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The Effects of Training on Action Observation: A Neuroarchaeological Investigation using EEG

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To my family

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Abstract

Like all organisms, humans have evolved from their ancestors. This process of evolution has not only changed the physical appearance of humans, but also shaped their cognitive mechanisms and abilities. Over time, humans have developed various cognitive abilities in response to specific events during their evolution. For example, living in more densely populated groups may have led humans to develop a cognitive mechanism to monitor others' actions, thereby increasing their chances of survival. Cognitive neuroscience seeks to answer, among other issues, questions regarding the cognitive processes that humans possess today as a result of evolution. Interdisciplinary studies are required to better understand how these processes function. Here, we introduce a relatively new field that combines neuroscience and archeology called *"neuroarchaeology"*, which can provide insights into the origins of *homo sapiens* cognition. Based on this interdisciplinary perspective, we focused on action observation and reported the results of our experiment that utilized EEG to investigate whether toolmaking training might have caused differential brain activity between groups during an action observation task. Our preliminary findings showed subtle differences between the experimental (trained) and the control groups. These results can serve as a valuable reference point for more extensive future studies in this area.

CHAPTER 1: Introduction

1.1 A New Discipline Emerges: Neuroarchaeology

At first glance, archaeology and cognitive neuroscience may appear as two highly unrelated fields of scientific inquiry because of their distinct study questions and methods. Archaeology, as a discipline, investigates anthropological inquiries regarding past societies and primarily uses ancestral remains as data, although not exclusively (Harris and Smith, 2001). Archaeology can provide unique answers into the understanding of human cognition. It can especially answer questions regarding the timing and place (evolutionary context) of human cognitive evolution (Wynn, 2002). The most common material evidence for the archeologists is the tools that our ancestors made with stones and that have come down to our day. Our ancestors used a method named “knapping”, which means striking one stone to the other with a certain power and a certain angle so that one of the stones will end up having a sharp edge that can be used for a variety of functions (Wynn, 2002). This relatively simple but very important motor repertoire of our ancestors may have a relationship with the development of some cognitive mechanisms such as visuo-spatial processes (Stout et al., 2000).

Cognitive neuroscience, on the other hand, is the study of the neural processes underlying cognition. Neuroscientists mostly do not aim to understand how a human cognitive ability emerged or what environmental conditions forced it to evolve the way it is today; rather they aim to understand how the mind works today, digging into this big question through different techniques.

Both archeology and neuroscience have contributed to the understanding of the human mind in their own unique ways but, to understand the human mind and answer our questions about it more in depth, we need more interdisciplinary studies. A relatively new scientific discipline that tries to fill that gap and meet archeology and neuroscience, is named *Neuroarchaeology* (Malafouris, 2009). Neuroarchaeology can be seen as application of neuroscience theories and methods such as neuroimaging to answer questions raised by archaeology (Stout & Hecht, 2015). For instance, Stout et al. (2008) conducted a study employing Positron Emission Tomography (PET), which revealed enhanced brain metabolic activity in areas that coincide with language-related regions while participants engaged in toolmaking tasks. Researchers posit that the utilization of tools may have facilitated the elaboration of specific brain regions, leading to the development of more advanced cognitive abilities in humans through this reciprocal interaction. This study can be regarded as a preliminary demonstration of how neuroarchaeology can address inquiries pertaining to human cognition. Neuroarchaeology can contribute to both the studies of archaeology and neuroscience. On the one hand, archaeologists can better understand which cognitive abilities were required by our ancestors to perform some behaviors such as toolmaking with the support of neuroscientific theories and methodology. On the other hand, neuroscientists can benefit from the material data strength of archeology to better understand how the interaction with materials and use of primitive technology that can be thought of as tools that made for a purpose (Renfrew et al., 2008) shaped human mind to solve mysteries of highly complicated human cognition. Stout and Hecht (2015) argue that anthropology stands as a prominent discipline that can assist neuroscientists in comprehending the evolutionary trajectory of cognitive abilities through comparative investigations across different human populations and various species. However, anthropology alone is insufficient to address inquiries regarding the specific circumstances that contributed to the development of these abilities, and archeology can fill the gaps of neuroscience-anthropology collaboration with its ability to show how interaction with materials shaped human cognition and when and in which context this interaction occurred. Neuroarchaeology will be a prominent and significant study field for both archeology and neuroscience in the coming years, as scientists from both disciplines aim to understand why the human mind works the way it does, how cognition is evolved, and what were the contributing factors for this evolution that makes our mind unique and highly sophisticated today.

1.2 Evolution of Cognition

After long years of philosophical and scientific inquiry, it is now widely accepted that the human brain is the organ that makes cognition possible. The human brain is a very complex system with billions of neurons (Azevedo et al., 2009) and trillions of connections between these neurons. This complex endeavor makes it possible for humans to solve the problems they face throughout the day. Like all organisms, humans have evolved from their ancestors. This process of evolution has not only changed the physical appearance of humans but has also forged their cognitive mechanisms and abilities. Over time, our ancestors have developed various cognitive abilities in response to specific events and ever-changing environmental demands during their evolutionary history. For example, living in more densely populated groups may have led humans to develop a cognitive mechanism to monitor others' actions, thereby increasing their chances of survival. Furthermore, Byrne and Bates (2007), argue the importance of socialization in the evolution of cognition, arguing that increased group member numbers require some cognitive abilities such as perception and memory for others.

The founding father of modern evolutionary theory, Charles Darwin (1871), noted some similarities between humans and non-human animals, and thought that studying these similarities could be informative in understanding human cognition. This idea has inspired the studies that focus on comparative psychology, which aimed to understand how human cognition is different from cognition in other animals, especially other apes, since they are humans' closest living relatives. In the early years of these studies, it was thought that absolute brain size is a reliable index of highly developed cognition and intelligence, but studies that show animals with not very big brains still show signs of developed intelligence. Research on birds has shown that they have a robust cognitive repertoire, including even some forms of reasoning (Emery & Clayton, 2004). Currently, an index of advanced cognition is not the absolute size of the brain; rather the relative size of the brain with respect to the whole body (Horik and Emery, 2011). Some studies have shown that among all mammals, humans have the largest relative brain size, followed by other primates and dolphins (Roth and Dicke, 2005). Many different hypotheses have been put forward to understand what could lead to large relative brain sizes in mammals. These hypotheses have focused mostly on socialization (Reader and Laland, 2002), mating (Emery et al., 2007), diet (Runbar and Schultz, 2007), and tool use (Lefebvre et al., 2004). The interaction of our ancestors with materials (i.e., tools) is thought to shape their and consequently our minds (Renfrew et al., 2008).

Material Engagement Theory (Malafouris, 2013) proposes that to understand the development and evolution of human cognition, it is necessary to consider how humans engaged with different materials (i.e., stone tools) throughout evolutionary history. Malafouris (2019), argues that the human mind cannot be localized within the brain and cannot be seen as something that is isolated in the body; rather it should be thought as an always ongoing process that becomes real with the interaction with materials and the environment. This conceptualization of the mind is a familiar view for the philosophy of mind literature. The "extended mind" view of cognition argues that the brain is not the sole location of the mind; rather, the mind is extended from the body and the interaction between body and environment is what constitutes cognition (Stout & Chaminade, 2007). This was a radical claim when it was first put forward, but it is now a widely discussed topic among philosophers of mind and cognitive scientists with many supporters. Moreover, in contemporary discourse, the perspective of cognition is often referred to as the "4E" framework, encompassing embodied, embedded, extended, and enacted cognition. While these concepts possess nuanced distinctions, they collectively challenge the conventional notion that cognition is confined to the body, particularly the brain (Menary, 2010). Archaeological investigations that center on the interaction between early hominins and tools have the potential to illuminate the connection between inner cognition and the external world. For example, *Homo habilis* (Leakey et al., 1964), is known as the first Homo genus that made long-lasting tools and used these tools efficiently although their ancestors are also thought to have made some basic tools (Jeffares, 2010). These toolmaking and tool use skills of Homo habilis may have led to the development of new cognitive abilities that were not present in earlier *Hominids.*

1.3 Toolmaking

One of the most unique features of humans is their behavioral traditions, which are often constituted by toolmaking skills (Stout, 2011). Toolmaking is a complex procedure that requires some kind of intentionality to use these tools later for a specific purpose. It is well documented that different species use tools for various reasons (Boesch & Boesch, 1990; Hunt, 1996; Jones & Kamil, 1973). Humans have been creating and using tools for a long time. Everything we create today as a product of engineering can be thought of as a tool that makes life easier for us and makes us gain time. However, the earliest tools that our ancestors are believed to have crafted and used were stone tools. (Semaw et al., 1997) which were made by hitting two stones against each other to make one of them sharp enough. Moreover, some societies in different parts of the world still make and use tools with stones (Gallagher, 1977). Human stone toolmaking technologies are mainly categorized into two different industries: namely Oldowan (Leakey, 1936) and Acheulean. Oldowan technology gets its name from the region Olduvai, Tanzania since stone tools related to this technology were found in that region. However, later research has shown that the earliest examples of Oldowan technology belong to 2.6 Myr. ago and were found in Ethiopia (Semaw et al., 1997; 2003; Semaw, 2006). Oldowan type of stone tools are characterized by basic forms of different stones that are not that much processed but used for different purposes (Toth & Schick, 2018). On the other hand, Acheulean technology is dated to approximately 1.8 Myr. ago and is characterized by more developed, processed stone tools (Lepre et al., 2011). Additionally, the hallmark of Acheulean technology lies in the presence of stone tools resembling hand axes and knives, which are specifically categorized as Large Cutting Tools (Favreau, 2023).

