTE	FCR	FCU	FPL	TE	ndDI1	ndTE
	Nut-cracking									
Novice	Hold	Mean	2.14	6.64	6.92	3.58	4.28	4.37	0.54	0.94
		SD	1.78	2.85	2.99	2.51	2.38	3.53	0.80	0.58
Intermediate		Mean	2.27	4.11	5.95	4.18	6.27	9.20	1.17	1.15
		SD	1.38	6.42	2.57	0.92	2.35	3.48	0.27	0.28
Expert		Mean	1.89	6.23	4.76	2.86	4.33	3.13	0.31	0.68
		SD	1.49	2.70	1.80	2.07	1.60	1.77	0.66	0.86
Novice	Aim	Mean	2.59	6.19	7.62	3.94	4.35	5.01	1.75	5.87
		SD	2.75	2.88	3.47	2.00	2.58	2.85	1.44	5.40
Intermediate		Mean	2.17	3.69	6.04	3.75	5.56	6.72	3.80	7.31
		SD	1.30	5.82	2.19	1.11	2.21	2.20	2.75	4.08
Expert		Mean	2.17	4.99	4.99	2.56	3.98	2.49	1.29	3.78
		SD	2.06	1.74	1.48	2.02	1.54	1.61	1.53	2.16
Novice	Execute	Mean	9.05	10.54	15.50	11.86	12.76	12.01	1.44	2.82
		SD	7.09	7.30	5.47	7.75	9.72	6.21	1.60	2.15
Intermediate		Mean	9.15	6.79	12.75	13.13	13.39	17.43	3.15	3.41
		SD	5.26	9.82	4.06	5.82	5.25	2.78	1.11	2.25
Expert		Mean	5.92	6.80	9.24	6.83	9.06	5.08	0.77	1.62
		SD	3.82	6.98	4.92	3.28	5.08	3.32	1.51	2.21
	Cutting									
Novice	Hold	Mean	1.29	2.29	3.32	1.46	1.96	3.81	0.37	0.78
		SD	1.18	1.93	1.32	0.89	1.50	2.62	0.38	0.55
Intermediate		Mean	1.40	2.38	3.16	1.69	3.16	3.90	0.54	1.36
		SD	0.50	3.21	1.91	0.93	0.89	1.04	0.46	1.00
Expert		Mean	1.19	1.65	1.88	0.99	1.78	1.43	0.32	0.30
		SD	0.77	1.44	0.78	0.53	0.71	1.67	0.53	0.40
Novice	Aim	Mean	3.16	1.70	1.66	7.96	2.99	2.00	2.36	2.14
		SD	1.83	1.31	1.09	3.98	1.23	1.38	1.31	1.87
Intermediate		Mean	2.90	1.65	1.86	11.30	2.81	3.22	3.02	2.26
		SD	1.12	0.95	1.12	0.68	1.41	0.82	1.66	2.38
Expert		Mean	1.23	1.54	0.97	3.84	1.50	1.52	1.97	1.53
		SD	1.54	0.69	0.66	3.34	0.56	0.35	2.34	0.84
Novice	Execute	Mean	12.55	11.39	6.90	14.76	7.64	8.93	5.43	5.75
		SD	9.11	7.30	3.48	10.46	2.28	4.44	4.41	4.35
Intermediate		Mean	9.34	6.77	6.07	20.87	5.98	8.81	4.81	5.49
		SD	6.01	4.09	4.43	6.34	2.82	3.43	5.86	1.26
Expert		Mean	6.02	10.07	5.70	7.94	4.74	8.63	4.30	2.58
		SD	5.00	2.79	2.34	10.74	1.52	5.57	2.54	3.28

observed on flake success rates, after controlling for pinch grip strength ($F(2, 17) = 3.95$, $p = 0.039$), while no significant effect was observed on hammerstone success rate, after controlling for power grip strength ($F(2, 21) = 0.07$ $p = 0.933$). Figure 6 displays the success rates of both tasks, against pinch and power grip strength, highlighting clear differences between the tool tasks.

3.3 | Hypothesis C

The line graphs in Figure 7 represent how average success rates varied across the three experience groups over 50 consequent trials, demonstrating starkly different results between the two experimental tasks. Success in the cutting task is distinctively different across

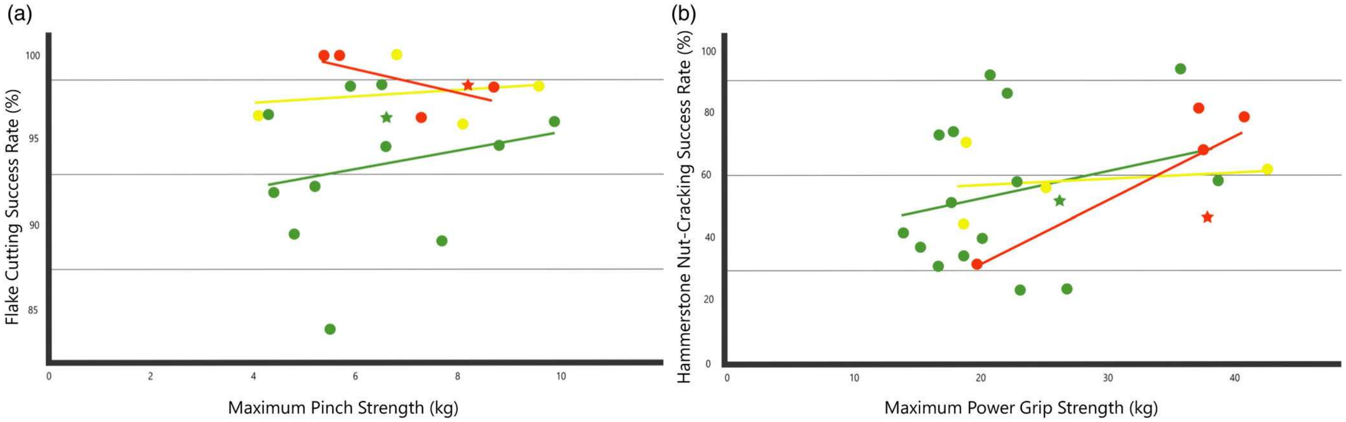

FIGURE 6 Success rates in tool-using tasks. (Green = Novice; Yellow = Intermediate; Red = Expert). Left-handed participants are indicated with a star symbol. The graph displays the success rates (in percentage) in the flake cutting (a) and hammerstone nut-cracking (b) tasks, plotted against the associated (pinch and power) grip strength of each participant. This graph highlights the clear difference between the experience groups in flake cutting and their extensive overlapping in the hammerstone nut-cracking task. This plot also highlights that strength is not the driving determining factor of success.

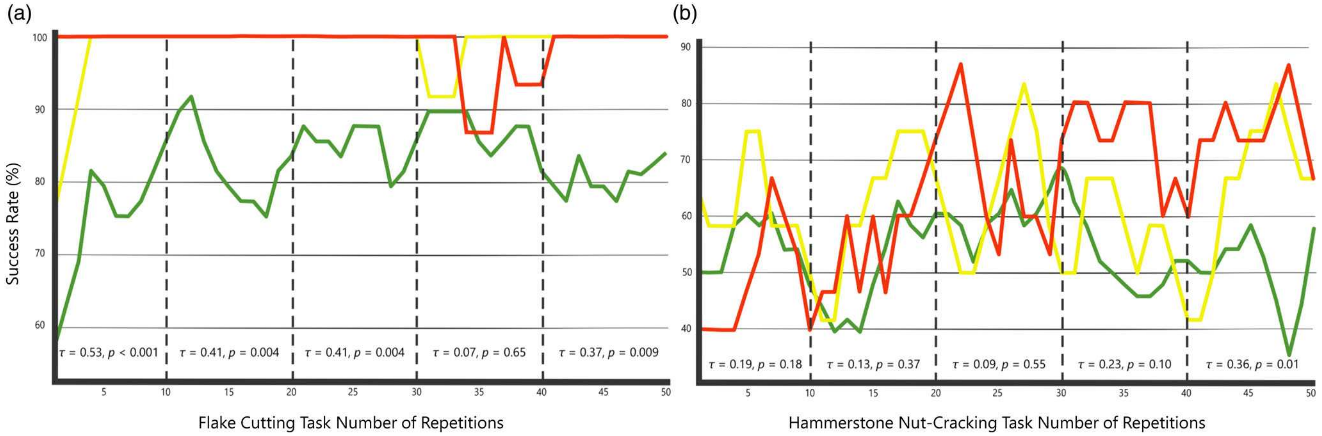

FIGURE 7 Line graphs of successes and failures by experience group (Green = Novice; Yellow = Intermediate; Red = Expert). The Y-axis demonstrates each experience group's average percentage of success for each repetition. The graph representing the flake cutting task (a) demonstrates the consistently higher mean success rate of the intermediate and expert groups across repetitions. The hammerstone nut-cracking task (b) shows a more complex pattern, with all three experience groups varying in their success. However, a distinct improvement can be seen around the 30th repetition, where the expert and novice groups begin to split. Dotted lines indicate repetition segments (the five "repetition sets") and the output of a Kendall's Tau test is reported for each set.

experience groups, with both the expert and intermediate groups consistently performing with higher success, compared to the novice group. However, in the nut-cracking task, there is much more variability observed throughout the repetitions. Success rates at the start of the task show a certain degree of randomness, with all three groups varying in their success rate. Nevertheless, from around the 30th repetition, the expert and the novice groups clearly begin to deviate from one another. Experts tend to become more consistently successful, while there is no visual improvement witnessed in the novice group. This trend is also reflected in the results of our correlation tests (shown for each repetition set within Figure 7), which indicated a significant association between experience level and success in four of the five cutting repetition sets, but only found such a correlation in the final nut-cracking repetition set (i.e., the last 10 repetitions). It should be noted, however, that the Tau coefficient indicates a moderate positive association (based on Kendall, 1938; Khamis, 2008). Taken together, while success in the nut-cracking task did not show to be significantly correlated with experience when analyzed holistically (see Figure 6), the last 10 repetitions show a statistically significant positive correlation between nut-cracking success rate and experience ($\tau = 0.36$, $p = 0.01$). In contrast, all except one of the five cutting task repetition sets were significantly correlated with experience, as expected.

These findings were also corroborated by our generalized linear models (i.e., the three repeated-measures binary logistic regression models). Figure S6 presents the average predicted probabilities of success ("1") for each experience group/model across the 50 nut-cracking trials, also providing the RMSE values of each logistic regression model for the first 20 versus the last 20 repetitions. The model representing the experienced knappers shows a decrease in error ("0") of 54.4% (from 0.51 to 0.29), whereas the other two experience groups show minuscule changes (0.2% and 1.8%, respectively).

4 | DISCUSSION

The overarching aim of this experimental study was to explore the factors affecting efficiency in early hominin stone tool use. First, we hypothesized that participants with extensive theoretical and practical experience and/or higher overall grip strength would be more efficient, both ergonomically and in terms of success, during both stone tool tasks, compared to those without experience or lower grip strength. Our results only partly confirmed this hypothesis (A). They showed that experience was a key factor in the successful completion of the flake cutting task, while this pattern was not observed for the hammerstone nut-cracking task. Importantly, in both tasks, expert knappers showed consistently lower effort (%MVC) in almost all muscles (Table 3, Figure 8, and Figures S1–S5). Interestingly, the muscles not exhibiting this trend for all steps/tasks (Table 3) were the hypothenar eminence and the FPL (in hammerstone Hold). The particular importance of these muscles for human-like tool use has been repeatedly highlighted in previous anthropological and experimental studies (e.g., Karakostis et al., 2018; Key et al., 2019; Kivell, 2015; 2023; Kunze et al., 2022; Marzke, 1997; Marzke et al., 1998), especially considering the FPL's absence in non-human primates and its apparent occurrence (based on muscle attachment morphology) in the earliest proposed tool-using hominins (e.g., Dunmore et al., 2023; Karakostis et al., 2021; Kunze et al., 2022). On this basis, the similar recruitment of these particular muscles between novices and experts in some steps/tasks might perhaps reflect the broader evolutionary importance of these muscles for general human-like manipulation, regardless of expertise.

Our second hypothesis (B) delved deeper into the differences expected between the two tasks, flake cutting and hammerstone nut-cracking. We expected that precise flake cutting efficiency may bear more dependence on stone tool-related experience compared to nut-cracking. In contrast, participants with higher grip strength were expected to have better efficiency in the hammerstone nut-cracking task. However, we found that only experience was shown to significantly influence flake cutting success, whereas no correlations with either strength or experience were found for the hammerstone nut-cracking task. In the latter, experts plotted similarly with both the intermediate and novice groups, demonstrating no significant differences in performance between the groups. Additionally, success rates did not significantly correlate with strength, indicating that the higher success frequency of the expert group in cutting was not due to increased grip strength (as shown in Figure 6). Altogether, these findings indicate that successful hammerstone nut-cracking may not be as

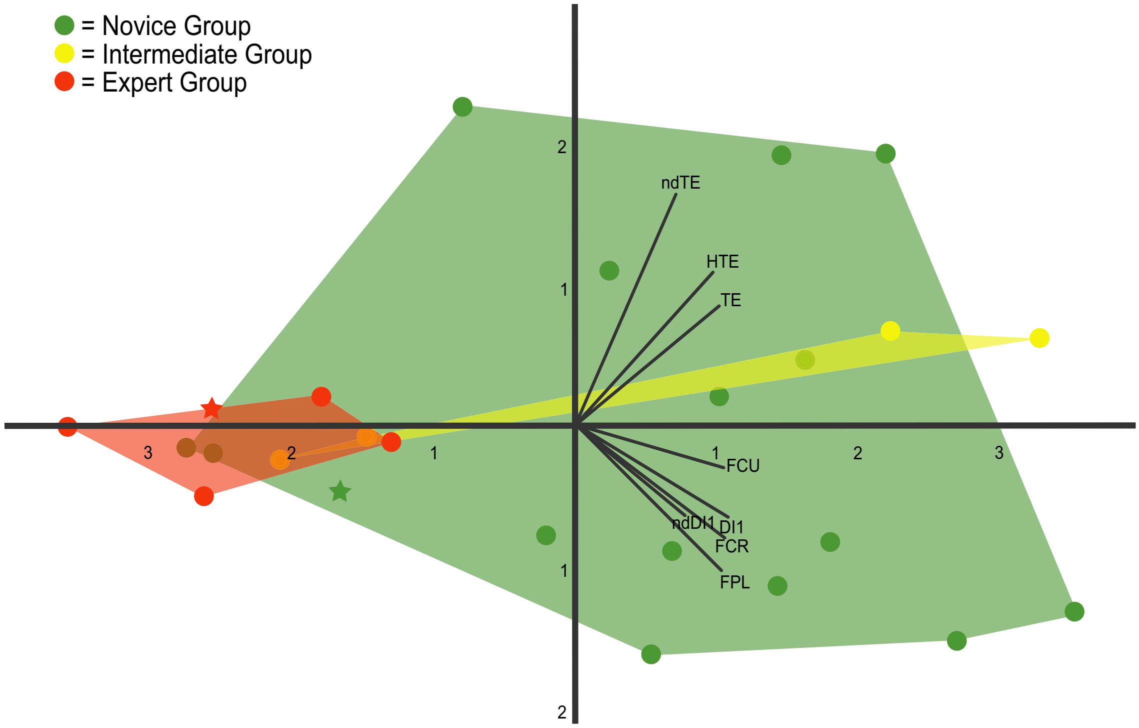

FIGURE 8 PCA plot (PC1 and PC2) summarizing muscle recruitment during the hammerstone nut-cracking Execute step, relying on values adjusted for participant grip strength. Individuals are color-labeled by experience level (Green = Novice; Yellow = Intermediate; Red = Expert). Left-handed participants are indicated with a star symbol. PC1 (55.94% of variance) clearly distinguishes the expert group from the novice group, with experts exhibiting far less muscular activation across all eight muscles.

dependent on experience as precise flake cutting is, suggesting that an increased ability to accumulate theoretical and practical know-how may have substantially benefited the successful performance of precise-grasping cutting activities in our evolutionary history.

Leading on from this, despite no significant correlation being found between hammerstone nut-cracking success and expertise overall, our hypothesis C did expect experts to show improvement rates higher than participants without stone tool-related experience. In the case of nut-cracking, this expectation is partly based on several accounts of the similarities observed between flake knapping and pounding techniques (Boesch & Boesch, 1993; Davidson & McGrew, 2005; Sugiyama & Koman, 1979). Our results confirmed this hypothesis, as experts displayed a gradual improvement during the last 20 repetitions of the hammerstone task, leading the last 10 repetitions to significantly (albeit moderately) correlate with the level of experience (Figures 7 and S6). Aligned with previous research by Bril et al. (2015) suggesting an ergonomic similarity between hammerstone nut-cracking and Oldowan flake knapping, we propose that the observed improvement in the expert group could likely be due to their extensive experience in stone tool production (knapping) bearing similarities to the hammerstone nut-cracking task. Furthermore, the immediately high flake-cutting success rates of participants with either practical and/or theoretical experience (Figure 7) suggest that stone tool knowledge allows quick comprehension of a non-familiar flake-cutting task at hand, without necessitating considerable trial and error.

4.1 | Comparisons with previous studies on efficiency

Our working hypotheses were addressed based on several aspects (proxies) of efficiency, which is broadly defined as the ability to perform a task without wasting materials, energy, and time. A commonly used measurement of efficiency involves the time taken to perform a task (e.g., Key & Lycett, 2014, 2018; Machin et al., 2007) or the total number of tries needed to carry it out (Key & Lycett, 2014). In this study, we focused on certain direct measures of tool-using efficiency that were often not considered in previous studies. In particular, by analyzing the muscular activation of all participants, we directly address the energy component of efficiency. Such an approach has previously been successfully employed in several studies aiming to understand the ergonomic and muscular requirements in lithic production and use (Hamrick et al., 1998; Key et al., 2020; Marzke et al., 1998). In the present study, participants were also asked to carry out the task within specific time intervals (see Materials and Methods), a design that enabled direct compatibility across individuals, tasks, and repetitions. Moreover, due to the increased number of repetitions (50) in this experiment, we were able to analyze improvement rates in the same step/task over time (thus being able to assess potential self-improvement per participant and experience level).

Our study also investigated whether certain biometric variables could be correlated to efficiency, as previous studies have reported. Key and Lycett (2018) reported that both hand size and grip strength were significant predictors of efficiency in stone tool use (Key & Lycett, 2018). Additionally, Rolian et al. (2011) found that individuals with longer thumbs and index fingers incurred relatively less muscular force and stress during stone tool use (Rolian et al., 2011). Our results did not show such an influence of grip strength on cutting efficiency, potentially due to the much greater impact of experience in this task. Additionally, Bril et al. (2015) reported that experienced participants performed better in both the hammerstone nut-cracking and Oldowan flake production tasks. Notably, even though our results did not show a significant effect of experience on nut-cracking, we did find significant improvement rates in experts toward the end of the nut-cracking task (last 10 repetitions; see Figure 7).

4.2 | Evolutionary implications of stone tool-using "know-how"

Several previous studies reported a significant effect of tool-related experience on efficiency, even when comparing experts to novice individuals who underwent basic training (Bril et al., 2012; Nonaka et al., 2010; Pargeter et al., 2020). While this is not entirely surprising, given that experts have undergone many years of practical training, comparing theoretical stone tool-related knowledge and practical "know-how" is under-researched within stone tool use (Bril, 2023). Snyder et al. (2022) categorized naïve participants into various naivety levels, including individuals with no knowledge of stone tools, those who had only "heard of" and "seen" stone tool use and knapping, and participants with "hands-on knapping experience". Regardless of experience, all participants successfully re-innovated knapping techniques (Snyder et al., 2022). Therefore, considering the results of that previous study on early stone tool knapping techniques, one would expect that our analyses would find that novice and expert individuals in this experiment might show similar efficiency trends. In terms of overall success rates alone, that was indeed the case for the nut-cracking task (but not for flake-cutting). Nevertheless, the intermediate group (i.e., participants with only theoretical experience in stone tool production and use) showed similar overall muscle activation levels to the novice participants, throughout both tasks. The experts (i.e., participants with practical expertise) were the only group with significantly lower overall muscular activation (Figure 9). Notably, this is despite the relatively high success rates of the intermediate group (compared to novices) in the cutting task. These trends highlight practical "know-how" as a key factor in consistent and improved early stone tool use efficiency, suggesting that practically experienced individuals have a clear advantage in understanding how much force is required to perform the task, without the expenditure of excessive energy, a trend that is not witnessed in the intermediate ("theoretical") group. These findings raise the possibility that an increased hominin ability to accumulate practical skill via 'trial and error' likely played a fundamental role in the energy-efficient use of early stone tools.

Furthermore, our results addressing the final hypothesis showed that stone tool "know-how" allowed experienced participants to self-learn less familiar tool-using tasks faster. In particular, the experts'

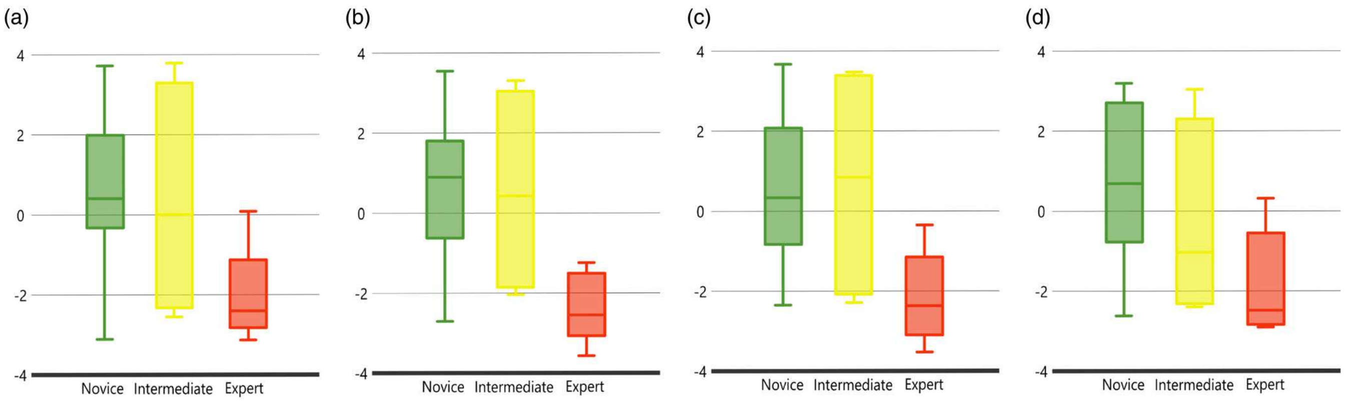

FIGURE 9 Boxplots of PC1 scores from the Aim and Execute steps of both tasks: (a) hammerstone Aim; (b) hammerstone Execute; (c) flake Aim; (d) flake Execute. These plots underline the substantial variation by experience (green = Novice; yellow = Intermediate, red = Expert) across steps. The experts' PC scores are consistently negative, reflecting relatively less muscular activation.

results allude to an ability to transfer their knapping skills to hammerstone nut-cracking faster than novice individuals. Their technical expertise likely assisted them in several aspects of nut-cracking, including experience in the calculation of necessary force (depending on the target material used), angle of blow, grasping pattern, aim, and muscle memory. This improvement within experts is also witnessed in Bril et al.'s nut-cracking and Oldowan flake knapping study (Bril et al., 2015), which reported that 100% of the experts successfully performed the nut-cracking task (same requirements for success were set in this study). Overall, these results raise the possibility that an evolved ability to self-learn through trial and error may have formed the basis for tool-using innovations that gradually led to the invention of more complex lithic technologies and refined subsistence strategies in hominins.

4.3 | Limitations and future possibilities

Due to the constraints of experimental research relying on living participants, it has to be underlined that, while many fossil hominins display fundamental similarities in their limb anatomy with modern humans, the various important differences in ergonomic requirements and morphology are still expected to affect manipulation patterns (e.g., Karakostis et al., 2021; Key et al., 2020; Kivell, 2015; Kunze et al., 2022; Marzke, 2013; Ricklan, 1987). Regardless of this bias, it is still reasonable to expect that the use of flake tools likely required similar precision grasping patterns, at least in hominin species (Napier, 1956 and 1962; Susman, 1991) that display several key human-like adaptations (e.g., a proportionally longer thumb; see Almécija et al., 2015; Kivell, 2015). Therefore, modern humans remain the best substitute for experimental studies such as this. Furthermore, it should be acknowledged that certain key anatomical differences between humans and non-human great apes (e.g., the absence of an FPL) prevent us from directly comparing this study's sEMG results to the hammerstone-pounding behaviors of non-human primates (from a biomechanical perspective of muscle coordination).

It is also important to note that, despite our best efforts to monitor muscles with special importance for lithic production and use, the chosen muscles are only a subset of all those involved in such manual activities. Additionally, sEMG is only applicable to superficial muscles. While the selection of muscles was based on previous studies' results and conclusions (e.g., Hamrick et al., 1998; Key et al., 2020; Marzke et al., 1998), additional muscles in the forearm and hand (both dominant and non-dominant) play an undoubtedly crucial role in human-like stone tool use. Nevertheless, it is worth noting that using an excess of electrodes can be technically problematic for practical reasons, as it can create difficulties in ensuring electrodes are monitoring the correct muscles intended. Second, the use of additional electrodes may also result in an excess of wires attached to the participant, increasing the chances of motion artifacts, and hindering the participants' natural range of motion.

Beyond the above limitations, this study poses several ideas for future possibilities. Of great importance is the continued development and application of this study's approach to other stone tool industries in the fossil hominin record. This could also be combined with comparisons of uni- versus bi-manual hammerstone pounding activities, considering that the latter are also observed in certain extant primate species (e.g., capuchins; see Falótico & Ottoni, 2016; Fragaszy et al., 2020). This is especially relevant given that Harmand et al. (2015) have suggested that Lomekwian hammerstones were likely wielded with both hands to strike against a stationary core resting on an anvil, based on replication experiments. Furthermore, in the future, we aim to integrate our sEMG analyses with synchronous recordings of brain activation patterns during stone tool use (e.g., via electroencephalography), which could potentially provide a basis to further explore cognitive aspects of efficiency in early stone tool use. Moreover, although we included two left-handed participants in this study, further work on the differences observed with hand preference could be developed in the future, based on a larger sample size of left-handed participants. Finally, our extensive sEMG recordings, which pinpoint the exact muscles and grips recruited during human hammerstone nut-cracking and flake-cutting activities (and their various

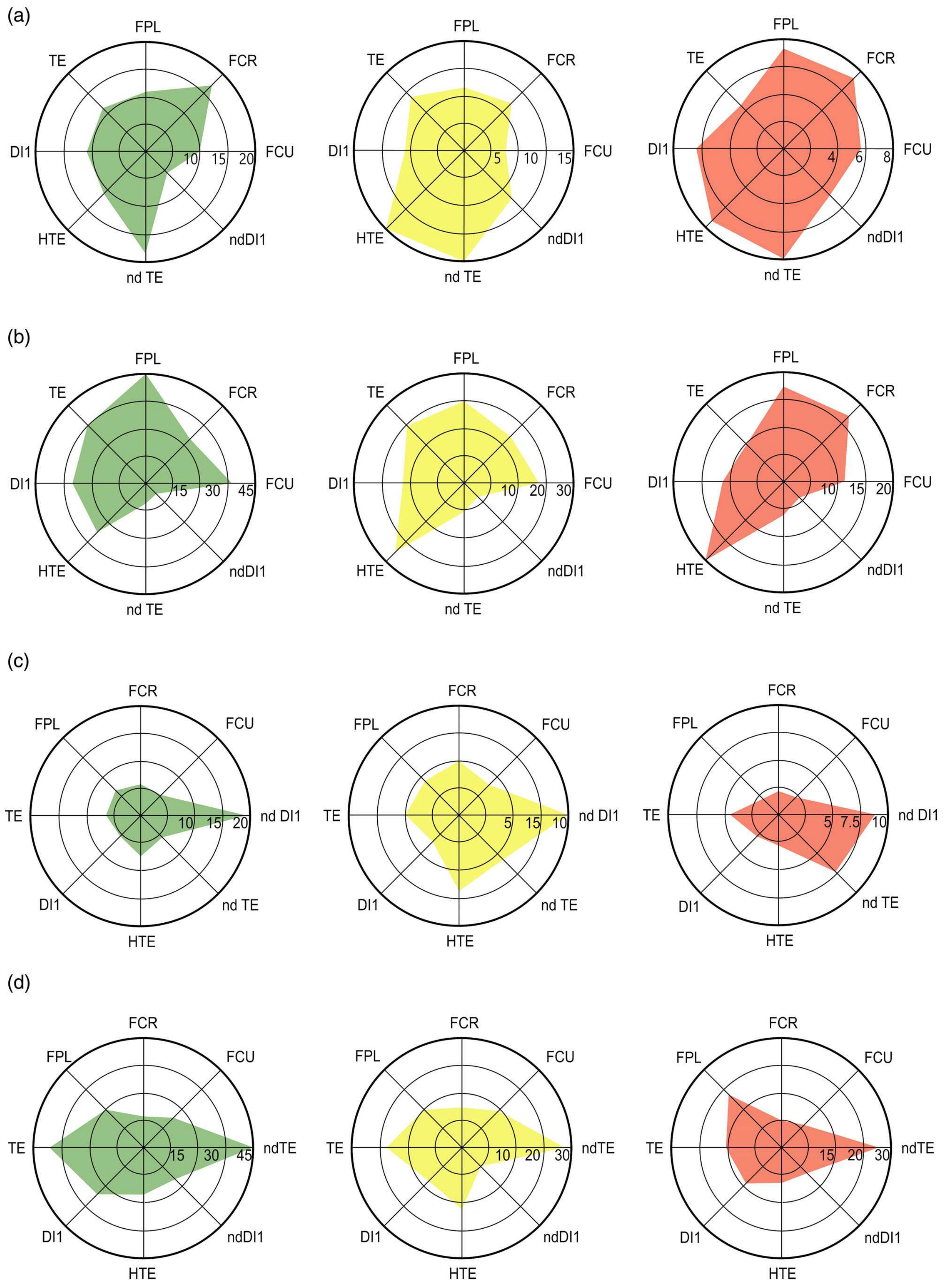

FIGURE 10 Radar Plots of %MVC values in action steps that showed significant differences by experience level: (a) hammerstone Aim; (b) hammerstone Execute; (c) flake Aim; (d) flake Execute. (Green = Novice; Yellow = Intermediate; Red = Experts). Radii values differ across plots (%).

steps), can contribute to developing more robust biomechanical hypotheses when reconstructing habitual manual activity or evolved dexterity in fossil hominins (e.g., Karakostis, 2024).

5 | CONCLUSION

Overall, this experimental study showed that practical "know-how" had the greatest influence on the efficient use of the earliest known cutting tools (flakes), a behavior that has been exclusively associated with hominins. In precise flake cutting, individuals experienced in stone tool production achieved higher overall success rates and improved ergonomic efficiency (less relative muscle recruitment). In line with our hypotheses, the flake-cutting task differed from its proposed predecessor (hammerstone nut-cracking), in which experts and novices showed similar overall success rates. Nevertheless, significant differences were observed in the rate of improvement over the last 10 repetitions. This suggests that experts with relevant skill sets were able to improve (i.e., "self-learn") in a less familiar task faster than those without. In our evolutionary history, such an ability to retain and accumulate practical knowledge likely facilitated the transfer of skills from one manual activity to another. This adaptability would have enabled early hominins to innovate in reproducing and developing stone tools, leading to the gradual diversification and sophistication of stone tool industries. Finally, the intentional production of a tool requires prior technical knowledge of its function and successful use. Considering also the results of a recent study on macaques that question the initial intentionality of hominin stone tool knapping (Proffitt et al., 2023), we propose that cumulative experience in efficient tool use (cutting) may have likely preceded the first intentional production of human-like stone tools (cutting flakes).

AUTHOR CONTRIBUTIONS

Brienna Eteson: Conceptualization (equal); formal analysis (lead); investigation (lead); methodology (lead); software (lead); validation (lead); visualization (lead); writing – original draft (lead). **Simona Affinito:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); validation (equal). **Elena T. Moos:** Formal analysis (supporting); investigation (supporting); methodology (supporting); resources (supporting); validation (supporting). **Fotios Alexandros Karakostis:** Conceptualization (lead); data curation (lead); investigation (equal); methodology (supporting); project administration (lead); resources (lead); software (equal); supervision (lead); validation (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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ENDNOTES

[1] It is worth highlighting that, in some non-human primate species, hammerstone pounding is performed bi-manually (Falótico & Ottoni, 2016; Fragaszy et al., 2020). Nevertheless, one-handed grips are typically observed in chimpanzee and macaque populations (Arroyo et al., 2016; Proffitt et al., 2023), as well as in experimental studies of hammerstone nut-cracking in humans (Bril et al., 2015).

[2] The status of the Lomekwian industry has faced controversy based on claims that the tools may not have been found in situ, casting doubt on their dating (Domínguez-Rodrigo & Alcalá, 2016), while authors of the paper propose that the discovery of Lomekwi 3 was found in spatio-temporal association with Pliocene hominin fossils, making them the oldest stone tools discovered to date (Harmand et al., 2015).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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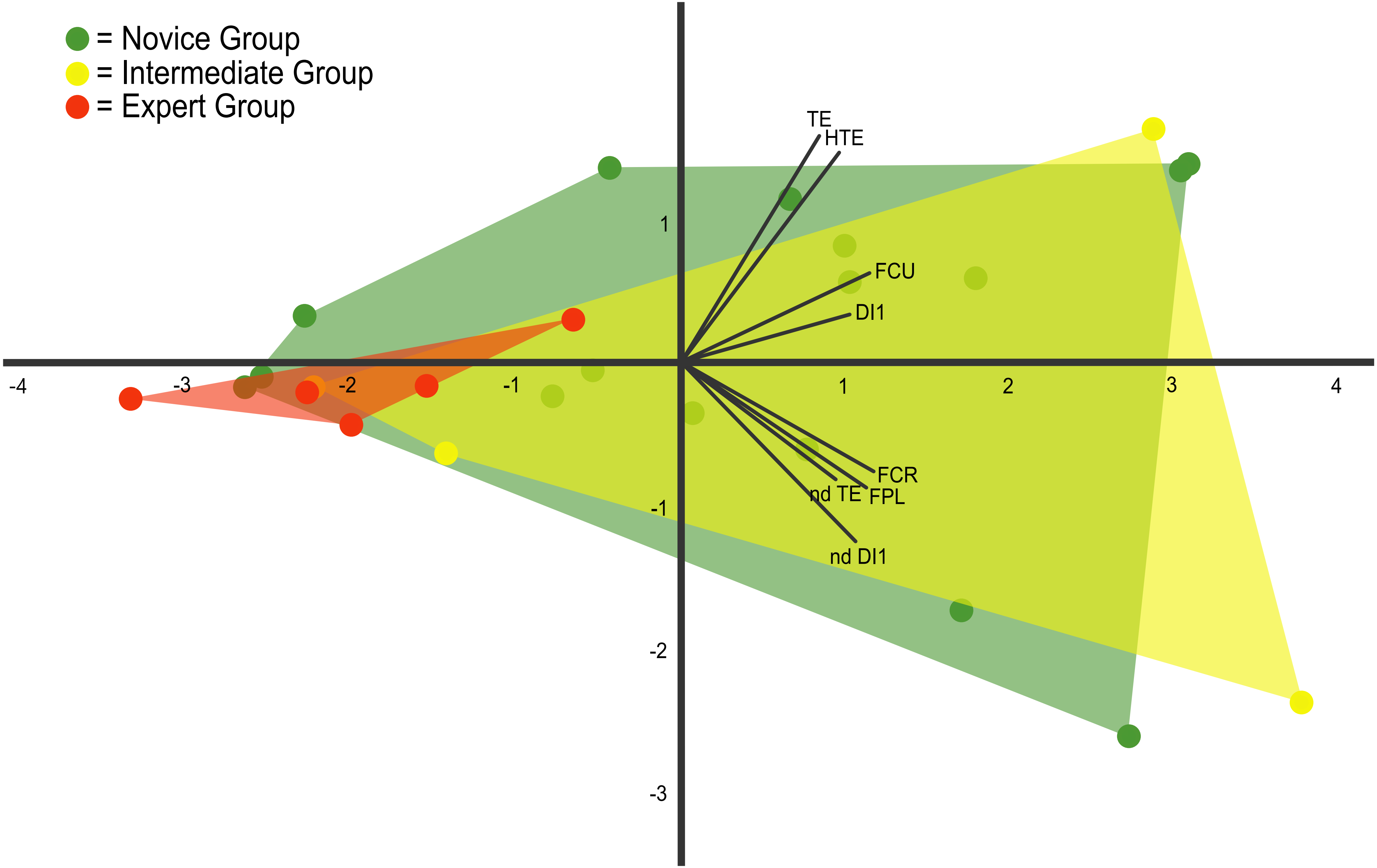
Supporting Information

Filename	Description
ajpa25019-sup-0001-FigureS1.pdfPDF document, 26 KB	**Figure S1.** PCA plot (PC1 and PC2) summarizing muscle recruitment during flake cutting Hold (size-adjusted on strength). Individuals are color-labeled by experience level. (Green = Novice; Yellow = Intermediate; Red = Expert).
ajpa25019-sup-0002-FigureS2.pdfPDF document, 26.2 KB	**Figure S2.** PCA plot (PC1 and PC2) summarizing muscle recruitment during flake cutting Aim (size-adjusted on strength). Individuals are color-labeled by experience level. (Green = Novice; Yellow = Intermediate; Red = Expert).
ajpa25019-sup-0003-FigureS3.pdfPDF document, 21.4 KB	**Figure S3.** PCA plot (PC1 and PC2) summarizing muscle recruitment during flake cutting Execute (size-adjusted on strength). Individuals are color-labeled by experience level. (Green = Novice; Yellow = Intermediate; Red = Expert).
ajpa25019-sup-0004-FigureS4.pdfPDF document, 21.4 KB	**Figure S4.** PCA plot (PC1 and PC2) summarizing muscle recruitment during hammerstone nut-cracking Hold (size-adjusted on strength). Individuals are color-labeled by experience level. (Green = Novice; Yellow = Intermediate; Red = Expert).
ajpa25019-sup-0005-FigureS5.pdfPDF document, 21.4 KB	**Figure S5.** PCA plot (PC1 and PC2) summarizing muscle recruitment during hammerstone nut-cracking Aim (size-adjusted on strength). Individuals are color-labeled by experience level. (Green = Novice; Yellow = Intermediate; Red = Expert).
ajpa25019-sup-0006-FigureS6.pdfPDF document, 224.3 KB	**Figure S6.** Graph showing the average predicted probabilities of success for each of the three experience groups across the 50 nut-cracking trials (“repetitions”), based on three repeated measures binary logistic regression models. The lower part of the figure presents the root-mean square-error (RMSE) values for each model/group in the first 20 versus the last 20 repetitions. Experienced knappers show an error decrease of 54.4%, whereas the change in the other groups is not considerable.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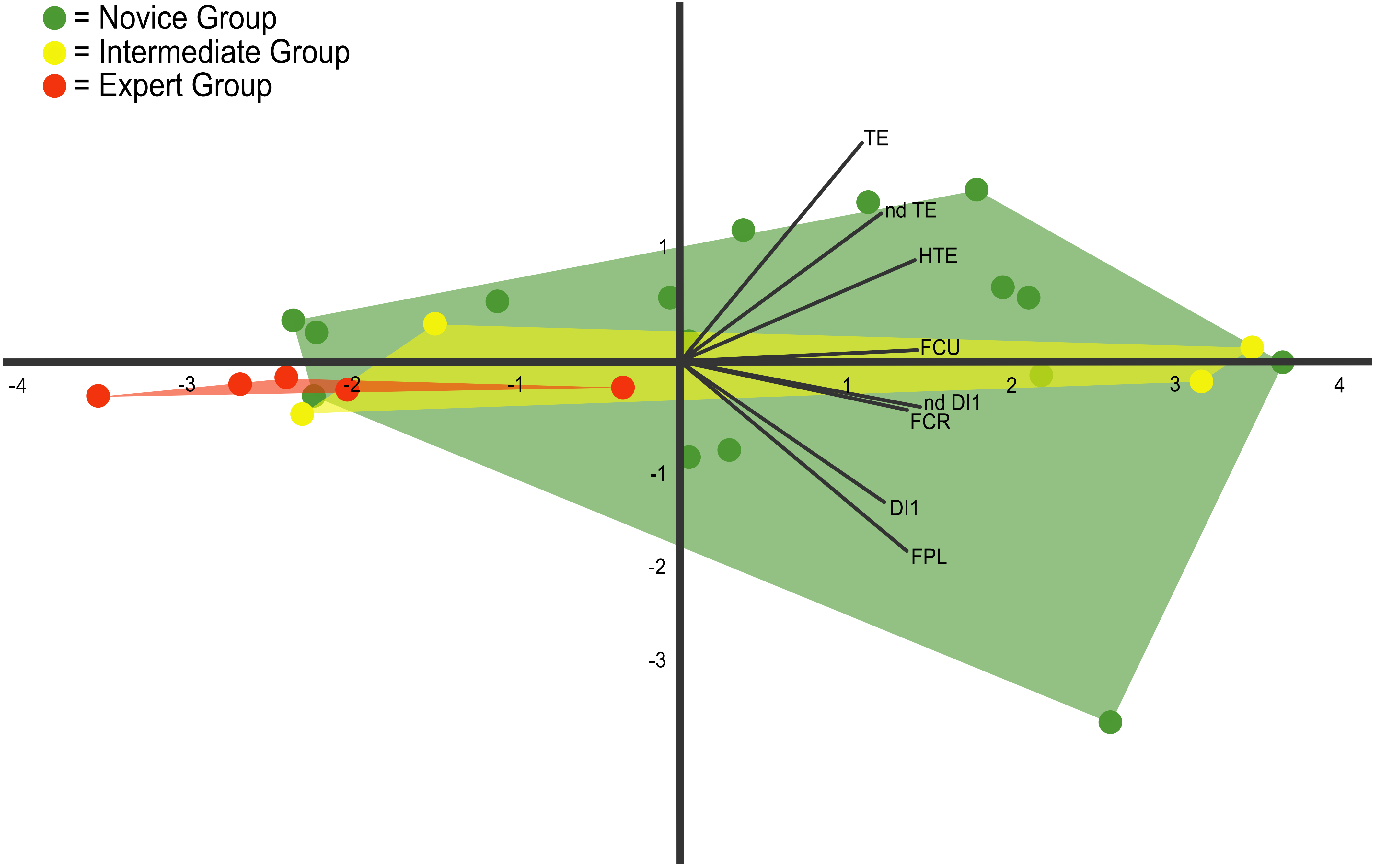
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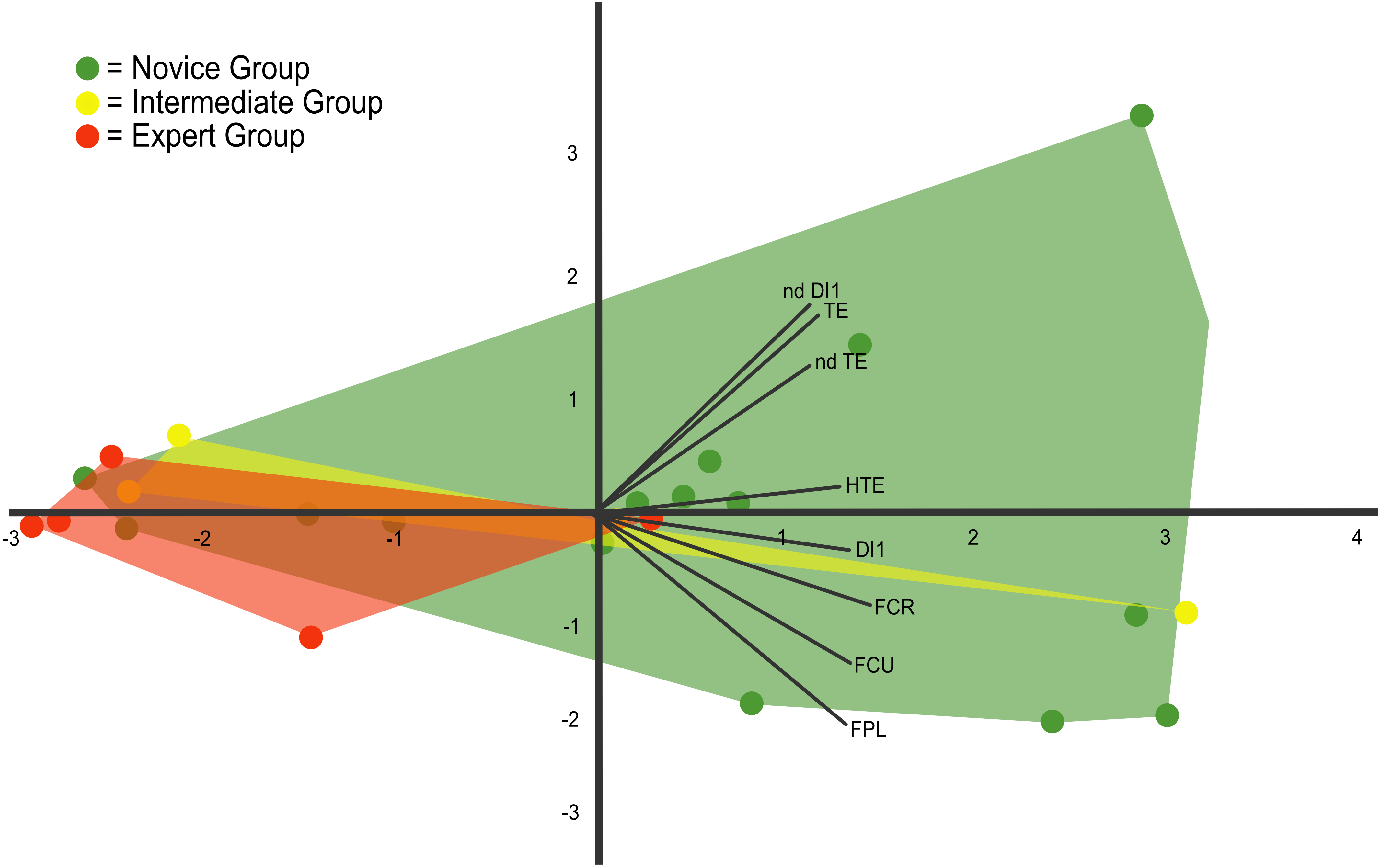
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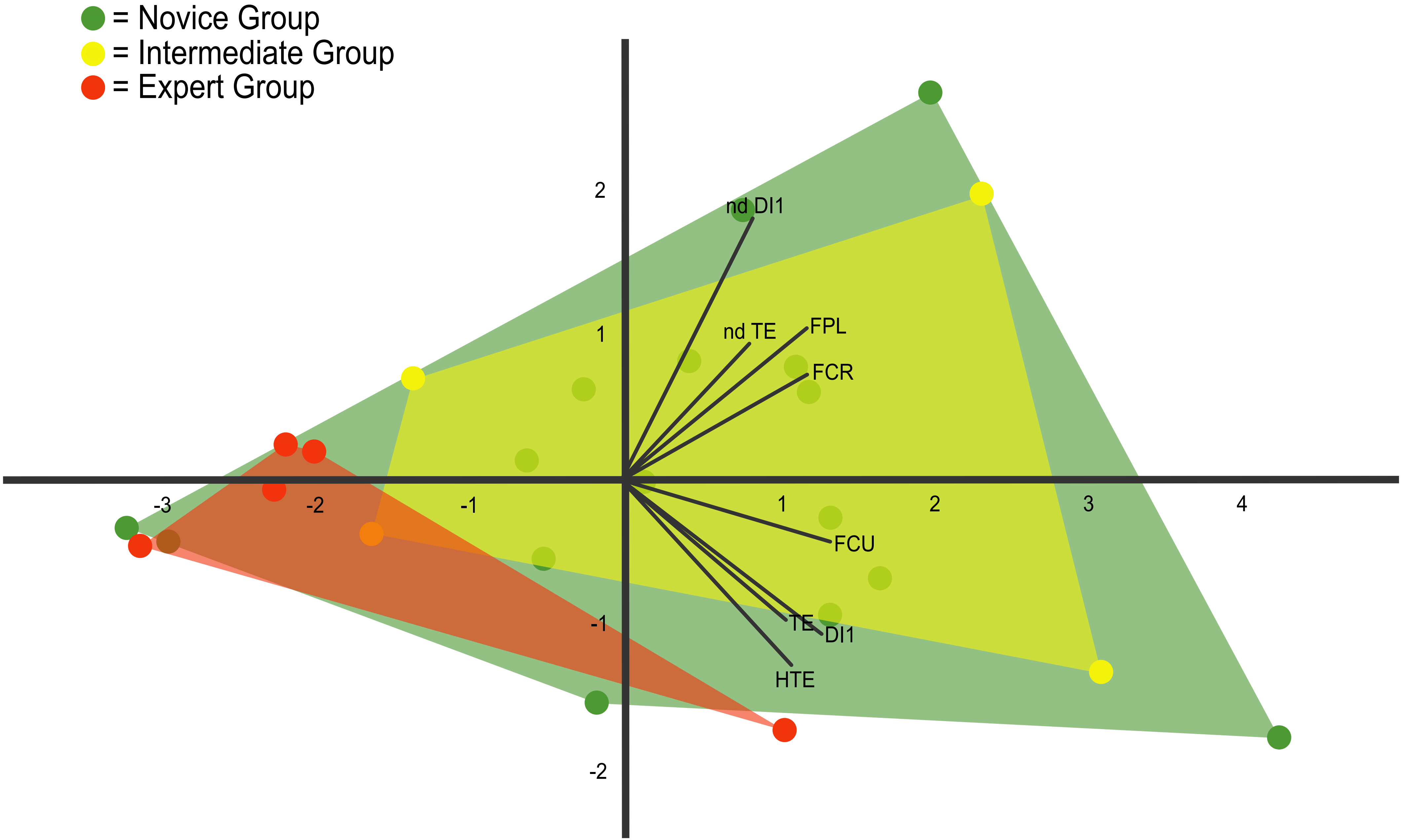
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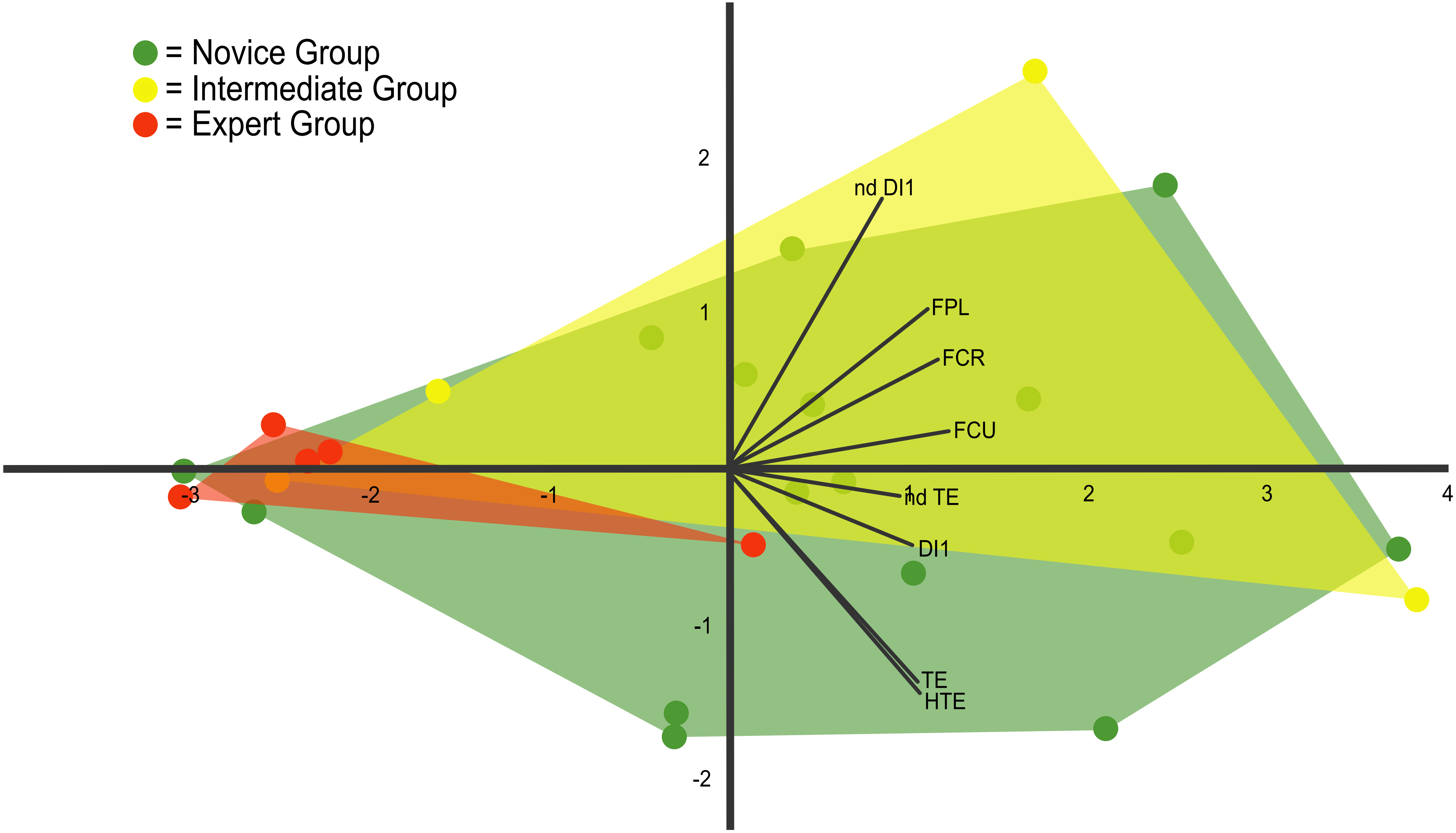
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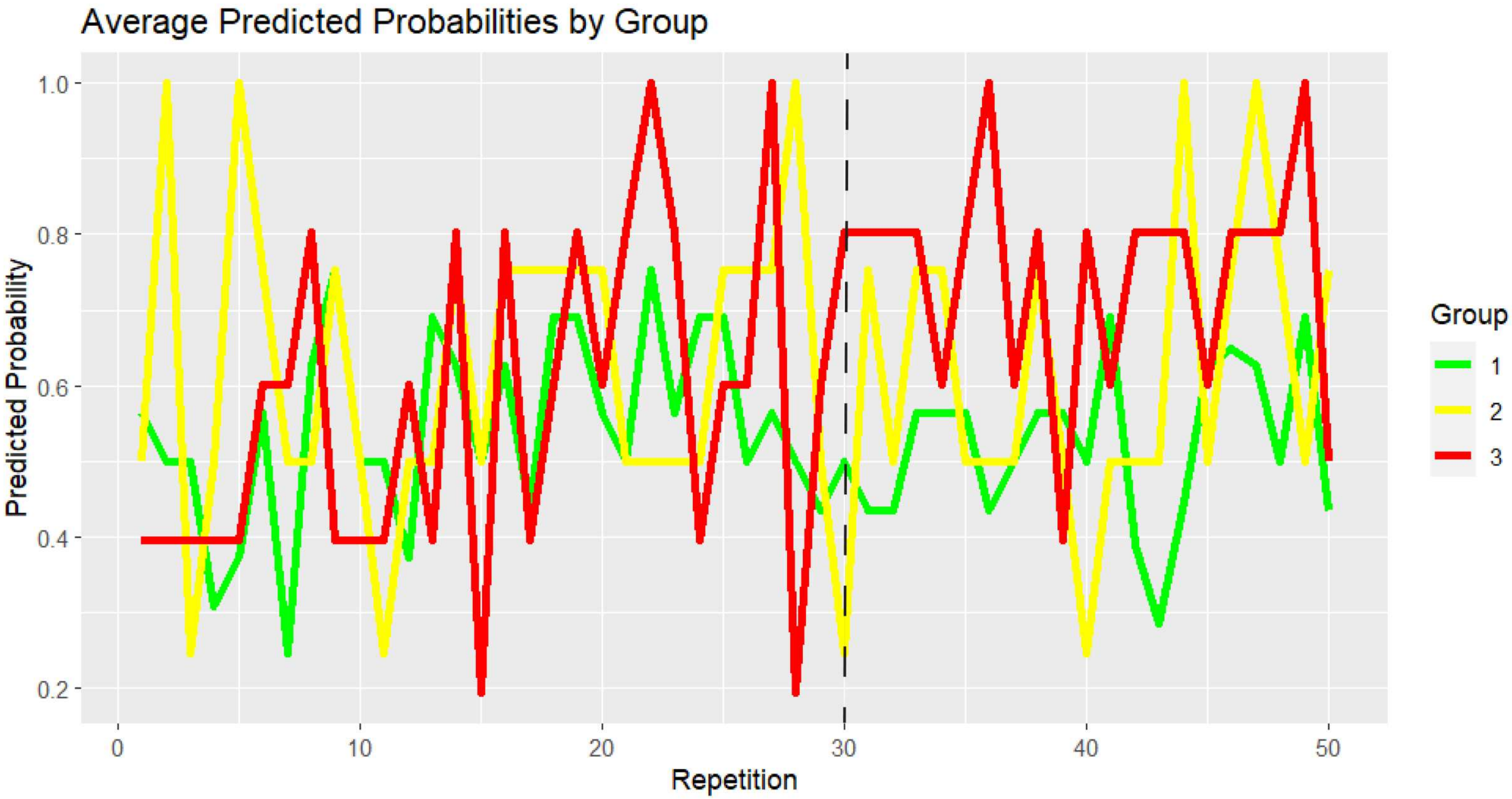