Another important event in the history of toolmaking is the use of clay to make pottery by our ancestors in different parts of the world, independently of each other (Kuzmin, 2013). Humans started making these clay-based products tens of thousands of years ago and then used them for different reasons such as cooking and storage of foods and for higher-thought reasons such as rituals (Rice, 1999). Moreover, it has been argued that our ancestors may have used these pots made with clay to boil some food to make them easy to digest (Kuzmin, 2013).

Both types of stone tools either made with Oldowan or Acheulean type and pottery made with clay were important tools for our ancestors' survival struggle because these tools helped them to solve problems they faced throughout the evolution, especially related to food. Furthermore, these different toolmaking strategies at different times of history contributed to the evolution of different cognitive and motor abilities in our ancestors that passed on to us by successful ancestors. Archaeological artifacts such as stone tools and pottery can provide insights to understand timing and reasons for the evolution of human cognition (Wynn, 2002).

1.4 Co-evolution of the Human Mind and Toolmaking

Not only the physical characteristics but also the cognitive abilities of humans are shaped by our ancestors' relationship with their surroundings and tools they made and used to manipulate their environment. It is well known that culture has an impact on cognition (Thompson et al., 2016) and toolmaking skills can be considered as a prominent part of human culture (Frey, 2008). Furthermore, tools are prominent artifacts that reflect our ancestors' cognitive abilities (Stout, 2002). For these reasons, it is widely argued that to better understand human cognition and its evolution, our ancestors' interactions with the tools they made should be well studied and understood.

The co-evolution of human cognition and primitive technology has been theorized to have started as soon as people began employing stone tools to modify their environment (Renfrew et al., 2008). Humans were using stone tools for at least 2.6 Myrs (Semaw et al., 1997), starting with the Acheulean tool technology, which covers more complex stone tools. Moreover, they have begun developing more complex behaviors that were not necessary for their earliest ancestors who only created simpler tools. These complex behaviors are accompanied by larger brain sizes, which can indicate the presence of more advanced cognitive abilities. (Ambrose, 2001; Diez-Martin et al., 2015; Klein, 2000). Coolidge et al. (2015) argues that the change towards increased complexity of tools used by our ancestors reflects the evolution of human cognition and endowment of mind with more sophisticated systems. Evolutionary pressures on the prefrontal cortex (PFC) seem to affect the development of different cognitive abilities, such as working memory (WM), which may have in turn, made our ancestors able to produce complex Acheulean tools (Putt et al., 2019; Stout et al., 2015). A study using functional near-infrared spectroscopy (fNIRS) neuroimaging technique has shown that there is an overlap in the brain regions activated by Acheulean toolmaking and piano playing in modern humans (Putt et al., 2017). This discovery may suggest that the practice of Acheulean toolmaking contributed to the development and refinement of brain networks enabling humans to exhibit proficiency in piano performance. This significant finding elucidates the potential role of early toolmaking skills in the acquisition and progression of more sophisticated cognitive abilities. Furthermore, it has been argued that the practice of Acheulean toolmaking potentially facilitated the further evolution of the superior temporal gyrus (STG). This proposition stems from the notion that the production of more complex tools such as hand axes necessitates the integration of higher-order planning with auditory feedback generated during the knapping process. It has been speculated that increased utilization of STG in this context may have contributed to the advancement of neural networks responsible for the perception of speech in humans. Enhanced speech perception abilities, in turn, may have played a pivotal role in the development of language skills among ancestral populations. There exists a pronounced asymmetry in many language abilities that predominantly favors the left hemisphere in nearly all individuals (Corina et al., 1992). Moreover, the left hemisphere appears to play a significant role in the integration of the sensorimotor and cognitive processes. It is plausible that these asymmetries in the functioning of the left hemisphere contribute to the shared cognitive mechanisms underlying the use of complex tools (i.e., motor skills) and language skills (Frey, 2008). Over the last 20 years, extensive studies have been conducted with the aim of understanding which brain regions and cognitive abilities accompany the use of these complex tools. Research showed that cognitive abilities such as causal reasoning (Johnson-Frey, 2003), sensorimotor abilities (Stout & Chaminade, 2007), and language (Stout et al., 2008) co-evolved with the complex tool-use skill of humans. Malafouris (2015) argues that human cognition is an evolved entity with its unique capacities, but it is not complete in itself. The human mind continues to evolve, it is an ever-going process and for this continuous process it is important to keep in mind its interaction with materials in the environment. He named this interactive process as *metaplasticity* (Malafouris, 2013), and puts forward the Blind Man's Stick Hypothesis, that talks about a blind man who utilizes a stick to perform his daily tasks, to explain how incomplete human cognition interacts with environment with tools to complete his or her cognition.

The interaction between tools and the human mind seems to be reciprocal; complex cognitive abilities lead to the production of more complex tools that direct the evolution of cognitive abilities, as a sort of virtuous cycle (Jeffares, 2010). Since our ancestors learned how to make these complex tools and passed this information on to their offspring, we can argue that observation of others' actions was also a prominent cognitive and behavioral repertoire of humans.

1.5 Action Observation

Humans possess a network named Action Observation Network (AON), which enables them to understand the goals and intentions related to observed actions, not only the actions performed by the individual, but also enables them to imitate observed actions more precisely (Caspers et al., 2010). Additionally, the activity of AON helps humans to predict the actions of others (Balser et al., 2014). AON exhibits a remarkable level of development in humans, enabling them to discern the intentions and objectives of others solely through the observation of their actions (Blakemore & Decety, 2001). Human gaze movements play a paramount role in facilitating the optimal functioning of the AON. The coordination between gaze movements and AON significantly contributes to the effective processing and interpretation of human actions. It has been argued that an observer's gaze movements, which track the hand movements of the individual performing an action, play a crucial role in facilitating the ability to understand and predict others' actions. This process generates a convergence between the visual and motor maps of the observer, specifically tailored to that particular action, thereby enabling the observer to comprehend the actions of others (Flanagan & Johansson, 2003). Given that humans rely on their eyes to meticulously observe actions from initiation to completion, comprehending the significance of eye movements becomes pivotal in deciphering the actions of others. By gazing upon the visual field, humans gain insights into their surrounding environment and acquire an understanding of unfolding events in the external world. During the observation of an action, whether performed by oneself or another individual, our eyes possess the ability to predict the trajectory of the performer's hand movements. Specifically, our gaze anticipates the location at which an action end. This predictive gaze movement activates the motor system that is required to perform the observed action, thus helping our understanding of the actions performed by others (Gredeback & Falck-Ytter, 2015). Furthermore, humans have the capacity to form a motor memory of an observed action within their motor cortex, akin to executing the same action themselves. This motor memory may serve as a beneficial resource, enabling the observer to perform the same action with enhanced precision if the situation necessitates it and if the action holds significant importance (Stefan et al., 2005). Moreover, action observation is not only beneficial for a better performance for the observer in terms of the execution of the observed action, but it can also be used as a tool for neurorehabilitation and can benefit people with neurological problems such as stroke (Buccino, 2014; Celnik et al., 2008; Ertelt et al., 2007).