RMSE:
Novice: 0.487
Intermediate: 0.426
Expert: 0.512

→

RMSE:
Novice: 0.488
Intermediate: 0.419
Expert: 0.293

APPENDIX C

Mind Over Muscle: Neural and Biomechanical Signatures of Expertise in Early Stone Tool Use

Neuromechanical Signatures of Expertise in Early Stone Tool Use

By Brienna Eteson, Simona Affinito, and Fotios Alexandros Karakostis

Manuscript under submission

Mind Over Muscle: Neural and Biomechanical Signatures of Expertise in Early Stone Tool Use

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Abstract

Understanding the cognitive and biomechanical foundations of early hominin tool use remains a central focus in human evolutionary research. Although interdisciplinary work on early lithic technologies has explored each of these aspects separately, few experimental approaches have directly examined the interaction between neural and muscular systems during stone tool production and/or use. This study adopts a recently developed interdisciplinary approach to explore the impact of cumulative tool-related expertise on the dynamic brain-body interplay required for early hominin stone tool use. Our experimental design compares Experts (with extensive practical knapping experience), Intermediates (with only theoretical knowledge), and Novices (with neither) performing two of the earliest known stone tool behaviors in the fossil record: hammerstone nut-cracking and Oldowan-style flake cutting. Using simultaneous EEG and sEMG recordings, we analyzed neural activity in the left-frontal, premotor/motor, and left-parietal cortices alongside muscular activation in the hands and forearms. Results show that, during flake cutting, Experts display distinct beta-band neural activity in the left frontal and premotor/motor regions, and to a lesser extent in the left parietal region, accompanied by reduced muscular activation. In the nut-cracking task, Experts show reduced muscular effort and slightly elevated premotor/motor involvement, though to a much lesser degree. Importantly, Experts also present significant neural differences between tasks, suggesting task-specific cognitive strategies related to motor planning and coordination. In contrast, Novice participants demonstrate greater reliance on higher muscular effort and left-lateralized parietal regions, likely reflecting increased engagement of visuospatial processing and understanding tool function and mechanical knowledge. Altogether, these findings underscore the intertwined nature of cognition and biomechanics in humanlike stone tool use and highlight cumulative practical knowledge as a driving force in early hominin behavioral evolution. They also encourage future experimental research on increased sample sizes to adopt integrated methods that jointly consider neural and muscular dynamics, to evaluate tool-using efficiency more holistically.

Keywords electroencephalography (EEG); electromyography (EMG); stone tool use; hominin behavior; experimental neuroarchaeology expertise

1. Introduction

As an integral part of hominin life, tools have enabled us to interact with nature in ways that would be otherwise impossible (Ambrose, 2001). The emergence of stone tool production and use appears to have coincided with other traits unique to the genus *Homo*, such as encephalization and restructuring of the brain (Stout et al., 2008). Over the past two decades, research has increasingly focused on the cognitive and biomechanical demands necessary to produce and use lithic technology (Hamrick et al., 1998; Key et al., 2020; Macchi et al., 2021; Marzke et al., 1998; Putt, Wijeakumar, and Spencer, 2019; Stout et al., 2000, 2015). As one of the oldest known hominin tool industries, the Oldowan has remained a central focus of this line of research (Ambrose, 2001; Faisal et al., 2010; Morgan et al., 2015; Plummer et al., 2023; Semaw, 2006) since its original discovery and first formal description in 1934 (Leakey, 1934; see de la Torre, 2011). Studying its characteristics and behavioural implications has become integral to understanding more about hominin evolution, enriching our hypotheses on the implications of brain reorganisation and encephalization, settlement in a range of environments, precise tool production and modification, and material transportation and selection (Toth and Schick, 2018).

Until recently, the field of experimental neuroarchaeology has predominantly focused on the production of stone tools rather than their use (Putt, Wijeakumar, and Spencer, 2019; Stout et al., 2000, 2015), leaving an important aspect of hominin lithic behavior (i.e., its practical function and utility) less thoroughly explored. Additionally, recent research on capuchin monkeys unintentionally producing Oldowan-like flaked tools (Proffitt et al., 2016, 2023) offers valuable insights. Proffitt and colleagues propose that some early stone flakes may not have been intentionally crafted as sharp cutting tools initially but rather originated as byproducts or waste from other tool-related activities, such as nut-cracking, which were subsequently recognized and deliberately replicated. This perspective complements the idea that the earliest cutting tools could have emerged gradually as a secondary outcome of other behaviors like hammerstone pounding, which is a practice documented among early hominins as well as some non-human primates (Arroyo et al., 2020; de la Torre et al., 2013; Goren-Inbar et al., 2002).

However, hammerstone pounding (observed in various primate species) differs markedly from Oldowan-style flake cutting, which has not been observed in non-human primates in the wild. Namely, these activities require different grip types and levels of force to perform such tool use tasks (Eteson et al., 2024), with hammerstone pounding typically recruiting a spherical power grasp (e.g., Bril, Parry, and Dietrich, 2015; Falótico and Ottoni, 2016; Fragaszy et al., 2020) and Oldowan flakes representing the oldest direct evidence for a forceful pad-to-side precision grip and an intentional cutting action (e.g., Susman, 1991). This adaptation to utilizing a forceful-precision grip, wielding sharp-edged Oldowan flaked cutting tools, likely also provided an advantage to hominins, such as increased access to food (Linares-Matás and Clark, 2022; Plummer, 2004; Plummer et al., 2023). Following the principle of parsimony, researchers have previously suggested that hammerstone pounding may have directly preceded Oldowan flake use (Panger et al., 2002). For this reason, a series of recent studies has relied on experiments to determine both the cognitive (Affinito et al., 2024) and biomechanical (Eteson et al., 2024) requirements associated with these two fundamental stone tool tasks that are inextricably linked.

Previous archaeological experimental works, which either relied upon direct muscle recordings or brain imaging techniques, have crucially expanded our understanding of the biomechanical and neurological requirements during early stone tool production and use. Their results have helped in identifying the key muscle groups (Key et al., 2020; Marzke et al., 1998) and brain regions (Putt, Wijeakumar, and Spencer, 2019; Stout et al., 2000, 2015) involved in early stone tool production and use, assessing the phase of the task that recruits the highest cognitive and muscular activity (Affinito et al., 2024; Eteson et al., 2024), and exploring the role that expertise plays on stone tool task performance (Bril et al., 2012; Bril, Parry, and Dietrich, 2015; Eteson et al., 2024; Nonaka, Bril, and Rein, 2010; Pargeter et al., 2020).

Relying on this fundamental groundwork, this study aims to explore the effect of practical expertise on both cognitive and muscular efficiency during these two fundamental early stone tool tasks: forceful hammerstone pounding (nut-cracking) and precise Oldowan-style flake cutting. We used simultaneous EEG and sEMG recordings to capture patterns of neural and muscular activity in participants with varying levels of stone tool experience. In our previous research (Eteson et al., 2024), we found that knapping Experts exerted less muscular force across monitored muscles compared to the Novice participants during the execution of the same two stone tool tasks. Here, relying on the same experimental model and data, we analyze the combined cognitive and muscular activation during these tasks to determine patterns that emerge based on participants' level of expertise. Based on Affinito et al. (2024), who found that the preparatory ("Aim") phase elicited the highest beta activity, we have chosen to focus on this phase of the task in this study (also see other neurological studies on tool use, such as Johnson-Frey, Newman-Norlund, and Grafton, 2005). In line with previous neurological research (Affinito et al., 2024; Hecht et al., 2015; Putt, Wijeakumar, and Spencer, 2019; Stout et al., 2000, 2008), we will focus on three key brain regions of interest (ROIs), namely, the premotor/motor, left-frontal, and left-parietal. Despite both tasks recruiting some degree of bimanual coordination, we chose to focus in this study on the left lateralized frontoparietal region due to its role in motor planning, problem-solving, tool-related understanding, sequencing of motor skills, and goal-directed actions (Aydin et al., 2022; Brandi et al., 2014; Goldenberg and Spatt, 2009; Johnson-Frey, Newman-Norlund, and Grafton, 2005; Osiurak et al., 2021). Based on these conditions, we address the following two core hypotheses:

Hypothesis 1

Our previous sEMG study (Eteson et al., 2024, 2025) demonstrated that knapping Experts exhibited lower muscular activation without compromising task success during stone tool use. Meanwhile, other research has shown that individuals with practical tool-related experience display increased cognitive activity in key brain regions during the performance of various contemporary tool-using tasks (e.g., Bangert and Altenmüller, 2003; Hluštík et al., 2004; Landau and D'Esposito, 2006). Building on these findings combined, we hypothesize that, if cumulative practical experience in two of the earliest known hominin stone tool tasks (i.e., forceful hammerstone nut-cracking and precise flake cutting) enhances both muscular efficiency and cognitive engagement at the same time, then experienced individuals will show decreased muscular activation coupled with distinct patterns of neural activation in relevant brain regions (i.e., premotor/motor, left-frontal, and left-parietal cortices), compared to Novices. Such distinct cognitive activation expected in Experts may potentially reflect either increased neural engagement due to enhanced planning and control or decreased activation reflecting greater neuromuscular efficiency developed through cumulative experience.

Hypothesis 2

Oldowan flake cutting has been shown to be cognitively more demanding than hammerstone nut-cracking, particularly in the frontoparietal regions (Affinito et al., 2024). This is likely due to its assumed greater planning complexity (Bril, Parry, and Dietrich, 2015; Toth and Schick, 2018), reliance on precision grasping patterns (Ehrsson et al., 2000; Iturrate et al., 2018; Marzke, 2013; Susman, 1991), and exclusive association with hominin tool use (Bril et al., 2012; Harmand et al., 2015). Therefore, assuming that cumulative practical experience plays a more critical role in meeting the precise demands of flake cutting than those of forceful nut-cracking (as suggested by

Eteson et al., 2024, 2025), we expect Experts to exhibit more distinct patterns of neural activation in frontoparietal brain regions, along with reduced muscular effort during the flake task (compared to the hammerstone task). Based on previous studies, this increased neural activation is anticipated in Experts due to enhanced cognitive processing, as demonstrated in Landau and D'Esposito's (2006) study, which found that experienced participants show greater cognitive adaptability and, as such, increased cognitive activity when performing a more complex task. In addition, frontoparietal activity is known to increase during fine motor control, like that required during a flake cutting task (Ehrsson et al., 2000; Iturrate et al., 2018). Flake tools are held using a pad-to-side precision grip, which engages fewer muscles and allows for finer motor control (Susman, 1991). In contrast, relatively increased muscular activation is expected during the hammerstone task, due to the tool's larger mass and requirement for a powerful grasp often involving all five digits (Bril, Parry, and Dietrich, 2015; Domalain et al., 2017; Eteson et al., 2024; Marzke et al., 1998).

2. Materials and Methods

2.1 Subjects

Twenty-five volunteers (14 biological females and 11 biological males) participated in this EEG/sEMG experiment. Participants originated from 10 nationalities and were recruited from the University of Tübingen. Of the 25 participants, two of the volunteers (biological males) were identified as left-handed and are therefore excluded from statistical analyses (unless stated otherwise). Participants had no history of any neurological, psychiatric, or physical pathologies or disorders that may hinder the EEG or sEMG results. Participants ranged from ages 22 to 55 years. All volunteers provided informed consent, and the study received approval from the Ethics Committee for Psychological Research of the University of Tübingen. Participants were also categorized into three experience groups, based on their practical and theoretical knowledge of stone tool knapping. Novice participants were those with an absence of experience (*n* = 15), Intermediates were those with theoretical knowledge of stone tool production (*n* = 4), and Experts were categorized as participants with extensive theoretical and practical lithic knapping experience (*n* = 4).

2.2 Stone tools and materials

Forty-five stone tool replicas (26 replica Oldowan flakes and 19 hammerstones) were employed in this experimental study. An experienced tool knapper (ETM, see Acknowledgements) sourced and produced all stone tools used for this study, following documented proportions in the archaeological record. Sourced hammerstones were between 8 and 14 cm in length (Titton et al., 2018), while flakes were knapped between 5 and 7 cm in length (Gladilin and Sitliviy, 1987; Hayden, 2008).

In addition to the stone tools, macadamia nuts (*Macadamia integrifolia*) were used in the hammerstone nut-cracking task, as a substitute for oil palm tree nuts (*Elaeis guineensis*) (Arroyo et al., 2016; Bril, Parry, and Dietrich, 2015; Hirata et al., 2009), commonly consumed in the wild by non-human primates using hammerstones to crack open their hard shells (Arroyo et al., 2016; Hannah and McGrew, 1987; Proffitt et al., 2018). For more information on the macadamia nuts used in this experiment, see Affinito et al. (2024) and Eteson et al. (2024).

For the Oldowan flake cutting task, a leather substitute, known as pleather, was used. Pleather was used in this experiment to ensure consistency in torque, thickness, and toughness across all trials and participants. A "Z" pattern was stenciled onto each piece of pleather to indicate to participants where they should cut through the material. For additional information on the materials used in this experiment, see Affinito et al. (2024) and Eteson et al. (2024).

2.3 Experimental Design

This two-part experiment was performed in a shielded cabin at the Max Planck Institute for Intelligent Systems in Tübingen (see Acknowledgements). Participants were seated alone in the cabin, with a table in front of them. A striking platform (consisting of a wooden chopping board, with a foam sheet laid underneath), pleather squares or macadamia nuts, and a hammerstone or replica Oldowan flake. A camera was also positioned in a discreet corner of the room to capture the experiment. An instructional video detailing a full description of the experimental tasks, EEG/sEMG application, and contraindications for the day of the experiment was provided to all participants 24 hours in advance of their participation. In the first part of the experiment, participants were asked to crack open a macadamia nut using a hammerstone. For the second part of the experiment, participants were asked to cut a marked "Z" pattern through a piece of pleather using a replica Oldowan flake. Both tasks were performed in three consecutive actions: "Hold" the tool, "Aim" the tool at said material, and "Execute" the tool use action (see Figure 1 adapted from Eteson et al., 2024). In addition, a five-second rest period followed the Execute action. Each action lasted five seconds, and participants were notified of the start of each action via an aural cue played directly into the cabin for 30 milliseconds (ms). These cues were deliberately marked to isolate and analyze the changes in both cognitive and muscular requirements during each action phase. Participants performed a minimum of 50 trials for each part of the experimental task. Each trial was a total of 20 seconds long (5 seconds for each phase: Hold, Aim, Execute, and Rest). For a more detailed overview of each action, see Affinito et al. (2024) and Eteson et al. (2024).

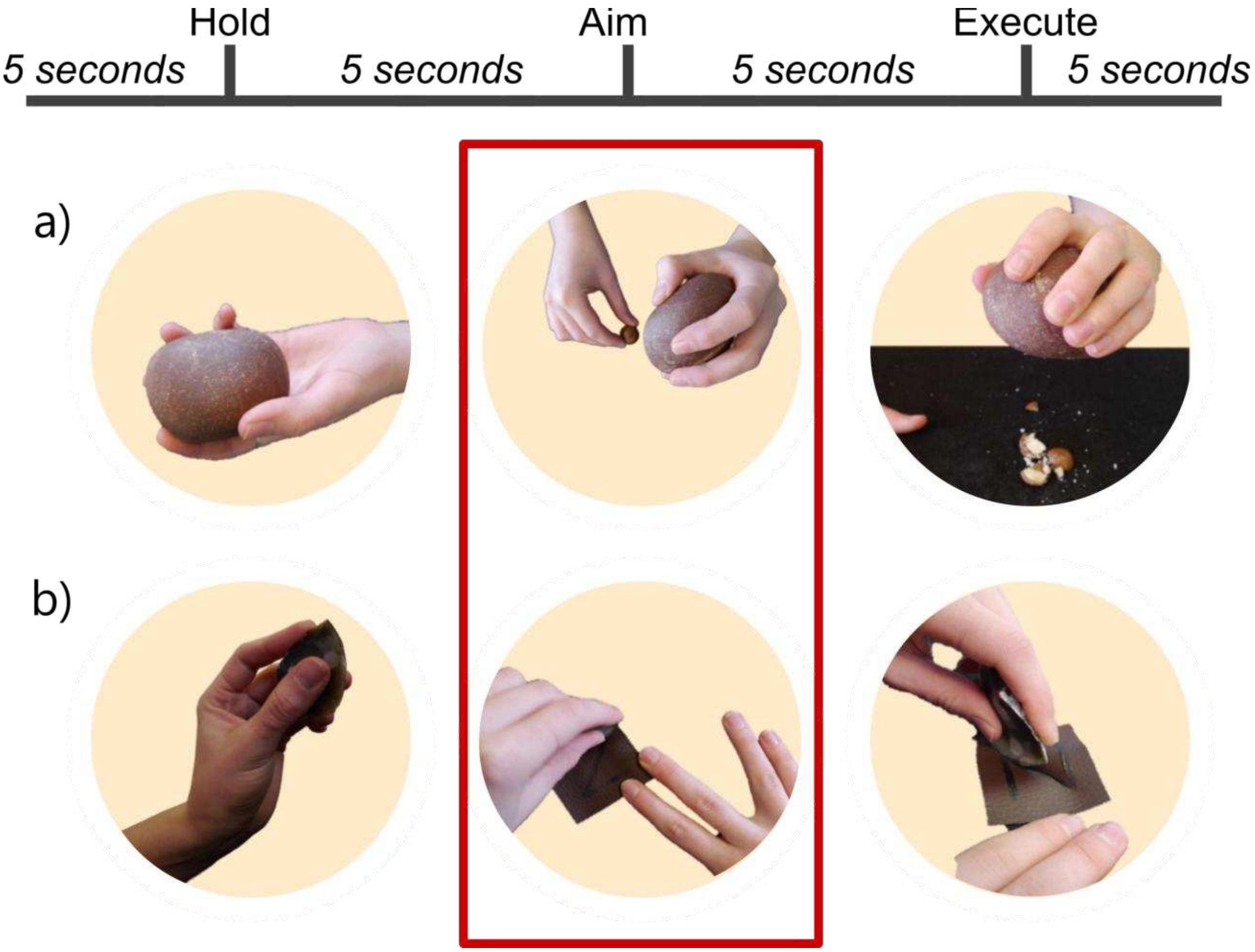

Figure 1. Stills of the experimental steps depict the three phases (Hold, Aim, Execute) recorded in each task, hammerstone nut-cracking task (a), flake cutting task (b). Each step was performed for 5 s. Illustration adapted from Eteson et al., 2024.

2.4 EEG and sEMG Recordings

This study followed the detailed protocol presented in Eteson et al. (2025), including step-by-step guidelines and clarifications for future use (dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1). All signals (EEG and sEMG) were recorded using Brain Vision Recorder (version 1.24.0101, Brain Products GmbH, Gilching, Germany), and a sampling rate was set at 2500 Hz to capture both EEG and sEMG signals. Cognitive activity was monitored using a 32-channel EEG cap with the international 10-20 system configuration, and a BrainAmp amplifier. The online central electrode FCz reference was used for recording. All EEG electrodes were filled with electrode gel to enhance connection to the participant's scalp and ensure an impedance below 25 kΩ (Laszlo et al., 2014; Leuchs, Pizzamiglio, and Bellomo, 2022; Mathewson, Harrison, and Kizuk, 2017). Muscular activity was recorded using a BrainAmp ExG amplifier and 8 BIP_2AUX Adapters for bipolar sEMG electrodes on 8 muscles in the hand and forearm (see Table 1 for a list of all EEG and sEMG channels analyzed in this study). Recommendations from the European standards for surface electromyography (SENIAM project) were followed for sEMG application and recording (Stegeman and Hermens, 2007). Bipolar electrodes were positioned directly over the muscle belly, aligned with the muscle fibers, onto clean skin with a small amount of abrasive conductive gel. The electrodes were then secured with kinesiology tape. Correct placement was assessed using exercises to activate those specific muscles (Key et al., 2020; Standring, 2021, see Eteson et al., 2024). BrainVision Recorder software (Version 1.24.0101, Brain Products GmbH, Gilching, Germany) was used to monitor and record both EEG and sEMG simultaneously during task performance. Before the experiment started, participants performed a series of maximum voluntary contractions (MVCs) to record everyone's maximum strength for each muscle. Participants performed a power grip and a pad-to-pad pinch grip using Baseline BIMS power "grip" and "pinch" strength dynamometers (Functional model, Fabrication Enterprises, New York). Each test was performed three times, and measurements were recorded for five seconds and repeated in both the dominant and non-dominant hand. The participant's highest measurement (kg) was also recorded as biometric data. Markers were then created before recording to denote each phase of the experimental tasks, i.e., Hold, Aim, Execute, and Rest. These markers were manually triggered in response to the auditory stimulus, recorded in the software as an AUX channel. This allowed us to accurately sync our markers with the auditory sound in the preprocessing stage. For more details on the recording setup, refer to Eteson et al. (2025).

Table 1. EEG and sEMG channel selection for PCAs based on ROIs (EEG) and muscular activity (Standring, 2021) in the hand and forearm (sEMG). Muscle abbreviations are as follows: DI1, first dorsal interosseus; FCR, flexor carpi radialis; FCU, flexor carpi ulnaris; FPL, flexor pollicis longus; HTE, hypothenar eminence (consisting of abductor digiti minimi, flexor digiti minimi, and opponens digit minimi); TE, thenar eminence (consisting of abductor pollicis brevis, flexor pollicis brevis, and opponens pollicis). Non-dominant muscles were also recorded due to the use of the non-dominant hand to stabilize the object during task preparation. These muscle abbreviations are: ndDI1, non-dominant first dorsal interosseus; ndTE, non-dominant thenar eminence.

Task	**EEG ROI**	**Corresponding EEG channels**	**sEMG channels**
flake Aim	premotor/motor	FC1, FC2, C3, C4	DI1, FCR, FCU, FPL, HTE, TE, ndDI1, ndTE
flake Aim	left-frontal	F3, F7	DI1, FCR, FCU, FPL, HTE, TE, ndDI1, ndTE
flake Aim	left-parietal	P3, P7	DI1, FCR, FCU, FPL, HTE, TE, ndDI1, ndTE

hammerstone Aim	premotor/motor	FC1, FC2, C3, C4	DI1, FCR, FCU, FPL, HTE, TE, ndDI1, ndTE
hammerstone Aim	left-frontal	F3, F7	DI1, FCR, FCU, FPL, HTE, TE, ndDI1, ndTE
hammerstone Aim	left-parietal	P3, P7	DI1, FCR, FCU, FPL, HTE, TE, ndDI1, ndTE

2.5 EEG and sEMG Preprocessing

All EEG and sEMG data were preprocessed using the BrainVision Analyzer software (Version 2.2, Brain Products GmbH, Gilching, Germany) following guidelines set out in Eteson et al. (2025) (for more details on the preprocessing, see the step-by-step protocol dx.doi.org/10.17504/protocols.io.36wgqnxbygk5/v1). We reviewed all raw data for dead and particularly noisy channels to remove them from the dataset. Markers were then adjusted to align with the auditory stimulus AUX to ensure the data could be correctly segmented. EEG and sEMG data were then preprocessed separately.

- **sEMG**

sEMG data was downsampled to 500 Hz and filtered with a low cutoff of 20 Hz, and a high cutoff of 450 Hz, with a notch filter at 50 Hz to maintain the important frequencies for sEMG, whilst filtering out potentially interfering power line noise. sEMG data was then segmented to divide the data into phases from 0–4000 ms epochs (Hold, Aim, Execute). The data was then rectified, transforming the signal to positive values. Rectification is a common technique used in sEMG studies, as the signal has a mean close to zero, prior to rectification, due to the fast oscillations of the muscles, which result in values in the data being both positive and negative. Each phase was then averaged, which created a mean segment from all repetitions performed (after cleaning, each participant had ≥46 repetitions due to noisy channels). Data was then exported into 0.4 ms epochs, which were then averaged again to create one data point for each muscle, per phase of the experimental tasks $\big(8\ (muscles) \times 3\ (phases)\big) \times 2 = 48\ (data\ points\ per\ participant)$.

MVCs were also preprocessed in the same way as the sEMG experimental data. However, instead of averaging, max markers (maximum data point in the MVC) were extracted from the MVC data and exported to use as a scale for which to create a %MVC value, to ensure participants' sEMG data was comparable despite varying individual strengths. This %MVC value is used for all statistical analysis and is calculated as: $(averaged\ sEMG\ data) \div (MVC\ value) \times 100$.

- **EEG**

EEG data were downsampled to 250 Hz and filtered with a low cutoff at 1 Hz and a high cutoff at 40 Hz. A notch filter at 50 Hz was also added, as with the sEMG, to filter out power line noise. Data was then re-referenced using the Reference Electrode Standardization Technique (REST) (Yao, 2001). Ocular artifacts were identified and removed using an automatic independent component analysis (ICA), and components were created to mark blinks and movements of the eye, along with other persistent muscular artifacts, using an inverse ICA transformation. The most prevalent patterns of muscular noise (including ocular artifacts) were selected for removal. Visual inspection was performed to ensure removal of selected components would not result in overcorrection. Channels that were removed during initial raw data inspection or displayed high levels of noise throughout were then interpolated by surrounding channels. Following interpolation, the entire task was segmented from the Rest period of the data. Segments of 15,200 ms were produced, encompassing all three phases per task. These segments were then baseline corrected from -200–0 ms. Baseline correction is usually performed before the start of a task ("Baseline Correction," 2024; Liland et al., 2011); however, to avoid task-related activity during baseline correction for both the Aim and the Execute phases, the baseline correction was performed prior to the start of the task, during the previous Rest phase. A conditional segmentation was then created to separate each phase, using the markers, from 0–1000 ms. Artifacts within the data were then identified based on several settings, such as a large, sudden increase in voltage, and maximum/minimum amplitude. Sections outside of these settings were then removed.

2.6 Data Analysis

As with the recording and preprocessing, we followed the protocol laid out in Eteson et al. (2025). For EEG, the preparatory action phase was segmented from 0–1000 ms, to capture the initial second of each task. For sEMG, the action phase was segmented from 0–4000 ms to capture the full muscular activity of the action phase. Before exporting the EEG data, a Fast Fourier Transformation (FFT), with a 10% Hanning window, was performed on the participants' trials. All trials (≥40, in line with standard parameters (Graham, 2021) were then averaged to create one data point for each phase, per participant. Mean beta activity (μV) between 12.5–30 Hz was then exported for each task. Mean beta activity was extracted due to the known association with increased activity during motor tasks (Athanasiou, 2018; Enders and Nigg, 2016; Eoh, Chung and Kim, 2005; Kirstein, 2008; Stern, 2005; Xavier, Su Ting and Fauzan, 2020). Grand averages were then created based on experience groups (Novice, Intermediate, and Expert). Grand averaged mean spectra data were used to produce FFT topographic maps for each experience group during the two Aim phases (flake and hammerstone), and Difference topography maps (calculated by subtracting the EEG signals of one condition from another to visualize the spatial distribution of these differences and highlighting regions where the EEG activity differs between the two conditions, revealing potential changes in brain activity) in Experts. All maps were generated in BrainVision Analyzer (Version 2.2, Brain Products GmbH, Gilching, Germany). Topographic maps within this study display the grand average of each experience group's EEG beta power across all channels, where amplitude is expressed as microvolts squared (μV^2). The maps do not account for or consider sEMG (muscular activation) interaction.

All statistical analysis on EEG and sEMG data was performed using the open-access software PAST (version 4.03; Hammer, Harper, and Ryan, 2001) and SPSS (version 29.0.2; Field, 2023). All plots and graphs were produced in PAST (Hammer, Harper, and Ryan, 2001) and modified in Inkscape vector graphics editor (version 1.3; Rogers, 2023).

EEG channel selection for further analysis was based on ROIs for our study. This technique is well known in EEG research, focusing on areas of the brain that have expected activity during stone tool tasks (Affinito et al., 2024; Hecht et al., 2015; Putt, Wijeakumar, and Spencer, 2019; Stout et al., 2000, 2008). The ROIs selected for analyses were the premotor/motor region (FC1, FC2, C3, C4), left-frontal region (F3, F7), and left-parietal region (P3, P7). Channels known to cause artifacts and are prone to noise during preprocessing[1] were removed from all analyses.

To address Hypothesis 1 and explore experience-based variation in brain-body interactions, univariate comparisons of individual EEG and sEMG channels between groups were not conducted due to the very small sample size of two of our experience groups and the discrepancy between group sample sizes (Field, 2023; Riffensburg, 2006). Considering that the focus of this study and methodology is on exploring covariance across different EEG and sEMG variables, we opted for a multivariate analysis prior to statistical comparisons. Therefore, two sets of three principal component analyses (PCAs) were run for each ROI (see above), either focusing on the flake or the hammerstone task (see Table 1 for all EEG/sEMG channels included for each PCA). PCAs were chosen to provide additional analysis on the proportional activation levels of the brain-body interaction by focusing on both EEG ROIs and sEMG channels. On this basis, PCA results provide additional context to the topographic maps by displaying EEG activation relative to sEMG activation. Therefore, topographic maps that display low beta power activation in a ROI (i.e., the frontal region) may show proportionally higher neural activity when plotted against sEMG channels of the hand and forearm in a PCA, if the participant has relatively low muscular activation, comparatively. Moreover, an additional PCA was conducted on the premotor and motor ROI, including the two left-handed individuals (see above, subsection "Subjects"), to explore potential effects of handedness in a brain region associated with limb control. Left-handed individuals were included in an additional premotor/motor ROI PCA due to the inclusion of both left and right hemispheric EEG channels. This allowed us to consider how left-handed participants plotted within their experience

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[1] Channels known to cause artifacts (based on Affinito et al., 2024) are Fp1, Fp2, FCz, TP9, TP10, FT9, and FT10.

groups, despite potential differences in hemisphere dominance, which is generally considered more variable in left-hand dominant individuals (Li et al., 2014). Additionally, there is contradictory evidence suggesting the left-hemisphere-dominance motion-planning hypothesis is crucial for motor function in left-handed people, as well as right-handed participants (Janssen, Meulenbroek, and Steenbergen, 2011; Sadeghi et al., 2021). Finally, an additional set of PCAs was run as participants have been shown to recruit their non-dominant hand more in the flake task, compared to the hammerstone task (see Eteson et al., 2025); therefore, we re-ran the ROI PCAs, excluding the two non-dominant hand channels (ndDI1 and ndTE) to determine whether any patterns of interest emerged.

These PCAs, which were used to explore variation across experience groups on a multivariate level (combining EEG and sEMG variables), were run based on a correlation matrix (i.e., on standardized values) to account for differences in variable scales between EEG (μV^2) and sEMG (%MVC) data. PCAs were conducted without assuming any pre-defined groups; participants were simply color-coded according to their experience level. Using the broken-stick model (Jackson, 1993), the relevant principal component (PC) axes were identified. Then, Shapiro-Wilk normality tests were run on extracted PC scores and, considering their significant result, non-parametric Kruskal-Wallis tests were then run on PC scores to determine significant differences between experience groups (Kruskal and Wallis, 1952; Field, 2013). When these tests found significant differences between experience groups, Dunn's pairwise post-hoc tests (with Holm-Bonferroni correction) were also performed to determine where these group differences lie (Field, 2013).

To adequately address Hypothesis 2 and thus compare practically experienced and unexperienced participants in terms of neuromechanical differences between flake and hammerstone use (i.e., hammerstone Aim and flake Aim), we decided to compare our Experts against the much larger and statistically robust group of Novices. Three PCAs (one for each EEG ROI and always including all sEMG channels) were run within each experience group being compared. As before, these PCAs were based on a correlation matrix, and the broken-stick model (Jackson, 1993) was used to determine the relevant PC axes. Since individuals are represented twice in each PCA (one for each task), to improve the visualization of the PCA patterns observed, intra-individual mean power values were calculated for the PCAs and subtracted from each task (for details on this technique, see Affinito et al., 2024, and detailed statistical protocol in Affinito et al., 2025). It is worth clarifying that PCAs were additionally run without this mean adjustment, showing equivalent patterns. The two Aim tasks were colored to differentiate, and no pre-defined group assumptions were made. Another set of two-tailed paired t-tests was then run on relevant PC scores, after checking for approximate normality, to determine significant differences between the two phases. Nevertheless, based on the extremely small sample size (n = 4 pairs), results should be interpreted with caution, despite a 2013 study showing paired t-test can theoretically provide attainable results with sample sizes >5 when within-pair correlation is high (de Winter, 2013). Drop Line graphs were also created from the PC scores to demonstrate whether the relationship between tasks was consistent across all Expert individuals.

Lastly, we would like to clarify that this study did not run a PCA with task comparisons against a control task, as this process has been already performed in our recent EEG study on the same experimental data, which consistently demonstrated relatively more frontoparietal engagement in both the hammerstone and flake Aim phases, when compared to the control task (Affinito et al., 2024).

3. Results

Analyses in this study are divided into two main sections corresponding to Hypotheses 1 and 2, each further subdivided according to regions of interest (ROIs) defined by EEG channel selections. In the first section (Hypothesis 1), we present the output of the multivariate analyses (PCAs) and subsequent tests on PC scores (Kruskal-Wallis and post-hoc analyses) to determine significant differences between experience groups. In the second section (Hypothesis 2), we present the PCA plots showing between-task variation within the Experts (or Novices), with two-tailed paired t-tests run on the relevant PC scores extracted. An alpha level of 0.05 was used for all statistical tests.

3.1 Hypothesis 1 – Comparison between Experience groups in both Aim tasks

PCAs were run to establish whether differences are observable based on specific ROIs collectively, and whether these ROIs display patterns of activity when analyzed collectively along with the sEMG activity of the upper limb recorded synchronously. The channels previously mentioned in Table 1 were selected as loadings for the following PCAs. The three-flake Aim PCA plots are presented in Figure 2, and hammerstone Aim PCA plots are presented in Figure 4. Details of the observed patterns for the Aim phase of each task are expanded on below.

3.1.1 Left-Frontal Region

- **Flake Aim**

From the topographic maps, Experts display high beta power in the left-frontal region, suggesting strong involvement of the executive functions, such as motor planning and decision-making. This effect is less pronounced in Intermediates and Novices, who still display beta power in the frontal electrodes, but show substantially lower levels than those in Experts. This indicates a potential reduction in the recruitment of higher-order cognitive control during the flake tool aiming phase.

In the initial PCA of the left-frontal region during the Flake Aim task, the first two principal components accounted for 55.26% of the total variance (PC1 = 35.61%, PC2 = 19.65%). However, an extreme outlier, defined as exceeding three times the interquartile range, was identified along PC2 in one Novice participant. Following the removal of this outlier, the PCA was re-run. In the revised analysis, only the first principal component was found to be meaningful, accounting for 38.79% of the variance, while PC2 contributed 14.98% (see Figure 2). The removal of the extreme outlier did not considerably change the patterns observed in this PCA. Despite no significant differences between experience groups in the exported PC scores (SI Table 1), the negative loadings of the left-frontal EEG channels lead Experts to plot differently from the other experience groups, which are widely dispersed along the PC1 axis. An additional PCA was run, excluding both non-dominant hand channels, and displayed 40.92% variance along PC1 (see Figure 3). In this PCA, PC1 further separates the Experts from the positive sEMG loadings and clearly distinguishes the Experts as having relatively increased left-frontal neural activation and decreased dominant muscular activation, compared to the other experience groups. No significant differences are observed in the PC1 scores (SI Table 2). A similar pattern is observed in all other ROIs analyzed in this study, which display further distinction between Experts and the other experience groups. Therefore, we provide details of this distinction in the left-frontal region in both tasks; for the other ROI PCAs, see SI Figures 1 and 2 and SI Tables 3 and 4.

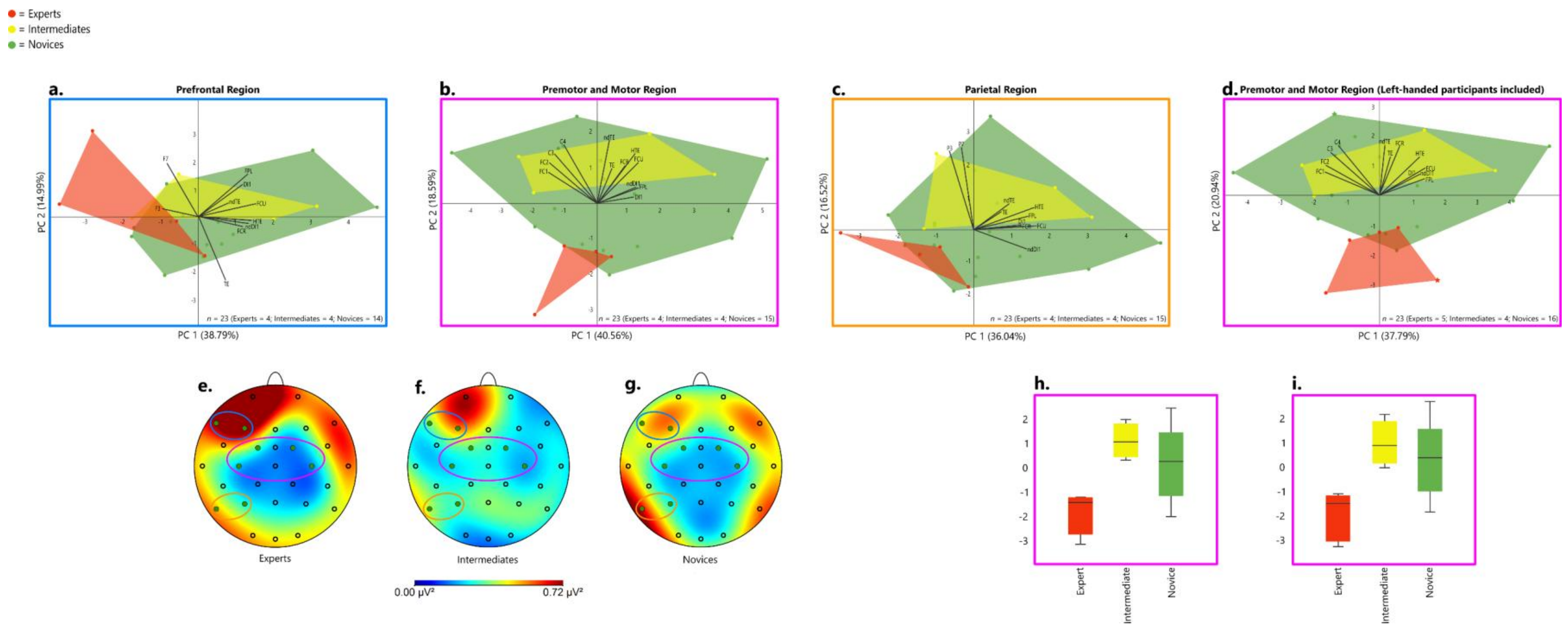

● = Experts
● = Intermediates
● = Novices
a.
Prefrontal Region
PC 2 (14.99%)
PC 1 (38.79%)
F7
F3
FPL
DI1
ndTE
FCU
HTE
ndDI1
FCR
TE
n = 23 (Experts = 4; Intermediates = 4; Novices = 14)
b.
Premotor and Motor Region
PC 2 (18.59%)
PC 1 (40.56%)
C4
C3
FC2
FC1
ndTE
HTE
FCR
FCU
TE
ndDI1
FPL
DI1
n = 23 (Experts = 4; Intermediates = 4; Novices = 15)
c.
Parietal Region
PC 2 (16.52%)
PC 1 (36.04%)
P3
P7
ndTE
TE
HTE
FPL
DI1
FCR
FCU
ndDI1
n = 23 (Experts = 4; Intermediates = 4; Novices = 15)
d.
Premotor and Motor Region (Left-handed participants included)
PC 2 (20.94%)
PC 1 (37.79%)
C4
C3
FC2
FC1
ndTE
FCR
TE
HTE
FCU
DI1
ndDI1
FPL
n = 23 (Experts = 5; Intermediates = 4; Novices = 16)
e.
Experts
f.
Intermediates
g.
Novices
0.00 µV²
0.72 µV²
h.
2
1
0
-1
-2
-3
Expert
Intermediate
Novice
i.
2
1
0
-1
-2
-3
Expert
Intermediate
Novice

Figure 2. Experience group comparisons focusing on the three EEG ROIs and sEMG channels during the flake Aim phase. PCA plots (**a-d**) demonstrate the differences between Expert (red), Intermediate (yellow), and Novice (green) participants in the left-frontal region (**a**), premotor/motor region (**b**), left-parietal region (**c**), and premotor/motor region, including left-handed participants (**d**). The PCA plots depict the first two components with EEG ROIs and all sEMG channels as loadings (see SI Tables 1, 9, 10, and 13). The topographic maps (**e-g**) represent the beta power of the three experience groups, red indicating higher and blue indicating lower values. PC scores that demonstrated significant differences between experience groups are displayed as box plots (**h-i**); PC2 (18.59%) premotor/motor region (**h**), and PC2 (20.94%) premotor/motor region including left-handed participants (**i**).