Knowledge that is acquired by observation can be imitated by the observer and can be passed to other people in the population but, more importantly, it can be passed to the next generations. To be a shared knowledge across the population and to be passed on to next generations, these learned characteristics should help individuals or populations in a way that can have a prominent impact on survival. Sophisticated action observation mechanisms should have helped our ancestors with their survival struggle in a variety of ways. For instance, observers can readily choose among possible responses within their repertoire and can be better prepared for the harmful actions of others. Moreover, learning from others is an important ability for both humans and other animals to survive (Rabbitt, 1966), and humans can learn motor sequences to perform an action by simply observing someone performing that action (Petrosini et al., 2003). An EEG study showed that action observation is an effective tool for learning and performing a motor task that reflects increased sensorimotor activity during observation and better performance in task execution (Gonzalez-Rosa et al., 2015). This ability of humans seems to have evolved very early in evolutionary history, since our ancestors learned so much knowledge and skills from their antecedents, such as how to make tools by observing them. This valuable ability, toolmaking, was an important contributor to the success of our ancestors since these tools could be used for a variety of scopes and this information has been passed on through generations. Those who observed better, mastered their skills better, became more successful, increased their chance of survival, and we are descendants of those who were successful. For this reason, observing others' actions while they interact with tools had substantial benefits to the observer throughout the evolution of our species. It is argued that humans learn these skills by internally representing motor actions taken by others while observing these actions and this is referred as *shared representation of action* (SRA). SRA is a well-supported hypothesis by the findings that there are overlapping brain areas that are activated for both execution and observation of action (De Vignemont & Haggard, 2008; Grezes & Decety, 2001). How the human brain creates these internal representations of actions and makes sense of the underlying intentions and goals of these actions is a prominent and highly debated study topic in the field of cognitive neuroscience.

1.6 Action Observation and Mirror Neuron System

A promising answer to the questions of how humans make sense of the actions of others is tentatively provided by the mirror neurons hypothesis. It empirically originates from an outstanding finding that showed that monkeys (macaques) have a subgroup of neurons in the motor region of their brain (F5), called *mirror neurons*, which are thought to help internally represent the observed action (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti & Craighero, 2004). Furthermore, although it is still a widely debated topic in the neuroscience literature, there is evidence from different studies utilizing different tools, from electrophysiological measurements to functional neuroimaging, which suggests that also humans possess these neurons (Rizzolatti et al., 2001). Action observation can be thought of as a process that is a part of this mirroring system that helps humans to monitor others' motor actions so that we do not commit the same errors, learn simply by observing, and perform better for motor tasks such as toolmaking. It is a well-known fact that social learning is an important part of human daily living because humans can learn different skills from others and imitate them just after observation (Bandura & Walters, 1977). Humans can even learn fine motor skills just by observing others who perform these skills (Carroll & Bandura, 1982, 1987, 1990). Furthermore, by observing others, humans can master the required motor skills to the level that they themselves perform these skills (Blandin & Proteau, 2000), so that their performance can be sufficient when they need to use these skills and perform related actions in the future. We can appreciate the importance of the cognitive system that allows humans to observe actions and understand the intentions of actions simply by observing, especially when we think about this system from an evolutionary perspective as gains that will increase survival chances for individuals and species. For instance, well-developed cognitive systems that are devoted to action observation may have helped our ancestors to better understand the actions that will lead to better internalization of motor skills such as toolmaking.

To understand how to make tools by observation, one needs to observe particularly hand movements, since hands are part of the body that convey much more information about the toolmaking process. In line with this idea, in a study using TMS to stimulate the motor cortex, it has been shown that when humans observe an action which is executed by others, neurons in the motor cortex of observers became more easily excitable, which is called as *motor resonance* (Fadiga et al., 1995). Furthermore, enhanced activation of mirror neurons especially for the hand movements of others could reflect the fact that these neurons' function is to help humans to understand and imitate observed actions (Rizzolatti et al., 2001) and this finding can be considered as an important support of the conceptualization of action observation processes in terms of mirroring system. In their eminent paper on mirror neurons, Rizzolatti et al. (2001) put forward evidence for the *direct-matching hypothesis.* This hypothesis suggests that monkeys and humans do not understand the action of others solely with the help of the visual system; instead, they give meaning to an action when the information coming from the visual system represented in the motor system matches with the action of the individual we observe. To understand the intention and goal of an observed motor action, an observer is required to internally represent that set of actions in his/her motor network (Rizzolatti, 2005; Rizzolatti & Fabbri-Destro, 2008). Acknowledging the role of mirror neurons in the functioning of action observation networks can help researchers to understand some pathologies that are mostly characterized by a deficiency related to understanding the goals of motor actions of others, such as autism spectrum disorders (Rizzolatti & Fabbri-Destro, 2008). Moreover, studies using EEG and fMRI with children showed that the action observation-execution matching system develops earlier than previously thought (Dapretto et al., 2006; Lepage & Théoret, 2006). These findings support the idea that the mirror neuron system used to understand others' actions is not a system developed with interaction with the environment; rather, it is an inherent system of the human brain that evolved in our early ancestors (but see e.g., Hickok, 2009, Caramazza et al., 2014, for some criticism of this theory).

Studies aiming to show which brain regions are employed for an action observation network are important for understanding how the activity of mirror neurons modulates the action observation system in the brain. A meta-analysis that consisted of data from 104 different neuroimaging studies utilizing fMRI or PET, in which participants were instructed to solely observe motor actions, found that activation in the Brodmann area 44 (BA 44, Broca's area) and 6 (BA 6, premotor area) were highly associated with the observation of actions. Moreover, while activation of BA 44 was more tightly associated with the observation of non-hand actions, activation of BA 6 was more closely associated with the observation of hand movements (Caspers et al., 2010). This finding is prominent to understand the relationship between the activity of mirror neurons and the action observation system, since it is thought that the BA 6 region in the human brain is functionally homologous to the F5 region of the macaque brain (Fink et al., 1997; Morin & Grèzes, 2008). To further understand the possible role of the activation of mirror neurons in the premotor area on action observation, we can refer to lesion studies, that show that a lesion in that region of the brain can cause a deficit of motion perception, which may negatively influence efficient engagement in action observation (Saygin, 2007).

A robust system of mirror neurons seems to be a promising candidate for explaining how humans developed a sophisticated culture that covers topics such as art, language, and obviously toolmaking. The prominent neuroscientist Ramachandran (2000) argues that even though other apes (i.e., chimpanzees) have a system that can be named as culture and use tools as well, they could not reach the complexity of human tools that we can appreciate today because their mirror neuron system has not reached the sophistication of humans. This approach towards action monitoring is promising because it can explain how and why humans developed an action monitoring system. However, only passively observing the motor actions of others may not be sufficient for this sophisticated toolmaking culture of humans. Humans often commit errors, which risk harming the process of this passed knowledge for generations. Observers should be able to differentiate which motor acts are appropriate and which are not to perform these motor movements in a more efficient way. Hence, it is also important to develop a cognitive system that is responsible for monitoring and detecting others' motor errors.

1.7 Error Monitoring

Imagine you are trying to learn how to make a kite by observing someone making a kite. As it has been argued above, you will have an internal motor representation of the hand movements of the person who is making the kite, but as you can appreciate, you also need to monitor and detect errors of that person to understand the action because humans are very likely to commit errors so often, and you should understand which erroneous actions interfere with the purpose of making a kite.

The error monitoring system is very closely related to the action observation system because both can be thought of as part of a human performance monitoring system (Pezzetta et al., 2018). To learn how to make a well-functioning tool, our ancestors not only needed to merely observe a set of motor actions, but they also conceivably needed to monitor and detect errors committed while making a tool. Error monitoring is a well-studied topic in neuroscience because of its crucial importance. Extensive research has shown that humans have a specialized cognitive mechanism responsible for the monitoring and detection of errors. Falkenstein et al. (1991) found that there are two Event-Related Potential (ERP) components that are related to error monitoring, detection, and error awareness in humans, and they labeled these components as Ne (Error Negativity, also called Error Related Negativity (ERN) e.g., in Gehring et al., 1993) and Pe (Error Positivity). Other studies from different laboratories have confirmed the existence of these two ERP components as brain’s response to errors (Gehring et al., 1993; Dehaene et al., 1994; Nieuwenhuis et al., 2001; Hermann et al., 2004; Endrass et al., 2007; Masina et al., 2019). Ne is defined as an increased negative amplitude over the frontal-central scalp electrodes that peaks around 20-100 ms after the error, while Pe is an increased positive amplitude over the parietal-occipital electrodes that peaks around 200 to 500 ms after the error (e.g., Falkenstein et al., 1991; Gehring et al., 1993; Falkenstein et al., 2000). These two ERP components have different roles in terms of error monitoring: Ne-ERN represents the detection of an error with an internal system probably without any awareness, while Pe reflects the fact that errors are consciously detected by the individual (Endrass et al., 2007; Nieuwenhuis et al., 2001).