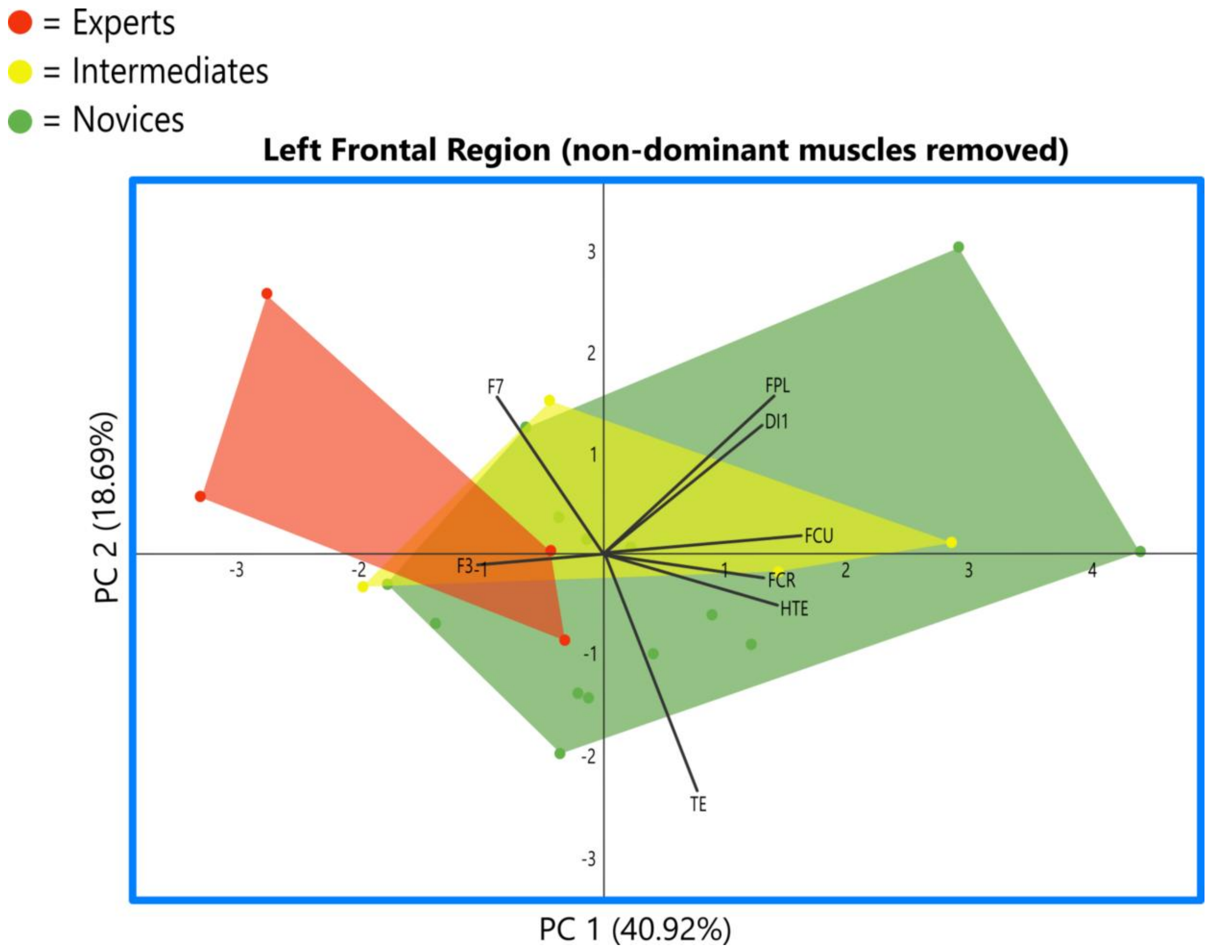


Figure 3. Experience group comparisons focusing on the EEG left-frontal region and dominant-hand sEMG muscles during the flake Aim phase. The PCA plot illustrates the differences between Expert (red), Intermediate (yellow), and Novice (green) participants. The PCA plots depict the first two components and EEG and sEMG channels as loadings (see SI Table 2).

- **Hammerstone Aim**

In the hammerstone Aim topographic maps, left-frontal beta power is relatively low in Experts, compared to flake Aim, and the other experience groups, who display predominantly higher beta power than Experts. Novices show moderate left-frontal beta power, whilst Intermediates display concentrated left pre-frontal activation, and moderate left-frontal activation. This pre-frontal region (Fp1 and Fp2), which shows high beta power in Intermediates in both hammerstone and flake tasks, was removed from analysis in our study due to these channels being potentially prone to noise (see Affinito et al., 2025; Eteson et al., 2025). This implies that the less experienced participants were engaging their executive functions during the planning phase of the hammerstone task more than the Experts.

In the hammerstone Aim left-frontal region PCA, representing a total variance of 53.90% between the first two PCs (PC1 = 34.45% and PC2 = 19.45%), an extreme outlier was detected again and removed from the analysis. A new PCA was run, excluding this extreme outlier. This new PCA made up 35.80% of the variance along PC1. Similarly to flake Aim, no significant differences were found between experience groups. However, a clear visual distinction is observed between the Experts and other experience groups: despite the topography maps displaying decreased neural activation in Experts, their values plotted negatively on PC1, driven by the left-frontal F3 EEG loading (and to a lesser extent, F7), demonstrating relatively increased neural activation. On the other hand, all sEMG channels show positive loadings, demonstrating relatively less muscular activation in Experts (see Figure 4). Intermediate and Novices' values are spread across PC1, plotting negatively and positively, resulting in a lack of significance found between the experience groups in the PC scores (SI Table 5). In the additional PCA, excluding both non-dominant hand muscles, PC1 accounted for 38.75% of the total variance. The overall pattern closely mirrors that of the original PCA with non-dominant hand channels included. Experts show a slight shift along PC1 toward the positive sEMG loadings, while still plotting predominantly negative with the left-frontal EEG loadings (see Figure 5). As with the previous PCA, PC1 scores did not show any significant differences between experience groups (SI Table 6). As similar shifts along PC1 are observed in the other two ROI PCAs for hammerstone Aim when non-dominant hand muscles are excluded, only the left-frontal PCA results are discussed here (for other ROI PCAs, see SI Figures 3 and 4 and SI Tables 7 and 8).

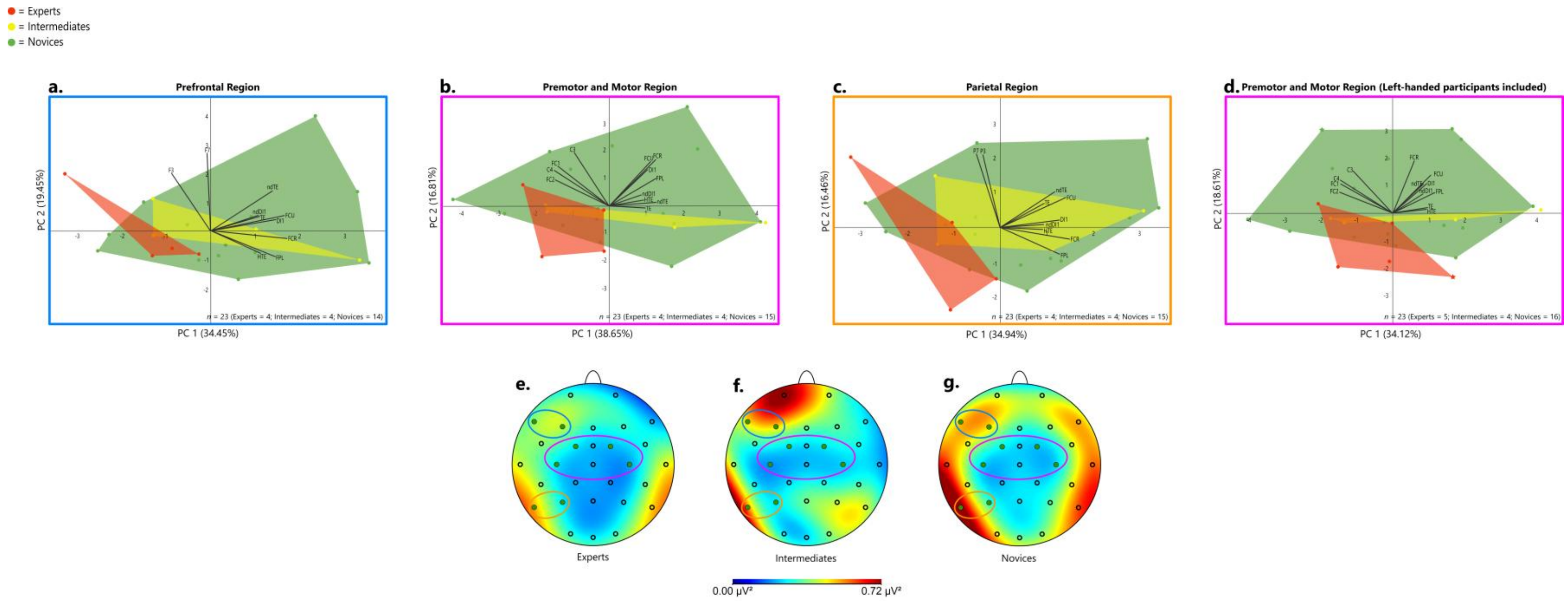

● = Experts
● = Intermediates
● = Novices
a.
Prefrontal Region
PC 2 (19.45%)
PC 1 (34.45%)
F3
F7
ndTE
ndDI1
TE
FCU
DI1
FCR
HTE
FPL
n = 23 (Experts = 4; Intermediates = 4; Novices = 14)
b.
Premotor and Motor Region
PC 2 (16.81%)
PC 1 (38.65%)
C3
FC1
C4
FC2
FCU
FCR
DI1
FPL
ndDI1
HTE
ndTE
TE
n = 23 (Experts = 4; Intermediates = 4; Novices = 15)
c.
Parietal Region
PC 2 (16.46%)
PC 1 (34.94%)
P7
P3
ndTE
FCU
TE
DI1
ndDI1
HTE
FCR
FPL
n = 23 (Experts = 4; Intermediates = 4; Novices = 15)
d.
Premotor and Motor Region (Left-handed participants included)
PC 2 (18.61%)
PC 1 (34.12%)
FCR
C3
C4
FC1
FC2
FCU
ndTE
DI1
ndDI1
FPL
TE
HTE
n = 23 (Experts = 5; Intermediates = 4; Novices = 16)
e.
Experts
f.
Intermediates
g.
Novices
0.00 µV²
0.72 µV²

Figure 4. Experience group comparisons focusing on the three ROIs and sEMG channels during the hammerstone Aim phase. PCA plots (**a-d**) demonstrate the differences between Expert (red), Intermediate (yellow), and Novice (green) participants in the left-frontal region (**a**), premotor/motor region (**b**), left-parietal region (**c**), and premotor/motor region, including left-handed participants (**d**). The PCA plots depict the first two components with EEG ROIs and all sEMG channels as loadings (see SI Tables 5, 11, 12, and 14). The topographic maps (**e-g**) represent the beta power of the three experience groups, red indicating higher and blue indicating lower values.

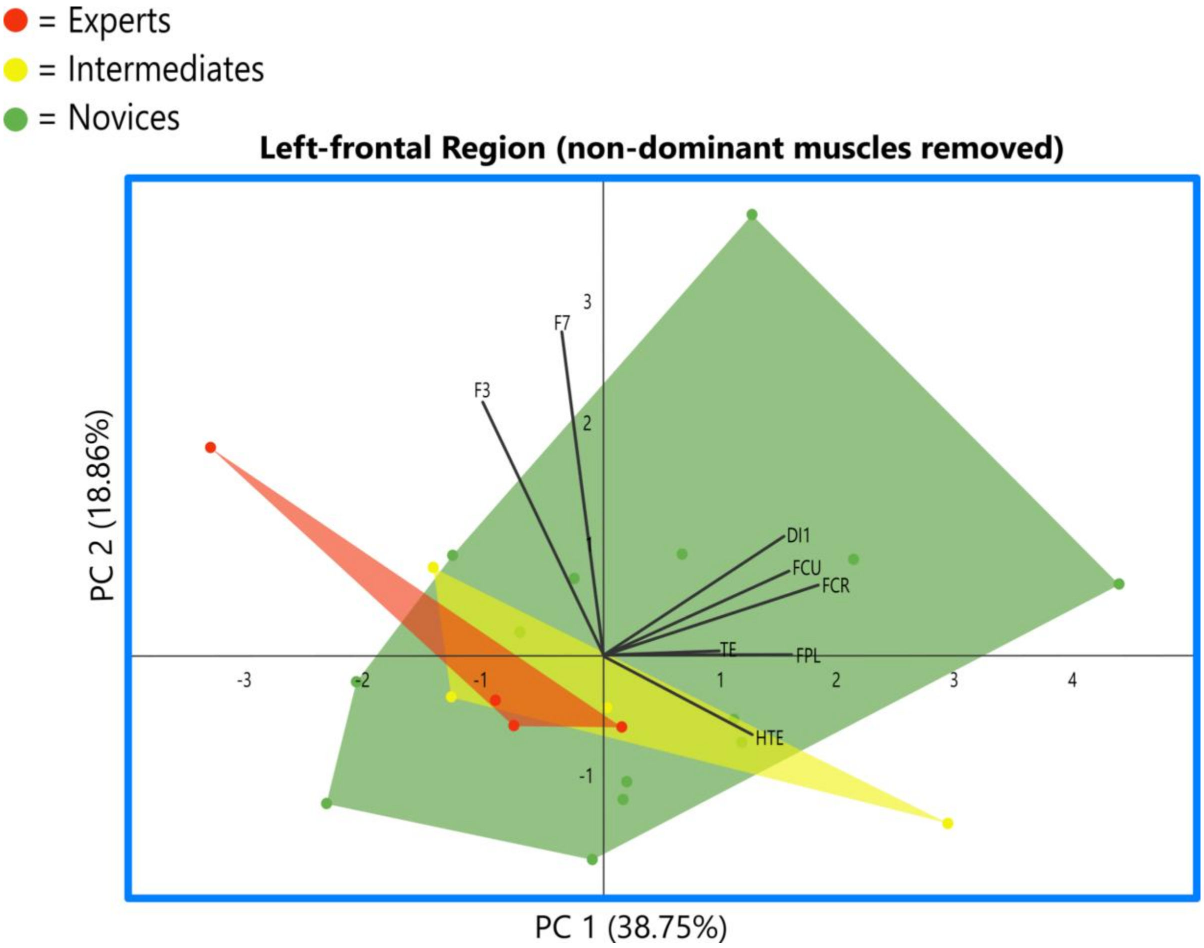


Figure 5. Experience group comparisons focusing on the EEG left-frontal region and dominant-hand sEMG muscles during the hammerstone Aim phase. The PCA plot illustrates the differences between Expert (red), Intermediate (yellow), and Novice (green) participants. The PCA plots depict the first two components and EEG and sEMG channels as loadings (see SI Table 6).

3.1.2 Premotor/Motor Region

- **Flake Aim**

Within the topographic maps, Experts exhibit a pronounced decrease in beta power in the premotor/motor region during the flake Aim task. In this case, the observed low beta power likely reflects a well-established phenomenon known as beta event-related desynchronization (ERD) (Crone et al., 1998; Pfurtscheller and Lopes da Silva, 1999; Zaepffel et al., 2013; Nakavashiki et al., 2014). Although visually marked by a reduction in beta power within the sensorimotor cortex, ERD is associated with increased cognitive-motor engagement during voluntary movement, often stimulus-driven and widely reported in event-related potential (ERP) studies. This interpretation aligns with findings from our previous EEG research (Affinito et al., 2024; Eteson et al., 2025), which demonstrated elevated cortical activation accompanied by decreased sEMG activity in Experts. This indicates strong motor engagement and task-specific activation. However, this desynchronization is markedly weaker in Novices and even more so in Intermediates, where the motor regions appear less engaged, reflecting a lower level of neural motor planning and recruitment during tool preparation.

In the PCA, the first two PCs together represent 59.15% of total variance (PC1 = 40.56% and PC2 = 18.59%). Along PC2, Experts are all positioned negatively, against all positive loadings of both EEG and sEMG channels, reflecting proportionally decreased muscular activation and beta ERD in practically experienced participants (see Figure 2). Due to non-normality of the PC2 scores (SI Table 9) (Shapiro–Wilk test: W = 0.76, $p = 0.04$), a Kruskal–Wallis test was conducted and revealed a significant difference between experience groups ($H(2) = 8.34$, $p = 0.02$). The subsequent Dunn's post hoc tests confirmed that Experts differed significantly from both the Intermediate ($p < 0.01$) and Novice ($p = 0.02$) groups. No significant group differences were observed along PC1.

As explained in Materials and Methods, an additional PCA was conducted that included the two left-handed participants, as EEG channels from both the left and right motor cortices were analyzed to account for bimanual tool use during the Aim task. PC 1 and 2 explained 58.73% of the total variance (PC1 = 37.79%, PC2 = 20.94%). While Experts now display a wider distribution along PC1, PC2 scores (SI Table 10) continue to show significant differences between experience groups ($H(2) = 9.16$, $p = 0.01$), indicating relatively increased cognitive activity and decreased muscular activation in Experts (see Figure 2). Dunn's post hoc analysis confirmed that these differences were driven by significant contrasts between Experts and both the Intermediate ($p < 0.01$) and Novice ($p < 0.01$) groups, preserving the separation across experience levels even with the inclusion of a left-handed Expert.

- **Hammerstone Aim**

In the hammerstone Aim task, as with the flake Aim task, Experts show strong indications of beta ERD over the premotor/motor region, although this appears slightly less pronounced than in the flake Aim task. Intermediates also show strong beta ERD, particularly in the left motor region, while Novices exhibit comparatively more beta power, likely reflecting less beta ERD, indicating reduced engagement in motor planning, initiating, and execution of voluntary movements, compared to the more experienced groups.

In the flake Aim premotor/motor PCA, PC1 makes up 38.65% of the total variance. The observed differences between Experts (negative values along PC1) and the other experience groups (positive and negative values along PC1) are separated by Experts' relative decrease in both cognitive beta power and muscular activation. The PC loadings show this separation is predominantly due to beta power increases of EEG channels (FC1, FC2, C3, and C4), likely reflecting beta ERD, and sEMG channels loading positively, reflecting decreased muscular activation in both the dominant and non-dominant hand in Experts (see Figure 4). However, despite this clear pattern, no significant differences were observed in PC1 scores (SI Table 11), as both the Intermediate and Novice experience groups plotted both positively and negatively across PC1. As with flake Aim, an additional PCA was run, including the two left-handed participants. PC1 (34.12%) and PC2 (18.61%) collectively made up for 52.73% of the variance, and EEG and sEMG predominantly maintained similar loadings to the previous PCA, with sEMG channels loading positively along PC1 and PC2, and EEG channels loading negatively along PC1 and positively along PC2. However, against the other Experts, the left-handed Expert plots positively along PC1, demonstrating relatively increased neural and muscular activation. Along PC2, Experts predominantly plot negatively against all EEG and sEMG loadings, displaying a relative decrease in muscular and neural activity, compared to Novices and Intermediates. Again, neither PC1 nor PC2 scores display significant differences between the experience groups (SI Table 12).

3.1.3 Left-Parietal Region

- **Flake Aim**

In the final ROI, Novices demonstrate the highest beta power among the experience groups, in the left-parietal region, likely reflecting an increased reliance on visuospatial processing and sensorimotor integration. In contrast, Experts show moderate-to-low beta power, suggesting a reduced requirement for active parietal involvement, like visuospatial processing. Intermediates exhibit the least beta power in this ROI, also demonstrating a reduced need for left-parietal engagement during task preparation.

However, the final PCA performed on flake Aim, focusing on the left-parietal region, reveals a slightly different narrative (PC1 = 36.04% of the total variance). As with the previous PCA graphs, Experts are distinguished from the remaining experience groups as they plot negatively along PC1, driven by less muscular activation and relatively increased neural activation (see Figure 2). Whilst the EEG loadings are small (-0.17 and -0.33), the parietal EEG channels load negatively along PC1, in contrast to all sEMG channels. Despite the EEG loadings perhaps being deemed as only representing a modest contribution to PC1, they remain the only loadings that plot negatively against all sEMG channels. Therefore, these loadings contribute to a greater proportional difference between the EEG and sEMG loadings, and these greatly affect the PC scores. Despite this clear separation, no significant differences were found between the experience groups in PC1 scores (SI

Table 13), again likely due to the widespread distribution of Intermediate and Novices' values, and perhaps also the small sample sizes.

- **Hammerstone Aim**

Finally, in the hammerstone Aim topographic map, similarly to the flake Aim task, Novices exhibit high beta power in the left-parietal region, potentially reflecting increased cognitive load in coordinating and visuospatial processing. Experts, by contrast, maintain relatively moderate, but comparatively lower beta power, whilst Intermediates exhibit moderate-to-high beta power, and fall between the other experience groups, displaying an intermediate pattern of activity.

In the final ROI PCA for the hammerstone Aim left-parietal region, PC1 represented a total of 34.94% of variance. Experts plot negatively along PC1, driven by the relative increase in the EEG loadings (P3 and P7), and a decrease in all sEMG muscle loadings (see Figure 4). As with flake Aim, the left-parietal loadings along PC1 are small (-0.20 and -0.28), but due to them being the only channels that load negatively, they are still considered to be important in the interpretation, behaving oppositely to the sEMG loadings, which all load positively. No significant differences between groups were observed in the PC1 scores (SI Table 14).

3.2 Hypothesis 2 – Comparison between Aim tasks in Experts

This hypothesis explores the expected differences between the two Aim tasks (flake and hammerstone) within the Expert (and Novice) group.

3.2.1 Left-Frontal Region

- **Experts**

In the left-frontal region, the Difference topographic map shows a strong differentiation, as flake Aim demonstrates substantially higher beta power activity. This difference between tasks indicates that neural activity related to decision making, planning, and problem solving is likely required to a higher degree during the cutting task.

In the PCA focused on the left-frontal EEG and all sEMG channels, PC1 and PC2 represent 81.13% of variance (PC1 = 58.39% and PC2 = 22.74%, respectively). PC1 clearly distinguishes between the two tasks, with EEG channels along with the non-dominant hand muscles loading negatively, whilst all dominant sEMG channels load positively. As hypothesized, flake Aim values plot negatively, showing relatively increased EEG and non-dominant sEMG muscular activity, whilst the opposite is true for hammerstone Aim, which displays relatively increased muscular activity (see Figure 6; see SI Figure 5 for PCAs without mean adjustment). After ensuring approximate normality, a paired t-test was run on PC1 and found a significant difference between flake and hammerstone on PC1 ($t(3) = 4.80$, $p = 0.02$), but no separation was observed between tasks along PC2 (see SI Table 15).

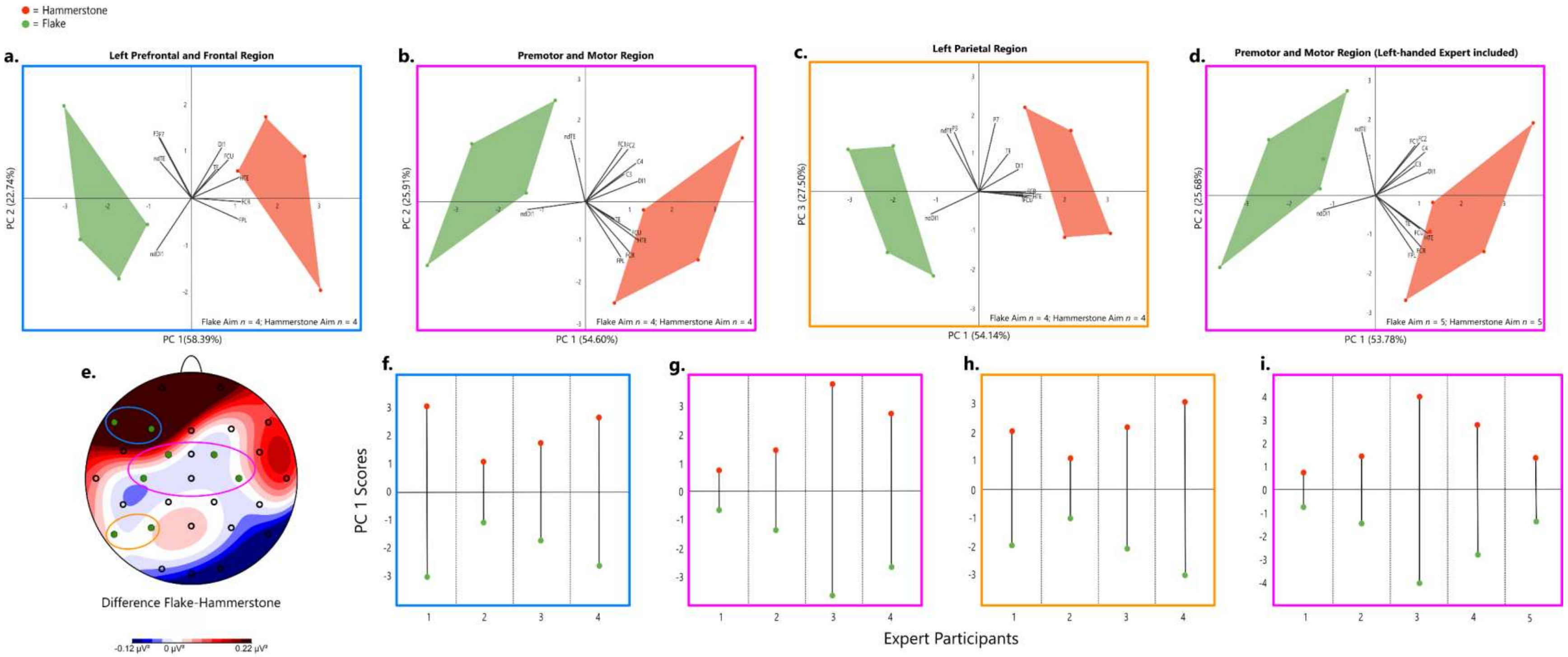

● = Hammerstone
● = Flake
a.
Left Prefrontal and Frontal Region
PC 2 (22.74%)
PC 1(58.39%)
Flake Aim n = 4; Hammerstone Aim n = 4
F3F7
ndTE
ndDI1
DI1
FCU
TE
HTE
FCR
FPL
b.
Premotor and Motor Region
PC 2 (25.91%)
PC 1 (54.60%)
Flake Aim n = 4; Hammerstone Aim n = 4
ndTE
ndDI1
FC1
FC2
C4
C3
DI1
TE
FCU
HTE
FCR
FPL
c.
Left Parietal Region
PC 3 (27.50%)
PC 1 (54.14%)
Flake Aim n = 4; Hammerstone Aim n = 4
ndTE
P3
P7
TE
DI1
ndDI1
FCR
HTE
FCU
d.
Premotor and Motor Region (Left-handed Expert included)
PC 2 (25.68%)
PC 1 (53.78%)
Flake Aim n = 5; Hammerstone Aim n = 5
ndTE
ndDI1
FC1
FC2
C4
C3
DI1
TE
FCU
HTE
FCR
FPL
e.
Difference Flake-Hammerstone
-0.12 µV²
0 µV²
0.22 µV²
f.
g.
h.
i.
PC 1 Scores
Expert Participants
1
2
3
4
5

Figure 6. Paired comparisons between hammerstone Aim and flake Aim in Experts, focusing on the three ROIs and sEMG channels. Mean power PCA plots (**a-d**) demonstrate the differences between hammerstone Aim (red) and flake Aim (green) in the left-frontal region (**a**), premotor/motor region (**b**), left-parietal region (**c**), and premotor/motor region including left-handed participants (**d**). The PCA plots depict the first two components with EEG ROIs and all sEMG channels as loadings (see SI Tables 15, 17, 18, and 20). The topographic map (**e**) represents the absolute beta power difference between flake Aim and hammerstone Aim in Experts. Darker saturation equates to stronger differences between the tasks. The drop-line plots (**f-i**) depict PC scores that display significant differences between tasks, hammerstone Aim (red) and flake Aim (green); PC1 (58.39%) left-frontal region (**f**), PC1 (54.60%) premotor/motor region (**g**), PC1 (54.14%) left-parietal region (**h**), and PC1 (53.78%) premotor/motor region including left-handed participants (**i**).

- **Novices**

For Novice participants, the Difference topographic map shows a more complex pattern, as both EEG channels F3 and F7 display a low-to-moderate difference between the two tasks; however, F3 displays increased beta power in the flake Aim task, whilst F7 displays decreased beta power in the flake Aim task. Compared to Experts, Novices show a less distinct pattern in the maps, suggesting both tasks required left-frontal activation, likely engaging in executive control, but in ways that EEG is unable to further dissect, due to its reduced spatial resolution.

The left-frontal region PCA (PC1 = 47.46% and PC2 = 21.40% variance) on Novice participants again shows an interesting distinction. Whilst Novices are clearly separated between tasks, with hammerstone Aim plotting positively along with all dominant-hand muscles, the EEG loadings separate along PC1 too, as discussed in the Difference topography maps. F7 plots positively, whilst F3 plots negatively with the ndTE (see Figure 7; see SI Figure 6 for PCAs without mean adjustment). Whilst the EEG and non-dominant loadings are small, they indicate that these tasks recruit different regions of the left-frontal area, and that the ndTE is likely particularly useful during the flake Aim task, which is also the case for Experts, due to the increased need to stabilize the pleather. This separation was found to be significantly different between the two tasks, $t(14) = -7.05$, $p < 0.001$, but no significance between groups was found in PC2 scores (SI Table 16).

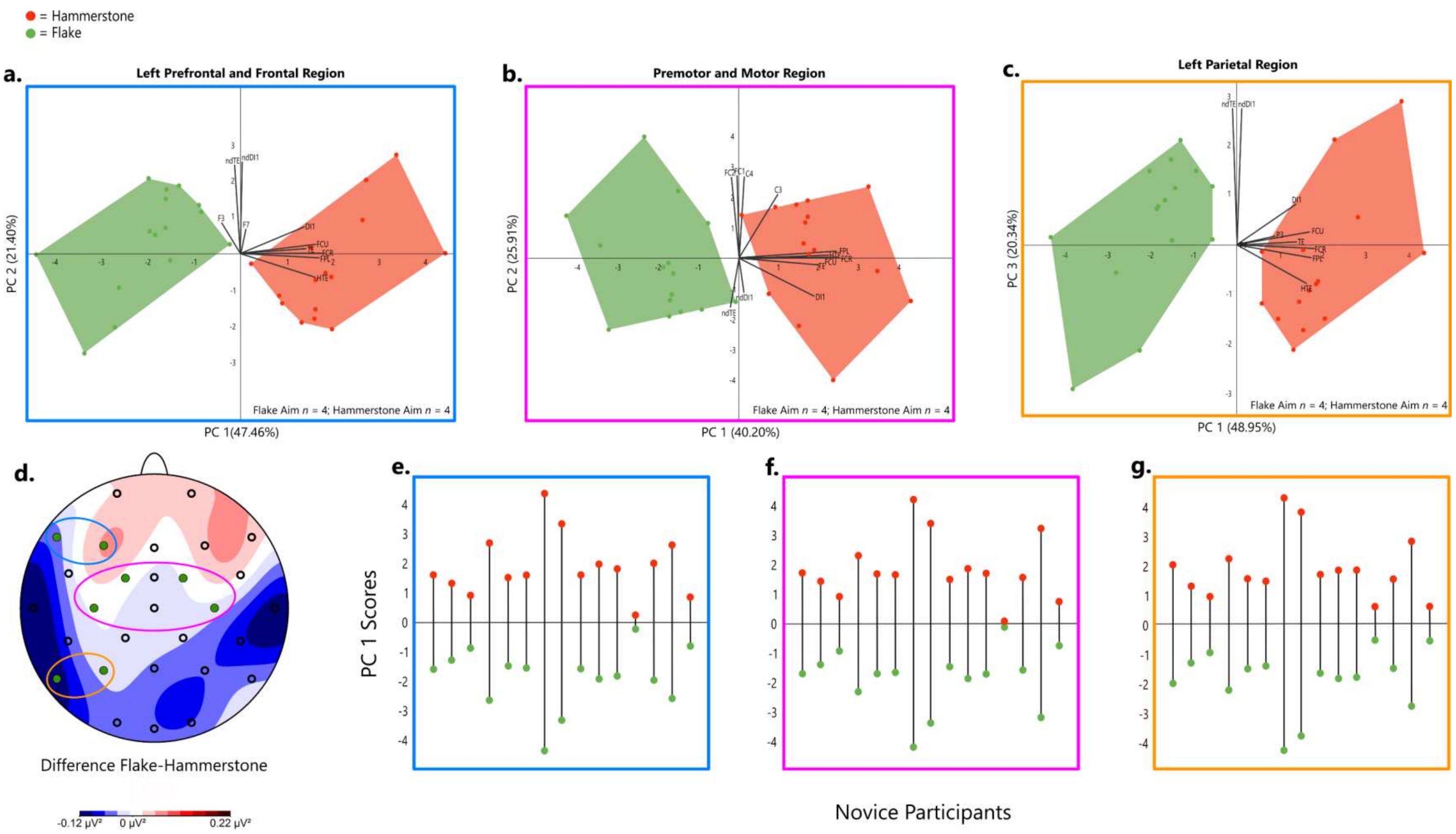

● = Hammerstone
● = Flake
a.
Left Prefrontal and Frontal Region
PC 2 (21.40%)
PC 1(47.46%)
Flake Aim n = 4; Hammerstone Aim n = 4
ndTE
ndDI1
F3
F7
DI1
FCU
TE
FCR
FPL
HTE
b.
Premotor and Motor Region
PC 2 (25.91%)
PC 1 (40.20%)
Flake Aim n = 4; Hammerstone Aim n = 4
FC2
FC1
C4
C3
FPL
FCR
FCU
TE
DI1
ndTE
ndDI1
c.
Left Parietal Region
PC 3 (20.34%)
PC 1 (48.95%)
Flake Aim n = 4; Hammerstone Aim n = 4
ndTE
ndDI1
DI1
P3
FCU
TE
FCR
FPL
HTE
d.
Difference Flake-Hammerstone
-0.12 μV²
0 μV²
0.22 μV²
e.
f.
g.
PC 1 Scores
Novice Participants
4
3
2
1
0
-1
-2
-3
-4

Figure 7. Paired comparisons between hammerstone Aim and flake Aim in Novices, focusing on the three ROIs and sEMG channels. Mean power PCA plots (**a-c**) demonstrate the differences between hammerstone Aim (red) and flake Aim (green) in the left-frontal region (**a**), premotor/motor region (**b**), and left-parietal region (**c**). The PCA plots depict the first two components with EEG ROIs and all sEMG channels as loadings (see SI Table 16, 19, and 21). The topographic map (**d**) represents the absolute beta power difference between flake Aim and hammerstone Aim in Novices. Darker saturation equates to stronger differences between the tasks. The drop-line plots (**e-g**) depict PC scores that display significant differences between tasks, hammerstone Aim (red) and flake Aim (green); PC1 (47.46%) left-frontal region (**e**), PC1 (40.20%) premotor/motor region (**f**), PC1 (48.95%) left-parietal region (**g**).

3.2.2 Premotor/Motor Region

- **Experts**

The Difference topographic map shows a small-to-moderate difference between tasks in the premotor/motor region in Experts. The map illustrates a slight decrease in beta power in the flake Aim phase compared to the hammerstone Aim, likely reflecting slightly stronger beta ERD, indicating enhanced motor demands, such as motor planning demands during the flake task. However, this difference between tasks is relatively small on the topography map.

In the premotor/motor region PCA, the first two PCs represented 80.51% of the variance (PC1 = 54.60% and PC2 = 25.91% respectively). Along PC1, all flake Aim values are positioned negatively, opposite the positive loadings of all EEG and dominant hand sEMG channels, with ndDI1 driving the negative loading on PC1. PC1 shows a clear visual separation between the two tasks, with flake Aim showing low activity (beta ERD), indicating increased neural engagement, whilst hammerstone Aim shows increased muscular activity in the dominant hand (see Figure 6). Additionally, whilst it must be interpreted with the necessary caution due to the low paired sample size (n = 4), a paired t-test confirmed that these differences in PC1 scores were significant ($t(3) = 3.15$, $p = 0.05$) (SI Table 17). When the left-handed Expert was included in the PCA, the values and loadings still demonstrated a similar pattern (see Figure 6), with PC1 (53.78%) and PC2 (25.68%) making up 79.46% of the total variance. In addition, due to the increased sample size when the left-handed participant was included (n = 5), a non-parametric Wilcoxon test could be run on the PC scores, which found a significant difference ($z = 2.02$, $p = 0.04$) between tasks on the PC1 scores (SI Table 18).

- **Novices**

The Difference topographic map for Novices indicates a minor difference between the two tasks in the premotor/motor region, displaying marginally higher beta ERD in the flake task, suggesting slightly higher activation of the motor network during cutting than when nut-cracking.

In tandem with the Difference topography maps, and to determine whether the above pattern in Experts is repeated in Novices, we ran a PCA including the sEMG channels as well. The first three PCs of the premotor/motor region represented 81.78% of the variance (PC1 = 40.20%, PC2 = 25.91%, and PC3 = 15.67%, respectively). Along PC1, the dominant-hand muscles drive the positive loadings, along with the EEG motor channels C3 and C4 (see Figure 7). Flake Aim values all plot negatively along PC1, leading to a clear separation between tasks that display significance (*t*(14) = -6.80, *p* <0.001). This likely reflects a small relative increase in the primary motor cortex during the flake Aim task (beta ERD), accompanied by a decrease in most sEMG channels. However, the non-dominant thenar eminence displays a small negative loading, as do the two premotor channels (FC1 and FC2), suggesting a relative increase in the ndTE and decrease (beta ERD) in the premotor region compared to the hammerstone task. PC2 and PC3 do not distinguish between the tool tasks in Novice participants (SI Table 19).

3.2.3 Left-Parietal Region

- **Experts**

In the left-parietal region, the topographic Difference map displays very little difference between the two tasks, reflecting that both tasks likely recruited similar beta power, suggesting both cutting and nut-cracking activated sensorimotor processing required for precise, goal-directed action in similar ways in Experts.

The final PCA conducted focused on the left-parietal EEG channels and all sEMG channels. The first two PCs here represented 81.64% of the variance (PC1 = 54.14% and PC2 = 27.50%). As with the other two ROI PCAs, the PC1 axis showcases a clear separation between flake and hammerstone Aim (see Figure 6). In PC1, the only negative loadings are those of the non-dominant hand muscles and the EEG P3 channel. All dominant sEMG channels and P7 load positively. Unlike the previous two PCAs, this PCA separates the EEG channels, demonstrating that these tasks display relatively more neural activity in specific regions of the left-parietal that require further investigation, which we are not able to distinguish between using EEG, due to its relatively low spatial resolution. However, a paired t-test did demonstrate, after confirming normality within the dataset, significant differences in PC1 (*t*(3) = 5.10, *p* = 0.02) between flake Aim and hammerstone Aim (SI Table 20).

- **Novices**

For Novices, the Difference topography maps displayed moderately strong differences in the left-parietal region, with a decrease in beta power in the flake Aim task. This indicates a stronger differentiation in Novices, when compared to the Experts' maps. Higher beta power during the hammerstone Aim task likely reflects an increased need for integrating sensory information and motor actions for tool manipulation.

In the left-parietal PCA (PC1 = 48.95% and PC2 = 20.34% of variance), all sEMG loadings, except ndTE and both EEG channels load, positively or near zero along PC1 for the hammerstone

Aim task, whereas flake Aim values plot negatively relative to these loadings (see Figure 7). This again suggests that PC1 is driven by dominant hand sEMG channels and the P3 EEG channel. ndDI1 and P7 channels also load positively, despite displaying small loadings. This shows a contrasting trend to Experts, who displayed relatively increased activation in the P3 EEG channel and both the non-dominant muscles for the flake Aim task. Despite differences between Experts and Novices, the Novice PC1 scores demonstrated a significant difference between the two tasks, $t(14) = -6.92$, $p < 0.001$ (SI Table 21). Additionally, the non-dominant hand muscles show strong positive loadings along PC2, with most flake Aim values plotting positively; however, no significant differences were present.

4. Discussion

This study provides the first direct experimental analysis of how stone tool experience influences both neural and biomechanical aspects of early hominin tool use. It addressed two main questions: whether Experts show distinct cognitive and muscular activation during the preparatory (Aim) phase of nut-cracking and flake cutting, and whether the precision of flake cutting (a task uniquely associated with hominins) elicits stronger neuromechanical differences than nut-cracking in Experts compared to Novices. Overall, despite the suboptimal sample sizes, our multivariate analyses revealed distinctive patterns of neuromechanical activation in our five knapping Experts (four right-handed and one left-handed participant), compared to the vast majority of Novice and Intermediate participants.

Regarding our first Hypothesis (H1), Experts display increased relative beta power in the left-frontal and premotor/motor regions during the flake Aim task, alongside reduced recruitment of all recorded muscles, compared to Novice and Intermediate participants. Contrary to expectations, however, Experts did not exhibit overall increased beta power in the left-parietal region but did still exhibit relatively increased beta power in the PCA (although loadings were small), when compared directly against other experience groups. This apparent discrepancy reflects the different information captured by the two analyses: topographic maps display EEG beta power spatially across the scalp for each experience group, while the PCA loadings, calculated from the EEG and sEMG channels, reveal patterns of covariance by measuring how the variables change when EEG and sEMG data are combined. Therefore, whilst Experts may not demonstrate the highest EEG beta power in some ROIs in the topography maps, they do display relatively more EEG activation, along with reduced sEMG activation in the PCA. During the hammerstone Aim task, Experts demonstrated reduced muscular activity across all recorded muscles, including those of the non-dominant hand. Overall, they showed consistently distinct patterns across EEG ROIs (Figures 2 and 4), while Novice and Intermediate participants exhibited much more variable multivariate patterns. Our findings also partially confirmed our second Hypothesis (H2), as the comparison between tasks in Experts displayed relatively more distinctive activation in the left-frontal and motor regions, paired with decreased muscular activation, in the flake task. The sub-sections below provide a more detailed discussion of our findings pertaining to each of the two hypotheses (H1 and H2).

4.1 Hypothesis 1: Distinct neuromechanical patterns in Experts

Our first hypothesis, which is built from our previous sEMG study (Eteson et al., 2024), proposed that Experts would exhibit increased activation across all ROIs, while also demonstrating reduced muscular recruitment during both the flake Aim and hammerstone Aim tasks, compared to Intermediate and Novice participants. In our previous study, we found that Experts displayed lower overall muscular activity than Novice and Intermediate participants during the execution phase of both hammerstone nut-cracking and flake cutting, without a significant decrease in their level of success (Eteson et al., 2024). Additionally, other studies on the cognitive requirements of general human tool use have observed experienced participants display increased activation in the ROIs analyzed in this study during task preparation and execution (Bangert and Altenmüller, 2003; Hluštík et al., 2004; Landau and D'Esposito, 2006). For instance, Landau and D'Esposito (2006) found that expert pianists exhibited increased activation levels in primarily right-lateralized prefrontal, sensorimotor, and parietal regions compared to non-pianists. Similarly, Hluštík et al. (2004) found that all participants showed expansion of the primary motor and somatosensory cortices after three weeks of manual (finger and wrist) movement training. Similarly, another motor task study found similar patterns in guitarists, who exhibited greater BOLD (blood-oxygen-level-dependent) signals in the precentral gyrus, left inferior parietal lobe, and prefrontal areas during motor preparation, when compared to non-guitarists (Vogt et al., 2007). As Yang (2014) indicates, experts tend to show increased activation in these brain regions, which are involved in action planning and comprehension. This suggests that motor training may help build more detailed and efficient patterns related to task performance.

Our analyses revealed distinct, experience-related patterns when EEG and sEMG data were analyzed in tandem. These findings align with a well-established body of literature on motor expertise, cognitive efficiency, and neural specialization (Bangert and Altenmüller, 2003; Hluštík et al., 2004; Landau and D'Esposito, 2006; Vogt et al., 2007). Specifically, the increased activation observed in the left-frontal and premotor and motor regions (beta ERD) among Experts during the flake Aim task aligns with previous research showing these areas are consistently involved in high-level executive functions such as motor planning, decision making, and working memory (Adin et al., 2022; Berchicci et al., 2012; Goldenberg and Spatt, 2009; Jones and Graff-Radford, 2021; Putt et al., 2019; Stout, 2011; Stout et al., 2008, 2015). They are also reported to contribute to refined and efficient motor control required for complex and fine-tuned movements acquired through extensive practice (Ehrsson et al., 2000; Landau and D'Esposito, 2006; Yang, 2014). These results add to a body of research demonstrating that, with increasing expertise, there is heightened engagement of prefrontal and premotor circuits during the planning and execution of manual tasks. In the context of stone tools, Bril et al. (2010) observed that only tool-use Experts in their study were able to make precise adjustments during knapping to achieve the required conchoidal fracture necessary to produce flakes. Experts were consistently more successful and more biomechanically efficient than the less experienced participants, suggesting that they can better recognize how different objects interact and affect one another, enabling them to adapt their movements to maintain efficient performance (Bril et al., 2010). This observation aligns with executive functions typically linked to increased activity in the left-frontal and premotor regions, as seen during the flake Aim task in our experiment.

As for the hammerstone Aim task, results do not align quite as well with the expectations of our first hypothesis. Whilst Experts were consistently more biomechanically efficient in terms of overall muscle recruitment compared to Novices (see Figure 4), their neural activation is less distinct compared to the flake task (see Figure 2) when analyzing the topographic maps. This result is particularly interesting due to our previous sEMG study (Eteson et al., 2024), which found that Experts did not exhibit higher overall success rates in the hammerstone task, compared to either Intermediates or Novices, perhaps suggesting that Experts recruited specific regions of the brain similarly to the Intermediate and Novice groups, due to comparable demands during the tool task, to ensure successful performance. However, despite this, Experts maintained similar rates of success during the nut-cracking task whilst seemingly displaying relatively more biomechanical efficiency (i.e., less overall muscle recruitment) and cognitive activity in the PCAs, when compared to the other experience groups.

Regarding the left-parietal region, previous studies have shown that Experts display increased parietal activity (Landau and D'Esposito, 2006; Vogt et al., 2007; Yang, 2014), due to the inferior parietal lobe's role in conceptualizing tool function, mechanical knowledge and problem-solving (Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Osiurak et al., 2021), combined with the superior parietal lobule's function of integrating sensory, motor, and visual information to guide and control movements, assisting in anticipating outcomes of observed actions. Yang (2014) suggests in their analysis of motor task studies that experienced participants seem to utilize the parietal region more effectively to process spatial and movement-related information. In contrast, we found that the left-parietal region, while displaying relatively increased activation in Experts in the PCAs, showed reduced overall activity compared to the Novices. Nonetheless, there are several difficulties encountered when directly comparing our results on stone tool use to those of previous motor studies on other manual tasks, which may likely explain the discrepancies we find between our results and those mentioned above.

Firstly, unlike the motor tasks in the studies mentioned above, the stone tool-use tasks employed in our study (particularly, the Oldowan-style flake cutting) do not require extensive practice to enable successful performance. Unlike the tasks in these studies utilizing Expert pianists or athletes, which necessitate years of specialized training, our tasks are based on common actions broadly known to our participants (i.e., cutting), even if the task details themselves (involving stone tool replicas) were novel. Secondly, it is important to note that EEG's limited spatial resolution prevents accurate detection of activity in specific deeper cortical structures or precise localizations within specific brain lobules (Boudewyn et al., 2018; Boyer et al., 2023; Gevins et al., 1994; Jiang, Bian, and Tian, 2019; Muthukumaraswamy, 2013). This limitation may have hindered our ability to accurately localize parietal activity from deeper within the cortical surface, which might be observable when using other brain-imaging techniques, such as fMRI (Sturzbecher and de Araujo, 2012; Zaretskaya, 2021), also used in the motor task studies we based our neural expectations on (Landau and D'Esposito, 2006; Vogt et al., 2007; Yang, 2014).

With regard to our Experts' lower left-parietal activation levels, it is worth noting that several other action observation studies on athletes (Babiloni et al., 2009, 2010; Zhang et al., 2019) revealed that expertise seemed to be related to lower activation levels, potentially evidencing the "neural efficiency" hypothesis (Dunst et al., 2014; Haier et al., 1988). This suggests that elite athletes achieve improved performance whilst consuming minimal neural energy. Even though this could partly explain the lower left-parietal activation of our study's Experts, it contrasts with their higher beta power levels in their left-frontal and premotor/motor regions during the precise flake cutting task. In this regard, instead of expecting or confirming lower brain activity across our Experts' brains, our findings may be reflecting how different regions are recruited based on expertise (Figures 2 and 4). As shown in the topographic maps, Novices exhibit slightly higher beta activity in the parietal region during both tool tasks, likely suggesting a greater reliance on processing novel visual, spatial, and sensory information to guide their actions (Carius et al., 2023). In contrast, Experts appear to rely more on premotor circuits, drawing on familiar motor patterns formed through extensive hands-on experience with similar tools and materials (Meister et al., 2005; Olsson and Lundström, 2013).