Further studies have shown that humans code the errors of others in the same way they code errors committed by themselves. Indeed, the electrophysiological signals for both types of errors are reflected by the same ERP components (Bates et al., 2005; De Bruijn & Von Rhein, 2012; Miltner et al., 1997; Van Schie et al., 2004). Moreover, these components for both types of errors are thought to originate from the same brain regions, and an fMRI study supports this argument (Jääskeläinen et al., 2016). These findings can illuminate the remarkable functioning of the motor action internalization system in humans, demonstrating its highly advanced nature. This sophisticated system enables humans to encode observed errors as if they were their own errors. Humans have been committing errors throughout their history, but not every error is the same in terms of its importance for our survival, as we can appreciate that some errors do not have a major influence, while others can have a substantial impact on humans. From this perspective, one can expect that, as the significance of an error increases, the electrophysiological response to that error will be more pronounced. In line with this expectation, studies that manipulated the significance of an error revealed that as the amplitude of ERPs that are related to error detection is sensitive the importance of errors to the individual: as the significance increases, amplitude increases (Hajcak et al., 2005; Maier et al., 2008).

1.8 Training and Action Observation

Training is one of the most important tools that humans have, to acquire a skill or to cultivate an already acquired skill further. When assessing the proficiency of individuals in a specific skill, it is anticipated that those who have received training in that particular skill will exhibit superior performance compared to individuals who have not undergone any training. How training influences performance is a prominent question to ask. From a neuroscience perspective, it is important to understand which brain mechanisms are related to and affected by training. In the context of motor tasks, training can be conceptualized as a mechanism that enhances the reactivity of the motor areas within the brain. Training creates memory in motor regions, and as mentioned above, even just the observation of a motor action can create these motor memories that will benefit the observer in terms of task performance. Research has shown that both physical and mental training can help individuals to learn better (Curlik & Shors, 2013). This ability of the human brain is attributed to its high plasticity. Even after a stroke, individuals can benefit from training to regain their motor movements to some extent (Nelles et al., 2001).

Another way to measure how training affects performance is to look at brain signals for a specific task if they differ after training. Action observation can serve as a tool to see if trained individuals observe actions in a different way than untrained individuals, and if so, how this difference is reflected in the brain signal. Calvo-Merino et al. (2005) aimed to understand whether the brain's response to an observed action is influenced by the observer's action repertoire. Researchers requested professional ballet and capoeira dancers watch both clips of ballet moves, and capoeira moves while participants were lying in the MRI scanner to record their BOLD signal. These authors found that expert ballet dancers exhibited increased BOLD signals for ballet moves compared to capoeira moves in brain regions that are part of the mirror neuron system and the pattern was reversed in capoeira dancers. These findings replicate earlier literature that shows that our brain simulates the observed motor actions, but further shows that the mirror neuron's activity is modulated by the previous motor experience of the observer (Calvo-Merino et al., 2005). Furthermore, showing that our mirror neuron system can differentiate ballet moves from capoeira moves, it is a highly sophisticated system that does not focus solely on gross movements to monitor an action. Another study that compared expert archers with naïve controls while watching a video showing archery found the same activation pattern. Although both groups exhibited increased activity in the premotor area as expected, hyperactivation was observed in the premotor regions of the expert archer's brain compared to the control group (Chang et al., 2011). Similar findings were obtained in a neuroimaging study that compared professional pianists with naïve controls (Haslinger et al., 2005). These studies show how expertise affects action monitoring, but a further interesting point would be to show how much experience with the observed action is enough to modulate the brain's response to the observation of that action. If expertise can have an influence, it can be expected that initial experience of novice individuals may also have an impact. Consistent with this anticipation, participants who had only a very limited experience with the observed action, specifically drawing novel characters on an LCD screen with a stylus, exhibited a distinctive electrophysiological signal compared to the control group. Participants in the experimental group who had imitation training on how to draw these characters displayed a larger desynchronization in the 11-13 Hz band compared to control participants who did not have any experience with the observed action (Marshall et al., 2009). Our action observation system is very sensitive to the motor experience we have with the action we are observing. Even a limited difference in experience can lead to different brain signals related to that action's observation. In a subsequent investigation conducted by the same researchers, it was discovered that the neural response to novel experiences was influenced by the level of experience. Participants who underwent more extensive training, including both visual and motor training, exhibited a greater degree of desynchronization (Quandt et al., 2011). An EEG study utilizing Time-Frequency (TF) analysis replicated the finding that experience with an action modulates the brain's response to the observation of that action; further, showed that even a semantic experience with the action (i.e., reading about the action), had an impact on the EEG signal, which is reflected by greater suppression of alpha and beta rhythms in a number of electrodes (Quandt & Marshall, 2014). Based on these findings, we can appreciate how much the human brain can benefit from training for a motor task, even if training is a "passive" one that only includes observation of the related actions. Experience with a motor task changes the brain's response to the set of motor acts that are required to perform the task. It has been thought that the brain's responsiveness to passive training is regulated by the activation of the Action Observation Network (AON). Studies mentioned above suggest that this responsiveness is sensitive to the repertoire of the observer. Observation of dance movements that participants were trained on causes activation of the AON, whether they are trained by physically experiencing those dance moves or just watching those dance moves from video clips (Cross et al., 2009). If we observe an action that is performed by a non-human animal (i.e., dog, monkey), this activation still maps to our motor system and activated related regions; however, if an action (i.e., barking) is not in our repertoire, it is not mapped to our motor system (Buccino, 2014). Expectedly, if the action that is observed is not a biologically plausible movement, motor regions of the brain do not respond to that action (Stevens et al., 2000). This finding supports the idea that AON is sensitive to the observer's motor repertoire.

Relevance

The aforementioned studies, spanning various techniques in both archaeology and neuroscience, collectively demonstrate the collaborative nature of these scientific disciplines in investigating the co-evolution of cognition and acquired skills such as toolmaking. The presence of diverse toolmaking technologies, ranging from stone tools to pottery making, appears to have played a role in the cognitive evolution of our species. Moreover, existing literature indicates that training and expertise in various motor skills, such as toolmaking or dancing, can induce changes in the brain's response to the observation of related motor actions. Integrating these findings in a study could provide valuable insights into understanding the impact of training on action observation and its implications for acquired skills. Additionally, such a study could offer insights into the neural changes associated with the invention and utilization of different tools. Consequently, it would hold significance for both archaeology and neuroscience, serving as an intersection point for the field of neuroarchaeology. In this context, we have designed a pilot experimental study to start to address these questions.

Rationale of the Current Study

The profound impact of human toolmaking abilities on our species' evolution is evident in our capacity to modify and exploit the surrounding environment. Technological advancements, such as toolmaking, may have influenced the evolution of cognition. This project aims to at least indirectly investigate what kind of functional changes occurred in the brain of the neolithic humans during their transition from working with stone to working with clay. This technological innovation likely led to the development of new skills, potentially resulting in changes within the brain regions responsible for motor control and cognitive systems that are responsible for action observation. Archaeologists study human skills by analyzing the material artifacts left behind by past societies. Cognitive Neuroscience plays a crucial role in studying skilled behavior and understanding the neural mechanisms underlying the observed variations in archaeological materials. The current project seeks to integrate these two research fields.

In pursuit of this objective, the present study explores the electrophysiological markers associated with action observation and error monitoring. By examining these electrophysiological signals, the aim was to gain insights into their interpretation and shed light on the co-evolution of cognition and toolmaking.

To achieve this, EEG data were recorded in two separate sessions, utilizing a 64-channel EEG system. Participants were assigned to either the experimental or control group. The experimental group underwent training on toolmaking skills, which served as the experimental stimuli, and this was the only systematic difference between the two groups.

It was expected that there will be no significant difference in electrophysiological signals between the two groups in the first session. However, in the second session, it was expected that there will be a significant difference between groups in terms of electrophysiological signal for observation of actions and detecting errors committed. This was based on the assumption that training on toolmaking skills, which serves as the experimental stimuli for the participants, will cause an enhanced activation of the motor system and will improve participant's ability to monitor errors, resulting in distinct neural signatures compared to the control group.

CHAPTER 2: Method and Materials

Project: Becoming an Expert

Using our knowledge of Neolithic craftspeoples' stone tools and ceramic vessels, a group of inexperienced volunteer archaeologists underwent training at the Laboratory of Experimental Archaeology and Research on Technology in Padova University, to manufacture stone and ceramic tools. The training aimed to replicate the raw materials, techniques, and knowledge transfer conditions resembling those of the Neolithic period. The participants' behavioral motor patterns and neural indices were monitored using an innovative technique: 3D hand movement analysis combined with simultaneous Transcranial Magnetic Stimulation and Electroencephalogram recording (TMS-EEG) at the Neuroscience of Movement Laboratory of University of Padova (NEMO). These measures allowed us to respectively assess changes in kinematics, TMS related activity patterns in the primary motor cortex (M1) and electrical activity patterns of the novice volunteers before and after acquiring the new skills in stone tools and pottery making. Here, only EEG results will be discussed, since results related to kinematics and TMS are not in the scope of this thesis and will be analyzed elsewhere.

2.1 Participants

The sample for this pilot experiment consisted of 28 students (13 females and 15 males, 26 right-handed, 1 left-handed and 1 ambidextrous) who were enrolled in the bachelor's and master's degree programs in archaeology at the University of Padova. Participants who accepted to attend the training were assigned to the experimental group. The experimental group consisted of 13 participants (8 females and 5 males, all right-handed) trained in both pottery and flintknapping, and the control group consisted of 16 participants (6 females, 10 males, 13 right-handed, 1 left-handed and 1 ambidextrous) who did not have any training. All participants had normal or corrected-to-normal vision and had no history of epilepsy or neuropsychiatric disorder and had no conditions that would make TMS inappropriate.

Participants' handedness was assessed using the Edinburgh Handedness Inventory (EHI, Oldfield, 1971). Although participation in the study was completely voluntary, participants received monetary incentives for their participation. Participants gave their informed consent to participate in the study, which was conducted in accordance with the ethical standards of the 2013 Declaration of Helsinki for human studies of the World Medical Association. The project was approved by the Ethical Committee for the Psychological Research of the University of Padova (approved protocol reference number: 4917).

2.2 General Procedure

The experiment consisted of two sessions for both experimental and control groups and there was approximately a one-month time gap between sessions. Participants were assigned specific dates and times for the experiment according to their available times. Participants were welcomed to the Neuroscience of Movement lab of the psychology department at the University of Padova for the experiment. Kinematics and EEG-TMS recordings began after participants filled the consent form for the participation in the study. Participants performed kinematic recordings before or after EEG-TMS co-registration. After the first session ended for all participants in both groups, training for the experimental group participants started. Participants were trained both on the knapping and pottery making by experts except one participant who only had training on pottery in that time gap. Training for the experimental group took place at the same time as a group training. Once training was completed, participants were welcomed to the lab again for the second session to see the effect of training Time passed between two sessions was 44 days on average (range of days= 13-63, SD=16.8) The stimuli and procedure were exactly the same for session 1 and session 2.

2.3 EEG Data Acquisition

The EEG data were recorded (sampling rate = 5000 Hz; online filter = 0.1–1000 Hz) using TMS-compatible BrainAmp amplifiers (Brain Products, Germany) from 64 Ag/AgCl electrodes mounted on a TMS-compatible elastic cap (EASYCAP GmbH, Germany). Impedance was ≤ 10 kΩ. All electrodes were referenced to FCz during the recording, while AFz was used as ground.

First, for each participant we measured their head circumference to find the proper EEG cap. Then we measured the distance between nasion and inion and inter aural distance to find the vertex of the head to be sure that our central electrode (Cz) and all other electrodes were in the correct position. All participants were informed about the EEG technique, EEG cap. Further questions from the participants about the EEG were answered to make them feel relieved since most of the participants were naïve to EEG.

EEG cap montage was performed. To reduce impedance and increase signal quality, we applied conductive gel and paste between the scalp and electrodes with a needle-free syringe and a cotton stick (Ilmoniemi & Kicic, 2009). After the EEG cap montage was done, another group of researchers started preparing participants for TMS application.

2.4 Experimental Stimuli

The stimuli for this experiment consisted of displays of eight video clips each lasting 1 second that showed an expert whose only hands can be seen while performing two different toolmaking technologies separated by fixation points. These were ‘Flintknapping’ and ‘Pottery’ conditions. Moreover, there were two sub-techniques for each condition which were named as coil building and spatula for pottery condition and, hard and soft hammerstone for flintknapping condition (Figure 1). For each sub-technique displayed, there was a corresponding video clip ending correctly and another ending with an error. A specialist was told to commit these errors so that it would be possible to observe if there were differences between correct and erroneous clips in terms of EEG signal. All stimuli were presented using E-Prime 2 (PTSNet), a commonly used software for psychology and neuroscience studies.

2.5 Experimental Task and Procedure

Participants were asked to take a seat in a comfortable chair in front of the computer that was used for the presentation of experimental stimuli while the EEG signal was recorded. Throughout the experiments all participants were only required to fixate at the frames that are shown in the center of the screen without moving their eyes and head as much as possible. The study consisted of 4 blocks with 32 trials each, a total of 128 trials, 16 repetitions of each video clip. Before each block, 8 TMS pulses were delivered to compute the MEP baseline and during the task the TMS pulse was delivered once every two trials. TMS was delivered in half of the repetitions of each video clip. Each trial in the experiment started with the presentation of a fixation cross, which lasted for a duration of 1 second. Subsequently, video clips, also lasting 1 second, were displayed at the center of the screen, with the final frame remaining visible for 600 ms. Following a precise timing protocol, TMS pulses were administered 759 ms after the initiation of the video clips, while the onset of the erroneous action occurred 600 ms after the initiation of the video clips. Order of blocks and conditions were randomized for each participant. Participants were asked if they needed a break between blocks to be sure they could sustain their attention throughout the experiment. In the beginning of each block, a text was displayed on the screen that reminded participants to relax and not move their eyes and body.