4.2 Hypothesis 2: Task-specific neuromechanical patterns in Experts

Our second Hypothesis (H2) expected Experts to show more distinct neuromechanical patterns between stone tool tasks (preparation for Oldowan-style flake cutting and hammerstone nut-cracking). This is based on our previous EEG study, by Affinito et al (2024), which reported that frontoparietal regions displayed increased activation during the flake cutting task, compared to the hammerstone pounding task, highlighting the neural mechanisms supporting precision-grasping tool use (e.g., Johnson-Frey, Newman-Norlund, and Grafton, 2005; Brandi, 2014). In addition, the use of cutting flakes is widely thought to postdate the earliest hammerstone pounding activities in hominin evolution (Bril et al., 2012; Harmand et al., 2015), requiring additional production steps when made intentionally (knapping to remove sharp flakes from a core), and offering greater resource access (Linares-Matás and Clark, 2022; Plummer, 2004; Plummer et al., 2023; Semaw, 2000). For these reasons, at least from certain respects, flake cutting is expected to be more cognitively demanding than hammerstone pounding. Landau and D'Esposito's (2006) findings also support this idea, demonstrating that Experts may show a greater cognitive adaptability, and as such increased neural activity, when performing a complex task, as opposed to a simple motor task. In addition, frontoparietal activity is known to increase during fine motor control, such as the one required for thumb-index precision grasping during flake tool use (Ehrsson et al., 2000; Iturrate et al., 2018). Ehrsson et al. (2000) also suggest that precision grasping activates both hemispheres (especially the ipsilateral premotor and rostral cingulate motor areas) even during unimanual tasks. In contrast, power grasping primarily engages the contralateral motor region. Increased muscular activation was also hypothesized during the hammerstone aiming task, due to the tool's significantly heavier mass than the flake, and requirements to perform a power grasp involving all five digits (Bril, Parry, and Dietrich, 2015; Domalain et al., 2017; Eteson et al., 2024; Marzke et al., 1998). In contrast, flake tools are held using a pad-to-side precision grip, which engages fewer muscles and allows for finer motor control (Susman, 1991).

In line with these predictions and the theoretical framework, during the flake Aim task, Experts in this study displayed increased EEG activation in both the left-frontal and premotor/motor regions, combined with decreased sEMG activation across dominant hand muscles (Figure 6). Although these results must be interpreted cautiously due to the small sample size of our Expert group (*n* = 4 right-handed participants), we do see a clear distinction in the left-frontal region between the two tool tasks in our Expert participants. This pattern is likely caused due to the additional working memory and motor planning required for more complex tasks, using fine-motor control and precision grips, when compared to simpler tasks or tasks involving power grasping patterns (Ehrsson et al., 2000; Iturrate et al., 2018; Lu, Kim, and Kim, 2023). This is consistent with the findings of a previous study proposing that the cognitive demands for hammerstone pounding activities are less than those for Oldowan flake knapping, which requires more complex mechanical knowledge (Bril, Parry, and Dietrich, 2015). Similarly, this trend has also been discussed in previous experimental studies on more complex stone tool tasks, such as Acheulean handaxe toolmaking (Putt, Wijeakumar, and Spencer, 2019; Stout et al., 2008, 2015). Overall, these findings suggest evolutionary pressure on executive functions (such as working memory, motor planning, and goal-directed behavior) during the early Pleistocene, driven by the growing demands of complex tool use and technological innovation (Putt, Wijeakumar, and Spencer, 2019).

Additionally, contrary to our expectation of overall lower muscle activation in Experts, we found that the non-dominant hand had relatively increased activation during the flake Aim task (Figure 6), despite both tool tasks requiring the non-dominant hand for stabilization. This may reflect the Experts' improved ability to understand the required torque, resistance, and force needed in the stabilization hand, to ensure the pleather was appropriately stabilized before task execution (i.e., cutting through the fabric) of the flake Aim task. Whilst also undoubtedly important during the hammerstone Aim task, stabilization from the non-dominant hand seems to have been required to a much lesser extent. This is likely due to the nature of the nut-cracking task, as sustained pressure applied to the nut was not necessary for successful completion of the task, unlike the flake-cutting task. However, the hammerstone task still recruited the dominant hand significantly more than the flake task, in line with our hypothesis (see Introduction). It is worth noting that a similar, yet less prominent and distinctive, pattern is present in Novices, in Figure 7. Whilst in the Novices' PCA, the non-dominant sEMG loadings are small, only the ndTE loading is negative, as are all flake Aim values. Whilst small, this loading likely represents the sustained pressure required by the thenar eminence to stabilize the pleather, and the motor coordination and action planning necessary to prepare for the cutting task.

Despite Experts' reduced overall muscle recruitment, when analyzing the premotor/motor cortex, Experts seem to show increased neural activation during the flake Aim task. This increased activation, as seen in Hypothesis 1, likely reflects increased neural activity and cortical engagement based on relatively low beta power in the premotor/motor region (see Figure 6). This increase in premotor/motor region activity is likely due to the fine motor control, movement precision, planning, and adjustment required to perform a forceful precision grip (i.e., use of an Oldowan-style flake) (Barany et al., 2020; Ehrsson et al., 2000; Iturrate et al., 2018). This aligns with our hypothesis and a previous study showing that, despite less muscular recruitment, Experts achieved greater success than their less experienced counterparts in the flake task (Eteson et al., 2024). Despite this, Novices again seem to mirror, at least to some degree, the patterns observed in Experts. Along PC1 of the premotor/motor PCA (Figure 7), Novices show a clear separation between tasks, predominantly from the increased activation of the dominant hand muscles in the hammerstone task. Additionally, whilst relatively small, channels C3 and C4 display positive loadings against the flake Aim task. This indicates relatively increased beta ERD in the motor region during the flake task, as seen in Experts. However, the premotor channels (FC1 and FC2) have small negative loadings, indicating lower neural activation (beta ERD) during the flake task, contrary to Experts. Whilst the proposed explanation that low beta power indicates higher neural activity in the motor region may at first appear confusing, we have previously suggested this in two previous studies that beta ERD appears to be the most appropriate explanation for the results of this experiment (Affinito et al., 2024; Eteson et al., 2025). In sum, although the observed low beta power in these regions may at first seem counterintuitive, prior work (Affinito et al., 2024; Eteson et al., 2025) supports beta ERD as the most plausible explanation, which, despite low beta power, reflects higher neural activation (Crone et al., 1998; Pfurtscheller and Lopes da Silva, 1999; Zaepffel et al., 2013; Nakavashiki et al., 2014).

Regarding the final ROI, the left-parietal region, the results suggest a more complex pattern of activation in Experts than initially hypothesized. Specifically, the two left-parietal EEG channels in Experts are separated along PC1, with loadings in opposite directions, indicating differential involvement of distinct parietal subregions across the two tool tasks (Figures 6). While these loadings are small, they do highlight activation patterns that likely reflect nuanced, within-lobe task-specific processing, which cannot be fully understood given the spatial limitations of EEG. Importantly, this pattern differs from that seen in Novices. The latter shows both parietal channels loading in the same direction, demonstrating greater left parietal activation during the hammerstone task, when compared to the flake task. This may indicate heavier reliance on visuospatial and sensorimotor integration to support unfamiliar tool use (Carius et al., 2023), whereas Experts may instead draw on more distributed motor-related networks shaped by prior tool-specific experience (Meister et al., 2005; Olsson and Lundström, 2013).

Finally, we included two left-handed individuals in two additional premotor/motor ROI PCAs (see Figures 2 and 4), due to EEG channels including both left and right regions of the premotor/motor cortices, and both tasks involving both the dominant and non-dominant hands. Interestingly, both left-handed participants plotted on the border of their allotted groupings in both the flake and hammerstone tasks. This may reflect what other studies have proposed, that left-hemisphere-dominance occurs in both left and right-handed people, during motor planning and function (Janssen, Meulenbroek, and Steenbergen, 2011; Sadeghi et al., 2021), with left-handed people generally also showing a more variable hemisphere dominance, whilst right-handed people predominantly show dominance in their contralateral hemisphere during motor control (Li et al., 2014). Contrastingly, the left-handed participants may also show bilateral activation, as with the right-handed participants, due to the bimanual nature of the task. Interestingly, the left-handed Expert does align with the other Experts, demonstrating a relative increase in premotor/motor activation (beta ERD) and decreased muscular recruitment (along PC2; Figure 2), whilst the Novice left-handed participant displays the opposite trend, aligning with the Novice group, displaying relatively increased overall muscular recruitment along PC2. Additionally, in PC1 of the hammerstone task PCA, a separation between Experts and the left-handed Expert is observable, with the left-handed Expert being driven by relatively lower beta power, likely representing increased neural activation (beta ERD) in the premotor/motor region and increased activation of the sEMG channels (Figure 4). This may reflect this participant's contralateral hemisphere dominance, as we know hammerstone Aim recruited the non-dominant hand less than in the flake task, or perhaps more simply, this could reflect relatively increased muscular activation. To fully explore the neural activation of left-handed participants during stone tool tasks, a larger sample size is needed.

4.3 Limitations and Future Possibilities

While this study offers valuable insights into the neural and muscular demands of early stone tool use, several limitations should be acknowledged. As previously mentioned, the spatial resolution of EEG, while effective for capturing real-time brain activity, is limited in its ability to precisely localize neural sources. Although there are various ways of improving spatial resolution in EEG, such as high-density EEG with increased numbers of electrodes monitored, our 32-channel electrode configuration was intentionally chosen to ensure compliance with our ethical guidelines and the practical feasibility of the complex and time-demanding experimental design required in our project.

Similarly, sEMG can only measure superficial muscle activity, and both EEG and sEMG are highly sensitive to artifacts, which can be difficult to fully eliminate in tasks involving large arm movements. Although we followed rigorous preprocessing protocols to mitigate these effects, we also removed specific channels from analysis that were particularly prone to large artifacts. sEMG can also become difficult to measure on particularly small muscles, due to signals being picked up from surrounding muscles. Therefore, smaller muscles were grouped into eminences that engaged in similar actions (i.e. thenar eminence). It is worth noting that we also acknowledge that we are not able to provide a complete repertoire of all the muscles involved in these two tool tasks, but followed guidelines from established studies (Hamrick et al., 1998; Key et al., 2020; Marzke et al., 1998) of particularly important muscles known for their role in precision and power grasping patterns. Unfortunately, it is practically implausible to monitor all muscles involved in tool use, particularly due to the constraints on the participants, i.e., affecting their range of motion, and coping with an excess of wires, which would likely increase the chances of motion artifacts.

Another key limitation of our study is the small sample size in both the Expert and Intermediate groups, which restricts the scope for rigorous statistical testing. However, given the rarity of participants with such extensive practical stone tool expertise, the distinctiveness of certain key findings, and the novelty of our integrative neural and biomechanical approach, we believe this study provides a valuable foundation for future research with larger samples to further explore the factors driving efficient stone tool use in human evolution. Finally, it is worth noting that, due to the controlled nature of this experiment, it was practically impossible to perfectly replicate all natural conditions of stone tool use. Environmental conditions within the experiment were, nevertheless, crucial to ensuring we could properly isolate cognitive and muscular activation during the tasks.

Future research could address some of these limitations by integrating EEG with imaging modalities offering higher spatial resolution, such as fNIRS or fMRI, or by expanding the number of electrodes used. Increasing the sample size, particularly of left-handed individuals and Experts, would allow for further exploration of differences in motor planning and brain lateralization. Finally, the field would also benefit from comparisons between the dominant (striking) and non-dominant (stabilizing) hand in bimanual stone tool production and use, given the observed bimanual coordination of extant primate species during hammerstone pounding activities (Falótico and Ottoni, 2016; Fragaszy et al., 2020), the suggestion of bimanual wielding during Lomekwian production (Harmand et al., 2015), and the known importance of the stabilizing hand (Kivell, 2015; Williams, Gordon, and Richmond, 2012; Williams-Hatala et al., 2018).

5. Conclusion

In summary, this study demonstrates that Expert stone tool knappers exhibit distinct brain-body interactions during two fundamental early stone tool tasks, particularly in contrast to less experienced individuals. Notably, Experts display increased activation in the left-frontal and premotor/motor cortices during the flake Aim task relative to hammerstone Aim, suggesting the importance of heightened motor planning and goal-directed action for the cutting task, as previously demonstrated when comparing nut-cracking to flake production (Bril, Parry, and Dietrich, 2015). These findings provide experimental support that the knowledgeable execution of early tool use, especially for flake cutting tools, whose intentional use is unique to hominins, requires increased neural engagement in brain regions involved in motor preparation and executive function, rather than reduced activation as it would have been expected based on the neural efficiency hypothesis (Kami et al., 1995; Landau and D'Esposito, 2006; Nakata et al., 2010).

From an evolutionary perspective, it is worth noting that these frontal and motor regions implicated in this study correspond to areas of the brain that underwent significant expansion within the hominin lineage. While our empirical results do not necessarily signify that stone tool use was the driving factor of this evolutionary process, they provide further support to the notion that the relative enlargement of these brain regions likely provided an evolutionary advantage for increasingly sophisticated and precise tool use (possibly as a result of exaptation) (Bruner, Battaglia-Mayer, and Caminiti, 2023; Hecht et al., 2015). Additionally, it is worth noting that, while Experts exhibited reduced muscular effort in the dominant striking hand, they showed increased activation in the non-dominant stabilizing hand during the flake task, underscoring the importance of assessing bilateral motor contributions to expertise.

Overall, our combined EEG/sEMG study uncovered interactions between neural and muscular systems that are likely overlooked in studies addressing either of these domains in isolation. In analyzing these methodologies in tandem, we provide a more comprehensive picture of how motor expertise is embodied and enacted, particularly in a domain such as lithic tool use (rather than production), which is currently under-researched within experimental archaeology. This innovative methodological framework opens new avenues for understanding how motor skill acquisition in the context of technology may have shaped brain and body interactions throughout hominin biocultural evolution. Lastly, this study cautions against simplistic interpretations of "efficiency" in cognitive terms: rather than less activation (brain power), Experts seem to develop a more focused and efficient organization of neural activity to match the demands of the task, relying on their valuable learned experience (Milton et al., 2007). In this sense, we propose that neural efficiency in humanlike stone tool use may be better understood as functional specialization and flexibility, rather than merely reduced cognitive load.

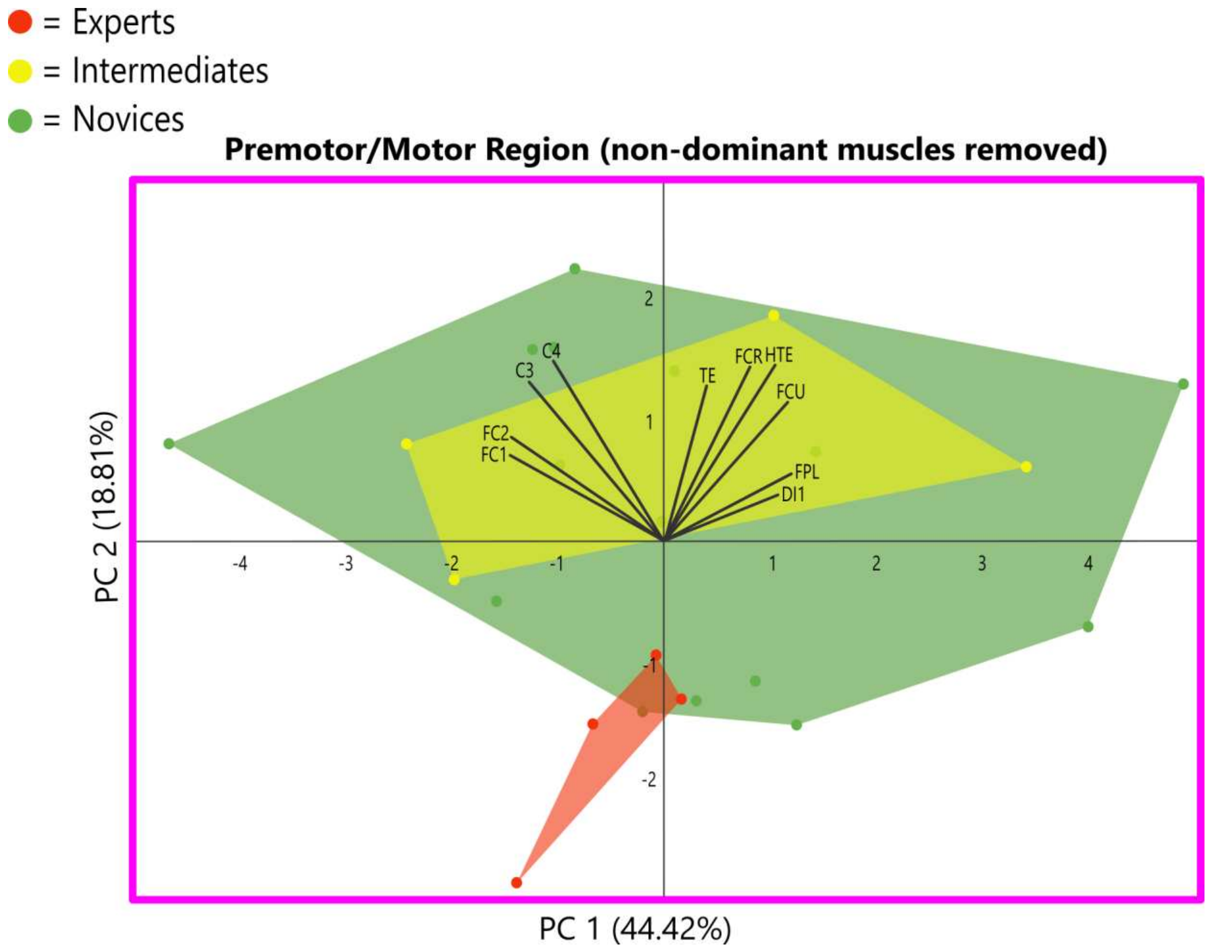
Supplementary Information

SI Table 1. Left-frontal region PCA statistics and loadings values for the flake Aim task comparing between experience groups, extreme Novice outlier removed.

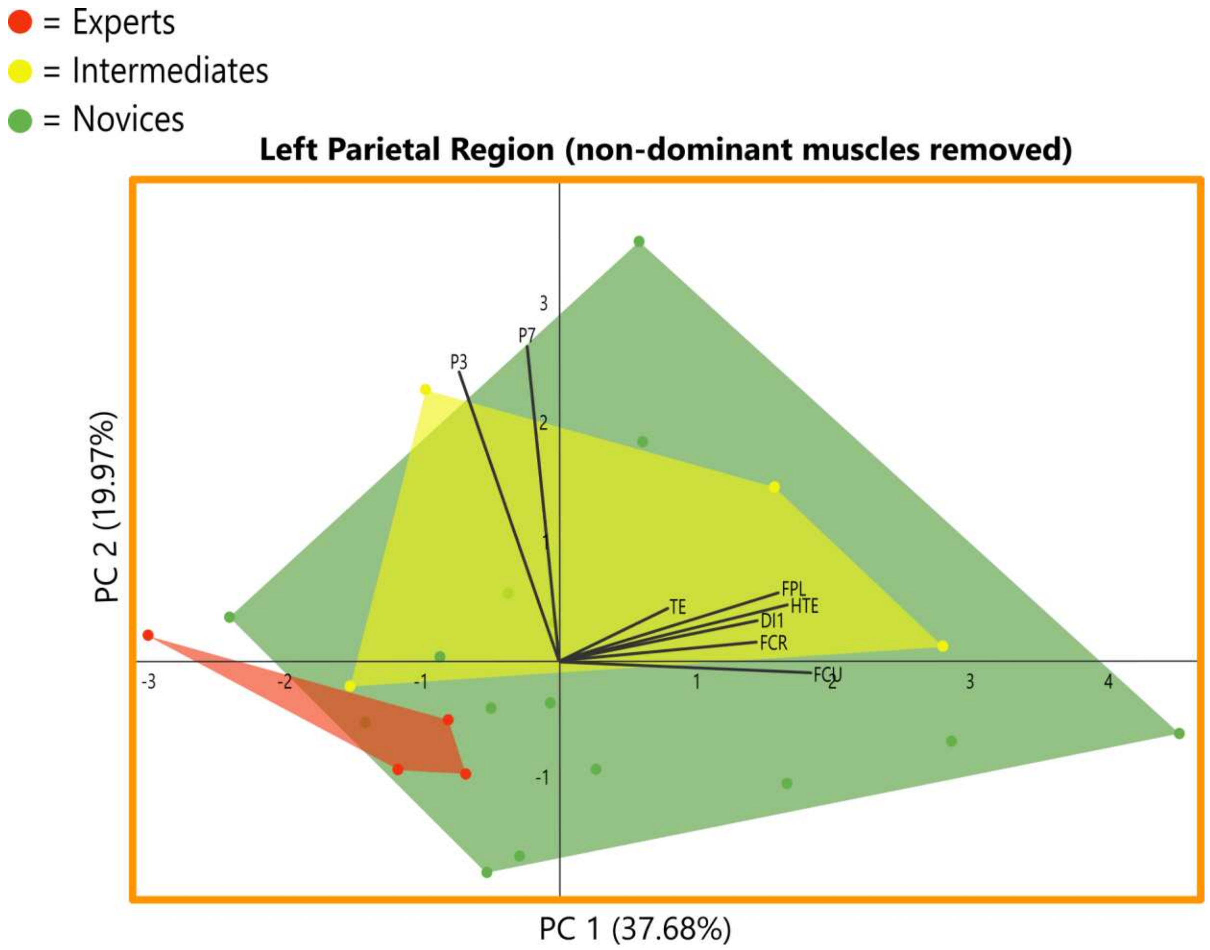
			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**F3**	**F7**
PC 1	3.88	38.79	0.63	0.76	0.63	0.82	0.71	0.39	0.72	0.43	-0.52	-0.44

SI Table 2. Left-frontal region PCA statistics and loadings values for the flake Aim task comparing between experience groups, excluding non-dominant muscles.

			Factor loadings							
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**F3**	**F7**
PC 1	3.27	40.92	0.66	0.73	0.68	0.83	0.72	0.40	-0.53	-0.45


Premotor/Motor Region (non-dominant muscles removed)

SI Figure 1. Experience group comparisons focusing on the EEG premotor/motor region and dominant-hand sEMG muscles during the flake Aim phase. The PCA plot illustrates the differences between Expert (red), Intermediate (yellow), and Novice (green) participants. The PCA plots depict the first two components (see SI Table 3) and EEG and sEMG channels as loadings.



SI Figure 2. Experience group comparisons focusing on the EEG left-parietal region and dominant-hand sEMG muscles during the flake Aim phase. The PCA plot illustrates the differences between Expert (red), Intermediate (yellow), and Novice (green) participants. The PCA plots depict the first two components (see SI Table 4) and EEG and sEMG channels as loadings.

SI Table 3. Premotor/Motor region PCA statistics and loadings values for the flake Aim task comparing between experience groups, excluding non-dominant muscles.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	4.44	44.42	0.63	0.61	0.47	0.68	0.70	0.23	-0.75	-0.63	-0.86	-0.86
PC 2	1.88	18.81	0.15	0.56	0.55	0.44	0.21	0.49	0.50	0.57	0.27	0.33

SI Table 4. Left-parietal region PCA statistics and loadings values for the flake Aim task comparing between experience groups, excluding non-dominant muscles.