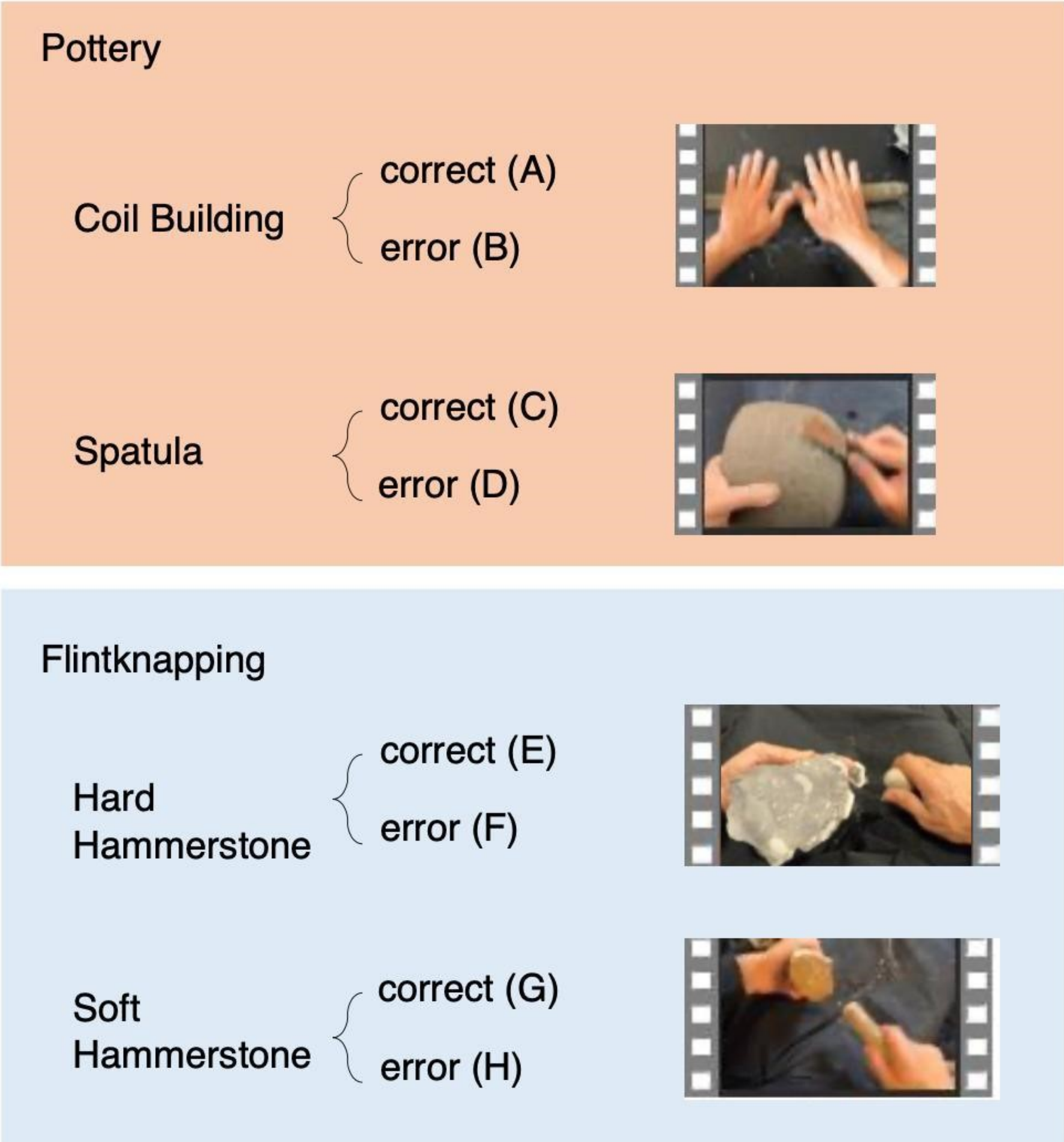


Figure 1. Frames taken from experiment, showing four different techniques. Coil Building and Spatula for Pottery making and Hard Hammerstone and Soft Hammerstone for Flintknapping. Participants were displayed these four techniques throughout the experiment. The experiment included correct and incorrect actions for all four techniques.

2.6 Training

During the training, participants in the experimental group, who had no prior experience in flintknapping and pottery making, received training from experts to acquire toolmaking skills. The participants were required to attend flintknapping and pottery training for a minimum of 24 hours. Throughout this training period, they learned techniques for knapping flint and shaping clay, using raw materials and tools that replicated those used in the Neolithic era. Most of the participants successfully completed the training, meeting the 24-hour requirement, except for three participants who did not reach 24 hours in one of the training sessions or in both training sessions. Additionally, one participant decided to discontinue the training after the pottery class (see Table 1). The training sessions were conducted as group activities, aiming to simulate the practices of Neolithic communities. At the conclusion of the training, the participants produced a total of 315 replicas of prehistoric stone tools and ceramic vessels (215 stone tools and 100 pots). These replicas will be valuable in assessing the impact of skill development on the production of archaeological materials. To ensure consistency, all participants were instructed to engage in the final flintknapping and pottery activities on the day prior to the second TMS-EEG session.

2.6.1 Pottery Training

During the initial session, the inexperienced participants received both theoretical instruction and a practical demonstration on the coiling technique and the use of tools, such as wooden or bone spatulas, to smooth the surfaces of the vessels. These techniques were based on records from the Neolithic period. The first day of the training focused on getting acquainted with the raw materials, while the subsequent days emphasized practicing the shaping of coils, the coiling technique, and the techniques for finishing the clay surfaces. The participants were tasked with creating a Neolithic-style pot within specific size parameters (approximately: 10 cm in diameter at the bottom, 20 cm in height, 15 cm in width, and 1 cm in thickness). Before the second TMS-EEG/kinematics session, participants were instructed to review and refresh their pottery-making experience. Table 1 provides an overview of the practical training sessions attended by each participant, as well as the timing of the refresh activities conducted prior to the TMS-EEG and kinematics sessions. The total duration of the training and refresh activities is also indicated in table 1, representing the overall experience each participant gained in practicing pottery.

2.6.2 Flintknapping Training

The training began with a theoretical overview, followed by hands-on practical activities. Most participants attended sessions on flintknapping conducted by an expert in the field. Additionally, they participated in study and documentation sessions, which involved examining and reconstructing the stone tools produced during the practical activities. Through this process, the knapping sequence was understood by reconstructing the flint core in reverse. Table 1 provides details regarding the theoretical introduction and the hours dedicated to the practical activities, which included observing flintknapping and refitting, as well as actively engaging in flintknapping. The table also displays the total time each participant spent on both theory and practice, demonstrating their progress in acquiring competence in stone toolmaking.

Table 1. Hours spent on the training for each participant.

Participants	Pottery Training			Flintknapping Training				
	Practical training	Refresh	Total active practice	Theoretical training	Knapping activity	Observation of knapping and refitting	Total active practice	Theoretical and practical
1	11	8	19	7.5	7.5	11	18.5	26
2	25.5	7	32.5	6	14	12	26	32
3	22	6.5	28.5	2	17.5	2	19.5	21.5
4	13	4	17	0	11.5	4	15.5	15.5
5	22.5	9	31.5	6	11.5	17.5	29	35
6	19.5	10.5	30	6	12.5	19	31.5	37.5
7	25.5	5	30.5	0	20.5	9.5	30	30
8	21	6	27	6	14	16.5	30.5	36.5
9	22.5	6	28.5	6	13.5	17.5	31	37
10	35.5	3.5	42	6	17	21	38	44
11	18.5	11.5	29	6	27	25.5	52.5	58.5
12	23	9.5	32.5	6	25.5	13.5	39	45
13	18	4	22					

Note. Numbers written in red color indicate the 24 hours limit has not been reached.

Participant 13 did not attend flintknapping training.

2.7 Data Analysis

2.7.1 EEG Pre-processing

All pre-processing and statistical analysis for EEG data was done by using MATLAB (The Mathworks, Inc.) software using scripts from EEGLAB (Delorme and Makeig, 2004) toolbox. Analysis of concurrent EEG and TMS followed the one described in Rogasch et al. (2017). We did not perform temporal alignment to TMS pulses because for half of our trials there was a TMS pulse and for the other half there was no TMS pulse. To enhance the performance of Independent Component Analysis (ICA), the TMS pulse artifact and the peak of TMS-evoked muscle activity within the time range of 0 (TMS trigger) to 6 ms were eliminated. In their place, constant amplitude data was substituted.

Upon visual examination, it was determined that there were no disconnected electrodes or trials exhibiting significant, non-repetitive artifacts. These types of artifacts, if present, could have negatively impacted the effectiveness of the ICA decomposition. Consequently, no manual rejection of channels or epochs was conducted during this stage, as it was deemed unnecessary based on the visual inspection results.

At this stage, it was observed that residual TMS-evoked muscle and electrical/movement artifacts persist in the data, extending beyond the initial 6 ms time frame that was previously removed. To address this issue, a preliminary Independent Component Analysis (ICA) was conducted using the FastICA (Hyvärinen & Oja, 2000) algorithm, following the recommendation of Rogasch et al. (2017). This ICA aimed to identify and manually select independent components (ICs) that specifically corresponded to these lingering TMS-induced artifacts, allowing for their removal from the data.

The presence of these artifacts can have a negative impact on the accuracy of Independent Component Analysis (ICA) when used for tasks such as recovering neural activity or eliminating physiological artifacts. Additionally, by removing these artifacts, it becomes possible to apply filtering techniques, potentially further enhancing the effectiveness of ICA decomposition (Vallesi et al., 2021). On average, 1.6 independent components (ICs) were removed at this stage (SD = 0.9, range = 0-5). This removal ensured that the EEG data for all participants were no longer contaminated by TMS-evoked muscular artifacts.

To process the data, several steps were taken. Firstly, the constant amplitude data surrounding the TMS pulse were interpolated using linear interpolation. Next, the EEG data underwent band-pass filtering using a Hamming windowed sinc Finite Impulse Response (FIR) filter, with cut-off frequencies set at 1 and 40 Hz. Subsequently, the FastICA algorithm was applied for the decomposition of independent components (ICs). An automated selection of brain components was conducted with the aim of removing residual TMS artifacts and artifacts associated with eye movements, blinks and muscular activity, channel's noise and other non-brain noise considering the classification results of the ICLabel plugin in the EEGLAB software (Pion-Tonachini et al., 2019), and the residual variances of the best-fitting equivalent IC dipoles calculated using the DIPFIT plugin in EEGLAB. Specifically, ICs with a brain label probability below 0.7 or a best-fitting equivalent dipole with a residual variance equal to or greater than 0.15 were excluded from further analysis. Prior to the rejection of components, a thorough visual inspection and labeling process were conducted for all the components. On average, 47.2 ICs (SD = 4.5, range = 35-56) were removed during this stage. Data was epoched from -1000 to 2000 ms around the onset of the video clips. The TBT EEGLAB plugin was used for the automatic rejection and interpolation of channels on an epoch-by-epoch basis. Epochs with more than six bad channels were excluded, otherwise the bad channels were interpolated in that epoch. Channels that were identified as bad in over 30% of the epochs were excluded and interpolated as well. For all the analyses we performed, we corrected for baseline, 200 ms before the onset of the video for the first part and 200 ms before the action in the second part.