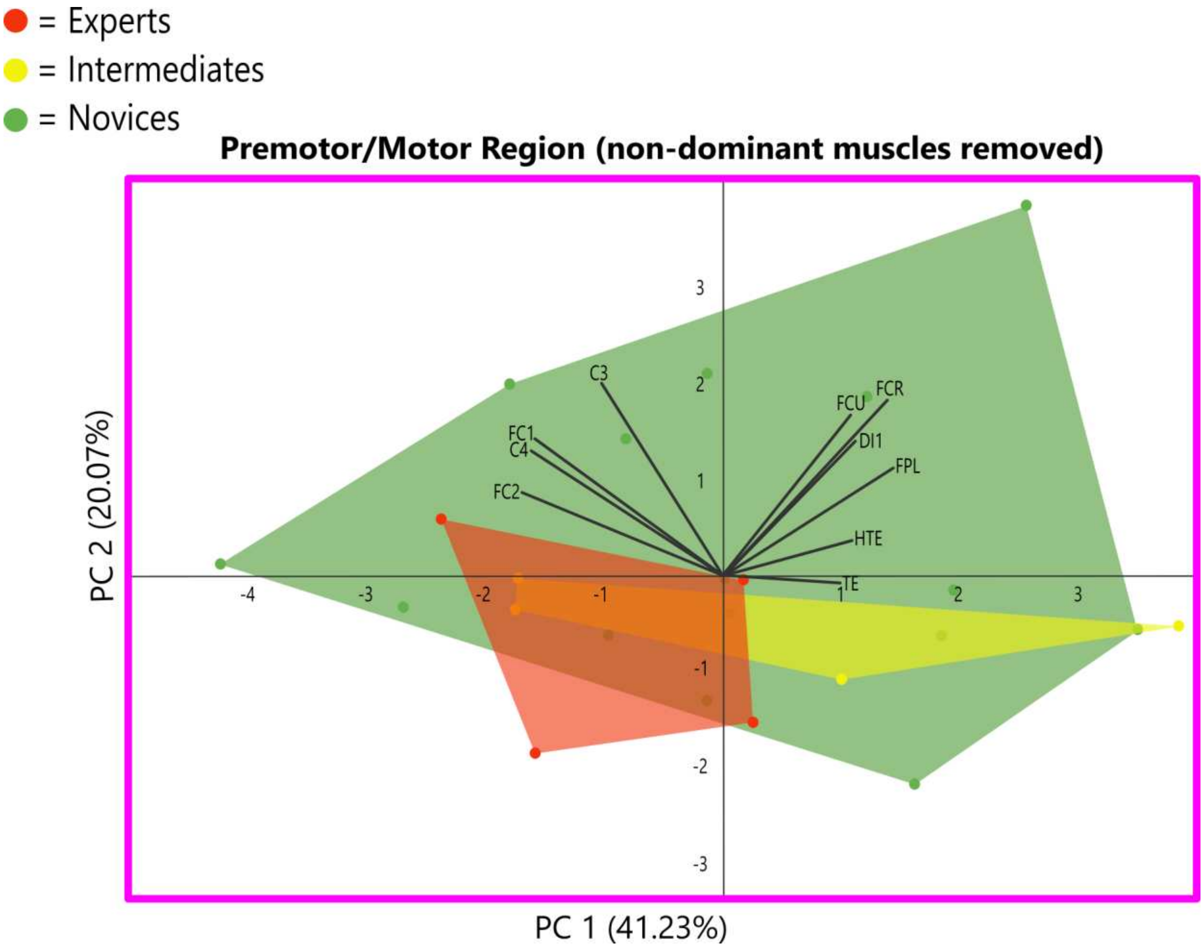
			Factor loadings							
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**P3**	**P7**
PC 1	3.01	37.68	0.67	0.78	0.68	0.84	0.74	0.36	-0.35	-0.11

SI Table 5. Left-frontal region PCA statistics and loadings values for the hammerstone Aim task comparing between experience groups.

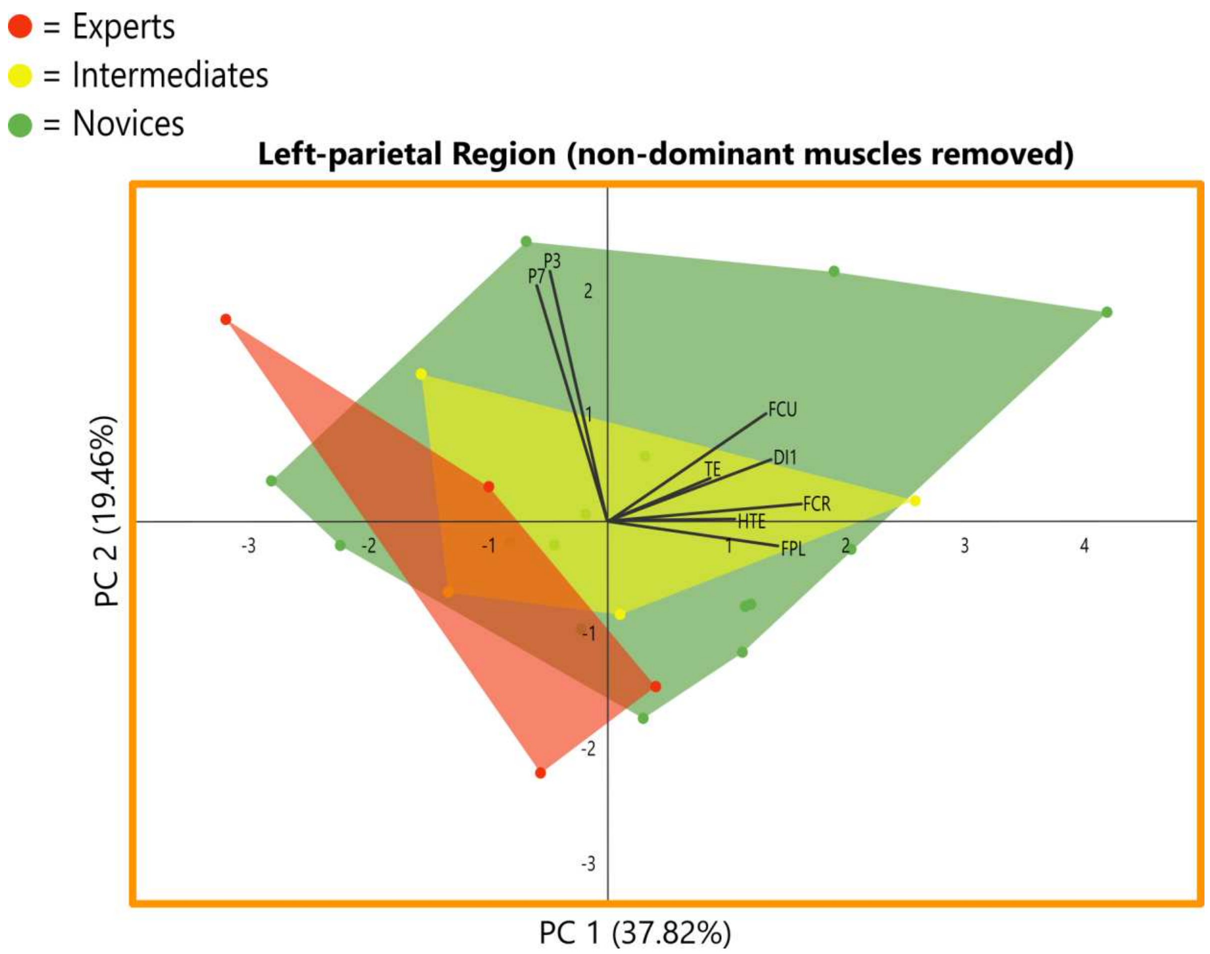
			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**F3**	**F7**
PC 1	3.58	35.80	0.69	0.52	0.81	0.78	0.68	0.51	0.50	0.65	-0.42	-0.04

SI Table 6. Left-frontal region PCA statistics and loadings values for the hammerstone Aim task comparing between experience groups, excluding non-dominant muscles.

			Factor loadings							
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**F3**	**F7**
PC 1	3.10	38.75	0.71	0.59	0.85	0.73	0.74	0.46	-0.46	-0.16



SI Figure 3. Experience group comparisons focusing on the EEG premotor/motor region and dominant-hand sEMG muscles during the hammerstone Aim phase. The PCA plot illustrates the differences between Expert (red), Intermediate (yellow), and Novice (green) participants. The PCA plots depict the first two components (see SI Table 7) and EEG and sEMG channels as loadings.



SI Figure 4. Experience group comparisons focusing on the EEG left-parietal region and dominant-hand sEMG muscles during the hammerstone Aim phase. The PCA plot illustrates the differences between Expert (red), Intermediate (yellow), and Novice (green) participants. The PCA plots depict the first two components (see SI Table 8), and EEG and sEMG channels as loadings.

SI Table 7. Premotor/Motor region PCA statistics and loadings values for the hammerstone Aim task comparing between experience groups, excluding non-dominant muscles.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	4.12	41.23	0.54	0.53	0.67	0.52	0.70	0.48	-0.49	-0.78	-0.76	-0.82
PC 2	2.01	20.07	0.47	0.12	0.61	0.56	0.37	-0.03	0.67	0.44	0.47	0.29

SI Table 8. Left-parietal region PCA statistics and loadings values for the hammerstone Aim task comparing between experience groups, excluding non-dominant muscles.

			Factor loadings							
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**P3**	**P7**
PC 1	3.03	37.82	0.72	0.56	0.86	0.70	0.76	0.45	-0.26	-0.32

SI Table 9. Premotor/motor cortex PCA statistics and loadings values for the flake Aim task comparing between experience groups.

			Factor loadings												
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	4.87	40.56	0.63	0.66	0.49	0.71	0.72	0.26	0.67	0.21	-0.72	-0.56	-0.84	-0.82
PC 2	2.23	18.59	0.07	0.53	0.40	0.43	0.16	0.37	0.17	0.67	0.52	0.62	0.33	0.43

SI Table 10. Premotor/motor cortex PCA statistics and loadings values for the flake Aim task comparing between experience groups, including left-handed participants.

			Factor loadings												
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	4.53	37.79	0.57	0.62	0.31	0.71	0.70	0.17	0.63	0.08	-0.74	-0.62	-0.84	-0.82
PC 2	2.51	20.94	0.28	0.49	0.62	0.35	0.22	0.49	0.28	0.64	0.55	0.61	0.30	0.39

SI Table 11. Premotor/motor cortex PCA statistics and loadings values for the hammerstone Aim task comparing between experience groups.

			Factor loadings												
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	4.64	38.65	0.54	0.49	0.66	0.59	0.66	0.51	0.46	0.66	-0.50	-0.78	-0.73	-0.77

SI Table 12. Premotor/motor cortex PCA statistics and loadings values for the hammerstone Aim task comparing between experience groups, including left-handed participants.

			Factor loadings											
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	4.10	34.12	0.50	0.49	0.31	0.56	0.61	0.51	0.43	0.45	-0.58	-0.78	-0.78	-0.79
PC 2	2.23	18.61	0.42	0.05	0.75	0.54	0.29	0.07	0.27	0.42	0.61	0.47	0.42	0.30

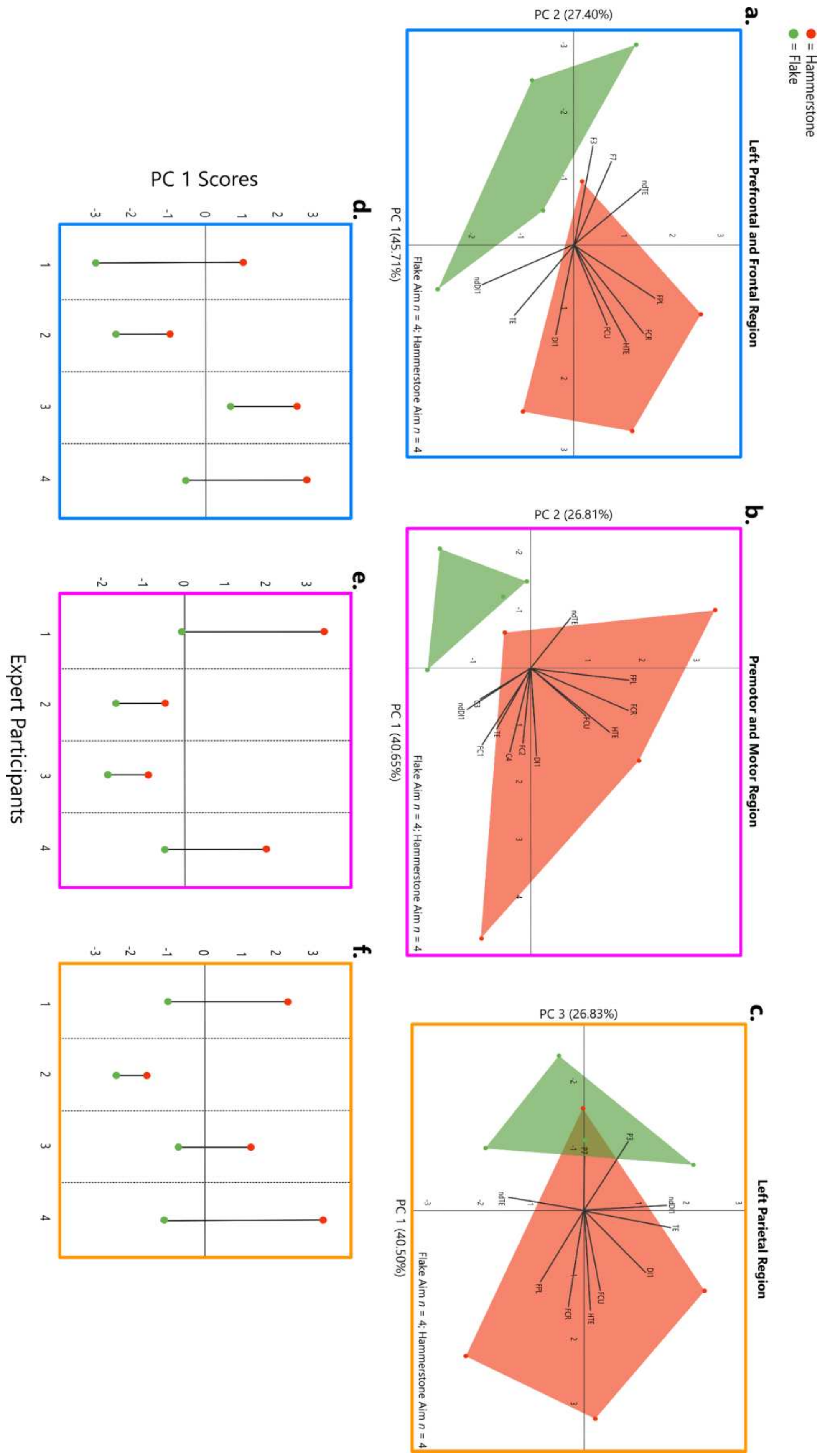
SI Table 13. Left-parietal region PCA statistics and loadings values for the flake Aim task comparing between experience groups.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**P3**	**P7**
PC 1	3.60	36.04	0.63	0.80	0.62	0.83	0.72	0.36	0.70	0.46	-0.33	-0.17

SI Table 14. Left-parietal region PCA statistics and loadings values for the hammerstone Aim task comparing between experience groups.

			Factor loadings									

Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**P3**	**P7**
PC 1	3.49	34.94	0.69	0.50	0.81	0.76	0.69	0.51	0.51	0.64	-0.20	-0.28

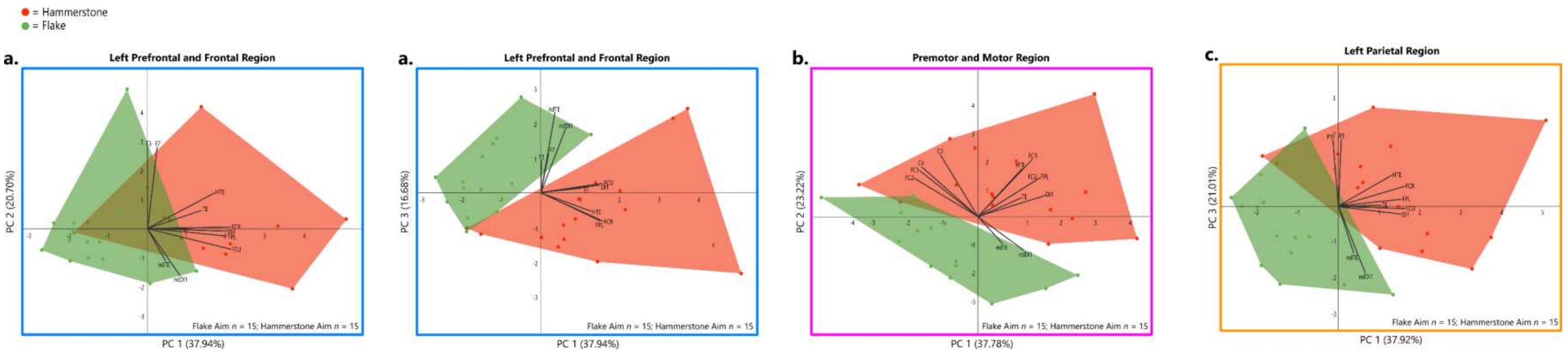


● = Hammerstone
● = Flake
a.
Left Prefrontal and Frontal Region
PC 2 (27.40%)
PC 1 (45.71%)
Flake Aim n = 4; Hammerstone Aim n = 4
F3
F7
ndTE
ndDI1
TE
DI1
FCU
HTE
FCR
FPL
b.
Premotor and Motor Region
PC 2 (26.81%)
PC 1 (40.65%)
Flake Aim n = 4; Hammerstone Aim n = 4
ndTE
FPL
FCR
FCU
HTE
C3
ndDI1
TE
FC1
FC2
C4
DI1
c.
Left Parietal Region
PC 3 (26.83%)
PC 1 (40.50%)
Flake Aim n = 4; Hammerstone Aim n = 4
P3
P7
ndTE
ndDI1
TE
DI1
FCU
HTE
FCR
FPL
d.
e.
f.
PC 1 Scores
Expert Participants
1
2
3
4

SI Figure 5. Paired comparisons between hammerstone Aim and flake Aim in Experts, focusing on the three ROIs and sEMG channels. Raw power PCA plots (**a-c**) demonstrate the differences between hammerstone Aim (red) and flake Aim (green) in the left-frontal region (**a**), premotor/motor region (**b**), and left-parietal region (**c**). The PCA plots depict the first two components with EEG ROIs and all sEMG channels as loadings (see SI Tables 22, 24, and 26). The drop-line plots (**d-f**) depict PC scores that display significant differences between tasks, hammerstone Aim (red) and flake Aim (green); PC1 (45.71%) left-frontal region (**d**), PC1 (40.65%) premotor/motor region (**e**), PC1 (40.50%) left-parietal region (**f**).

SI Table 15. Mean-adjusted left-frontal region PCA statistics and loadings values for Experts' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings										
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**F3**	**F7**
PC 1	5.84	58.39	0.60	0.96	0.99	0.74	0.94	0.46	-0.73	-0.66	-0.69	-0.68
PC 2	2.27	22.74	0.59	0.24	-0.04	0.44	-0.24	0.31	-0.61	0.41	0.70	0.70


● = Hammerstone
● = Flake
a.
Left Prefrontal and Frontal Region
PC 2 (20.70%)
PC 1 (37.94%)
F3
F7
HTE
TE
FCR
DIt
FPL
FCU
ndTE
ndDIt
Flake Aim n = 15; Hammerstone Aim n = 15
a.
Left Prefrontal and Frontal Region
PC 3 (16.68%)
PC 1 (37.94%)
ndTE
ndDIt
F7
F3
FCU
DIt
TE
HTE
FCR
FPL
Flake Aim n = 15; Hammerstone Aim n = 15
b.
Premotor and Motor Region
PC 2 (23.22%)
PC 1 (37.78%)
C3
C4
FC1
FC2
FC3
HTE
FCU
FPL
TE
DIt
ndTE
ndDIt
Flake Aim n = 15; Hammerstone Aim n = 15
c.
Left Parietal Region
PC 3 (21.01%)
PC 1 (37.92%)
P7
P3
HTE
FCR
FPL
TE
FCU
DIt
ndTE
ndDIt
Flake Aim n = 15; Hammerstone Aim n = 15

SI Figure 6. Paired comparisons between hammerstone Aim and flake Aim in Novices, focusing on the three ROIs and sEMG channels. Raw power PCA plots (**a-c**) demonstrate the differences between hammerstone Aim (red) and flake Aim (green) in the left-frontal region (**a-b**), premotor/motor region (**c**), and left-parietal region (**d**). The PCA plots depict all relevant principal components with EEG ROIs and all sEMG channels as loadings (see SI Tables 23, 25, and 27).

SI Table 16. Mean-adjusted left-frontal region PCA statistics and loadings values for Novices' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**F3**	**F7**
PC 1	4.75	47.46	0.77	0.90	0.97	0.91	0.94	0.79	0.02	-0.07	-0.23	0.07
PC 2	2.14	21.40	0.29	-0.24	0.00	0.10	-0.04	0.05	0.97	0.94	0.33	0.26

SI Table 17. Mean-adjusted premotor/motor cortex PCA statistics and loadings values for Experts' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings											
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	6.55	54.60	0.89	0.89	0.76	0.78	0.61	0.50	-0.98	-0.24	0.67	0.87	0.63	0.73
PC 2	3.11	25.91	0.25	-0.46	-0.62	-0.36	-0.68	-0.22	-0.09	0.77	0.34	0.48	0.67	0.65

SI Table 18. Mean-adjusted premotor/motor cortex PCA statistics and loadings values for Experts' paired comparisons of the flake and hammerstone Aim tasks, including the left-handed participant.

			Factor loadings											
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	6.45	53.78	0.88	0.89	0.77	0.75	0.63	0.53	-0.92	-0.26	0.65	0.84	0.67	0.75
PC 2	3.08	25.68	0.28	-0.45	-0.61	-0.39	-0.67	-0.29	-0.17	0.76	0.35	0.52	0.60	0.63

SI Table 19. Mean-adjusted premotor/motor cortex PCA statistics and loadings values for Novices' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings											
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	4.82	40.20	0.74	0.88	0.98	0.92	0.96	0.79	0.05	-0.08	0.38	0.05	-0.02	-0.07
PC 2	3.11	25.91	-0.39	0.03	-0.01	0.00	0.07	-0.07	-0.34	-0.51	0.65	0.84	0.85	0.84
PC3	1.88	15.67	0.13	-0.28	0.00	0.12	-0.04	0.01	0.92	0.81	0.31	0.12	0.30	0.27

SI Table 20. Mean-adjusted left-parietal region PCA statistics and loadings values for Experts' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**P3**	**P7**
PC 1	5.41	54.14	0.71	0.99	0.95	0.86	0.83	0.51	-0.85	-0.57	-0.44	0.29
PC 2	2.75	27.50	0.31	-0.02	-0.06	-0.08	-0.06	0.52	-0.32	0.81	0.83	0.96

SI Table 21. Mean-adjusted left-parietal region PCA statistics and loadings values for Novices' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**P3**	**P7**
PC 1	4.89	48.95	0.75	0.88	0.98	0.93	0.95	0.76	0.05	-0.06	0.48	0.01
PC 2	2.03	20.34	0.29	-0.27	-0.02	0.09	-0.09	0.02	0.96	0.96	0.06	0.01

SI Table 22. Raw left-frontal region PCA statistics and loadings values for Experts' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**F3**	**F7**
PC 1	4.57	45.71	0.78	0.83	0.76	0.70	0.46	0.61	0.34	-0.49	-0.86	-0.73
PC 2	2.74	27.40	-0.16	0.47	0.63	0.30	0.74	-0.53	-0.81	0.61	0.18	0.35

SI Table 23. Raw left-frontal region PCA statistics and loadings values for Novices' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**F3**	**F7**
PC 1	3.79	37.94	0.82	0.70	0.86	0.86	0.82	0.56	0.34	0.19	0.01	0.11
PC 2	2.07	20.70	-0.02	0.37	0.02	-0.20	-0.07	0.19	-0.48	-0.32	0.89	0.85
PC 3	1.67	16.68	0.08	-0.19	-0.29	0.10	-0.29	0.06	0.67	0.84	0.34	0.42

SI Table 24. Raw premotor/motor region PCA statistics and loadings values for Experts' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings											
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	4.88	40.65	0.93	0.68	0.45	0.51	0.14	0.65	0.44	-0.51	0.33	0.89	0.81	0.80
PC 2	3.22	26.81	0.06	0.71	0.87	0.50	0.88	-0.29	-0.55	0.35	-0.44	-0.18	-0.42	-0.06

SI Table 25. Raw premotor/motor region PCA statistics and loadings values for Novices' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings												
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**C3**	**C4**	**FC1**	**FC2**
PC 1	4.53	37.78	0.78	0.51	0.64	0.71	0.72	0.51	0.54	0.28	-0.43	-0.65	-0.68	-0.73
PC 2	2.79	23.22	0.25	0.55	0.66	0.44	0.45	0.22	-0.37	-0.29	0.71	0.57	0.53	0.45

SI Table 26. Raw left-parietal region PCA statistics and loadings values for Experts' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**P3**	**P7**
PC 1	4.05	40.50	0.61	0.97	0.94	0.78	0.69	0.17	-0.05	-0.10	-0.67	-0.53
PC 2	2.68	26.83	0.60	0.06	-0.15	0.16	-0.42	0.84	0.81	0.73	0.43	0.01

SI Table 27. Raw left-parietal region PCA statistics and loadings values for Novices' paired comparisons of the flake and hammerstone Aim tasks.

			Factor loadings									
Principal Component	**Eigenvalue**	**% of variance**	**DI1**	**HTE**	**FCR**	**FCU**	**FPL**	**TE**	**ndDI1**	**ndTE**	**P3**	**P7**
PC 1	3.79	37.92	0.82	0.69	0.86	0.86	0.83	0.56	0.35	0.19	0.03	-0.08
PC 2	2.10	21.01	-0.09	0.34	0.22	-0.03	0.08	0.01	-0.74	-0.52	0.74	0.75

Statements and Declarations

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Competing Interests

The authors declare no competing interests.

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Data availability

The dataset used in this study is available from the corresponding author upon request.

Ethics statement

The experiment was performed in line with the Declaration of Helsinki (1964; revised 2013). Ethical approval was obtained from the Ethics Committee for Psychological Research at the University of Tübingen, and written informed consent was secured from all participants prior to their participation in this study.

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