2.7.2 ERP Inferential Analysis

As a preliminary step, we performed Global Field Power (GFP) analysis on our data. GFP is a measure that allows researchers to quantify the amount of activity and is computed by finding the potential differences for each component that is reflected by finding the standard deviation (Lehmann & Skrandies, 1980). Each topographic map displays a distributed electrical activity that is reflecting the underlying brain activity and GFP helps us to measure standard deviation for each map to see activity patterns (Skrandies, 1990). GFP was measured for each participant and then we computed the average to have one GFP that reflects the average activity pattern of all participants (Figure 2). We utilized GFP since this was a pilot and exploratory study that aims to see preliminary results and although we had some expectations based on the literature, we did not have any concrete hypotheses.

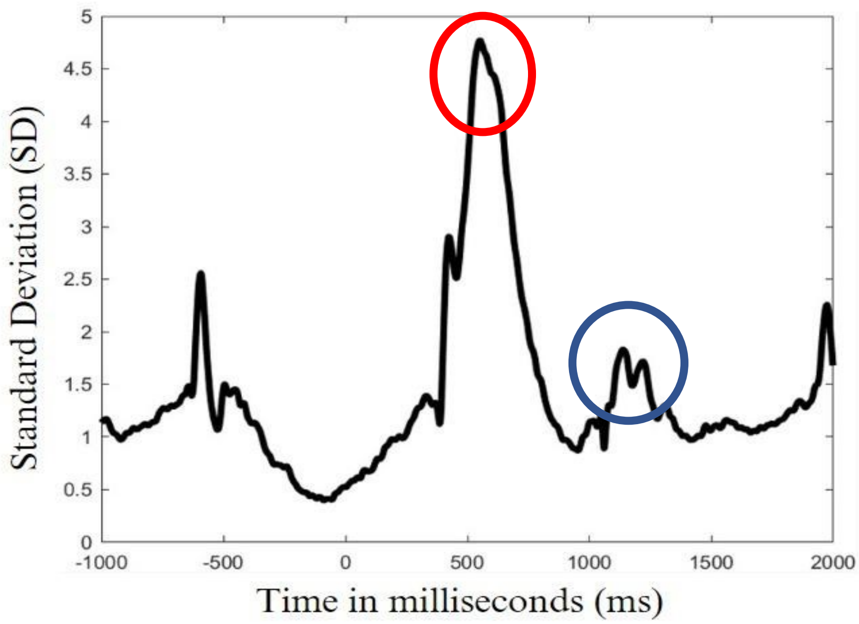


Figure 2. Global Field Power. Shows brain activity as a function of time, average of all participants. The prominent time windows are highlighted with red and blue circles.

Based on the GFP, we identified two distinct time windows that exhibited pronounced increases in brain activity, as indicated by the highlighted circles in Figure 2. Please note that the GFP was computed irrespectively of the experimental conditions. The first observed increase in brain activity occurred during the time interval from 500 ms to 700 ms, which corresponds to the time participants have seen the action, but action was not completed, and no error occurred yet in the trials with the erroneous action. Any differential activation observed within this time window may reflect a variation in the mechanisms underlying action observation specifically related to the observed actions. The second point of interest corresponds to the time range of 134 ms to 210 ms following the completion of the action in the video clips. Differential activation within this second time window may reflect the involvement of error monitoring mechanisms. We calculated the average activation values for these defined time ranges, resulting in two values: one representing the first observed increase in activity and the other representing the second observed increase in activity.

After the identification of the interesting time-windows based on GFP, we plotted the topoplot of the signal averaged in those time-windows and across participants, to find the channels that were responsible for that increased GFP. Based on the topographic map (Figure 3), the following channels were identified for subsequent analysis in the first time-window: PO7, PO3, POz, PO4, PO8, Oz, O1, O2. For this time-window, the mean signal was extracted for each technique. Then, a 2 groups x 2 sessions x 2 techniques mixed ANOVA was conducted. Since this was an underpowered pilot study, we also conducted uncorrected t-tests for each contrast.

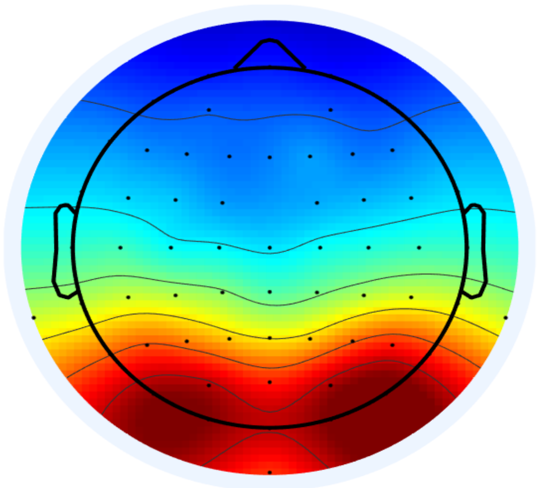


Figure 3. Topographic map of the activity pattern for the first time-window. The colormap indicates voltage in the range -7 µV – 7 µV.

For the second time-window, since the GFP might have reflected TMS evoked potentials, we projected the GFP separately for trials with TMS and without TMS. In the non-TMS trials, there was no evident activity in the GFP (Figure 4). Hence, the analysis in this time window was limited to the TMS trials.

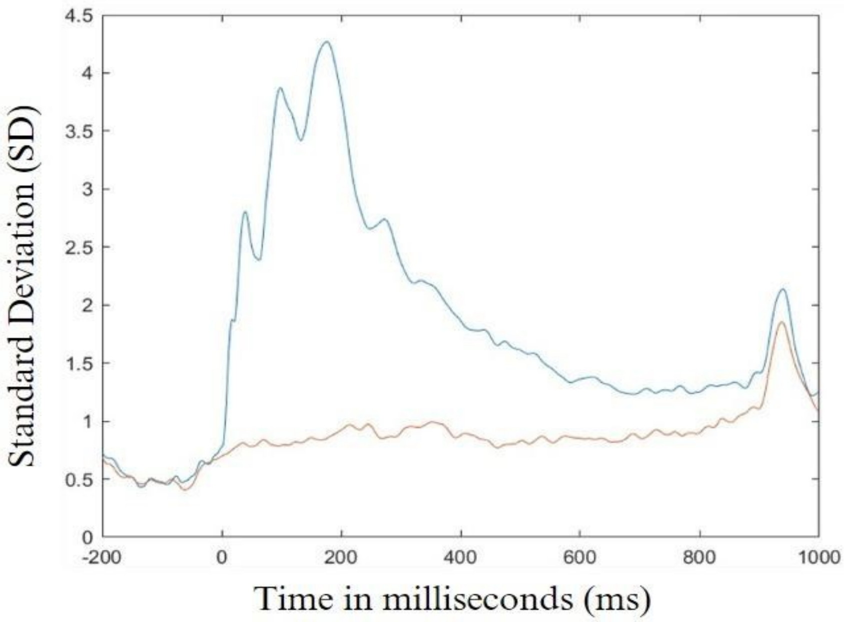


Figure 4. Global Field Power for TMS (blue line) and non-TMS (orange line) trials. 0 in the X axis represents the onset of TMS pulse.

Based on the topographic map presented in Figure 5, the specific channels that were responsible for the enhanced activation pattern in the GFP were identified for further analysis in the second time- window. These channels include FC1, FC2, Cz, and Fz.

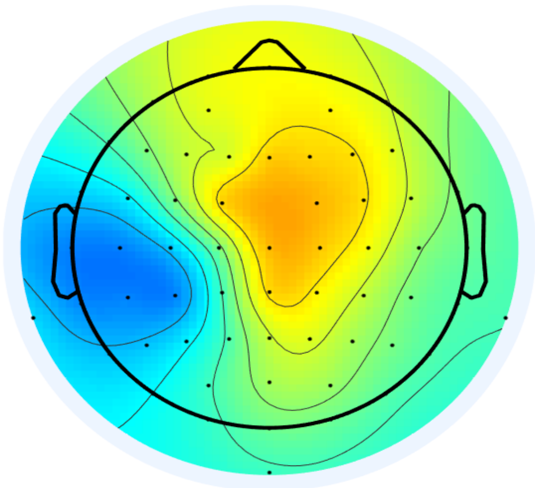


Figure 5. Topographic map shows the activity pattern for the second time-window. The colormap indicates voltage in the range -1.5 µV – 1.5 µV.

After detecting the channels of interest for the second time-window, we conducted a 2 sessions x 2 action (correct or incorrect) x 2 techniques x 2 groups ANOVA to see the main effects and interactions between factors. We also performed exploratory uncorrected t-tests for each contrast.

CHAPTER 3: Results

3.1 Results Regarding the First Time-Window: Action Observation

We separately show topographic maps for the experimental and the control groups for the first time-window (Figure 2, red circle), as well as pottery and flintknapping. Figures 6 and 7 show topographic maps that represent activity patterns for flintknapping and pottery in the identified time window.

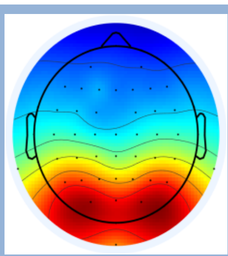
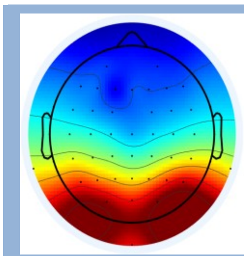
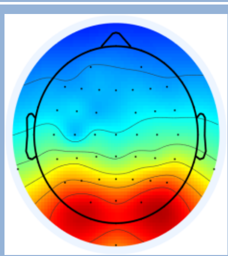
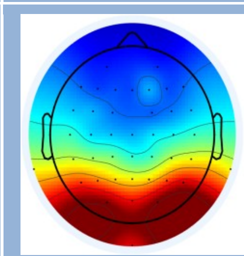
Flintknapping	EXP	CON
S1		
S2		

Figure 6. Topographic maps showing the activity patterns for groups both for first and second sessions, averaged for participants. For flintknapping technique, hard hammerstone, and soft hammerstone sub-techniques together. (S1: Session 1, S2: Session 2, EXP: Experimental group, CON: Control group). The colormap indicates voltage in the range -7µV – 7µV.

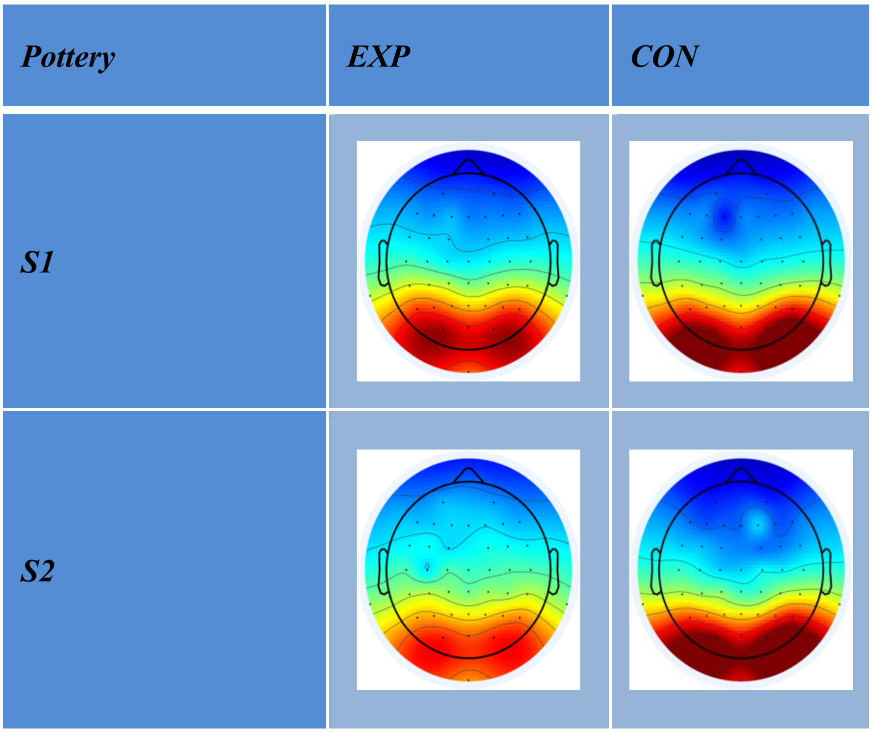


Figure 7. Topographic maps show activity patterns for groups both for first and second sessions, averaged for participants. For pottery technique, coil building, and spatula sub-techniques together. (S1: Session 1, S2: Session 2, EXP: Experimental group, CON: Control group). The colormap indicates voltage in the range -7 µV – 7 µV.

Table 2 shows the results of 2 x 2 x 2 mixed-ANOVA. This analysis did not reveal any statistically significant main effects for any of the variables examined. Furthermore, there was no significant interaction between variables. All calculated p-values in the analysis were greater than the predetermined significance level of $p < .05$.

Table 2. 2 (sessions) x 2 (techniques) x 2 (groups) ANOVA results.

	Sum of Squares	**df**	**Mean Square**	**F**	**p**
Session	4.129	1	4.129	0.620	0.439
Session * Group	9.923	1	9.923	1.491	0.234
Residual	159.720	24	6.655		

	Sum of Squares	df	Mean Square	F	p
Technique	1.292	1	1.292	2.184	0.152
Technique * Group	1.62e-5	1	1.62e-5	2.74e-5	0.996
Residual	14.190	24	0.591		
Session * Technique	0.227	1	0.227	0.460	0.504
Session * Technique * Group	1.575	1	1.575	3.185	0.087
Residual	11.870	24	0.495		

Note. Type 3 Sums of Squares.

Table 3 presents the uncorrected t-test results. When the two techniques were examined together, we observed a significant difference between groups in the second session (p = .046). However, when the tests were conducted separately for each technique, the significant difference between groups was exclusively observed for the pottery technique (p = .024).

Table 3. Contrasts that a t-test performed and related p values for two techniques together and separately.

Method	Channels	Contrast	*t*-value	*p*-value
Both	PO7, PO3, POz, PO4, PO8, Oz, O1, O2	S2 vs S1 EXP	-1.114	.289
		S2 vs S1 CON	0.423	.679
		S2_exp vs S2_con	-2.109	**.046**
		S1_exp vs S1_con	-0.919	.367
		(S2-S1)_exp vs (S2-S1)_con	-1.221	.234
Pottery		S2 vs S1 EXP	-1.528	.152
		S2 vs S1 CON	0.622	.545

Method	Channels	Contrast	*t*-value	*p*-value
		S2_exp vs S2_con	-2.405	**.024**
		S1_exp vs S1_con	-0.790	.437
		(S2-S1)_exp vs (S2-S1)_con	-1.631	.116
Flintknapping		S2 vs S1 EXP	-0.732	.480
		S2 vs S1 CON	0.132	.897
		S2_exp vs S2_con	-1.889	.071
		S1_exp vs S1_con	-1.142	.265
		(S2-S1)_exp vs (S2-S1)_con	-0.734	.470

Note. S1: Session 1, before training. S2: Session 2, after training. EXP: Experimental group. CON: Control group. Only for the first time-window, related to action observation. Significant results are written in bold.

To further explore the significant difference in the observation of pottery, considering that participants in the experimental group received training exclusively on the coil building sub-technique (see Figure 1), a 2 (groups) x 2 (sub-techniques of pottery) x 2 (session) ANOVA was conducted (Table 4).

Results of this ANOVA revealed a significant difference between the sub-techniques of pottery (p = .018). Specific sub-techniques employed in pottery making had a statistically significant impact on the observed outcomes. We did not observe any significant interaction between sub-techniques and groups or sessions.

Table 4. 2 (groups) x 2 (sub-techniques) x 2 (groups) ANOVA results for the pottery technique.

	Sum of Squares	df	Mean Square	F	p
Sub-technique	10.7332	1	10.7332	6.4051	**.018**

	Sum of Squares	df	Mean Square	F	p
Sub-technique * Group	0.9555	1	0.9555	0.5702	.457
Residual	41.8934	25	1.6757		
Session	4.9686	1	4.9686	0.6930	.413
Session * Group	17.7171	1	17.7171	2.4711	.129
Residual	179.2463	25	7.1699		
Sub-technique * Session	0.0473	1	0.0473	0.0758	.785
Sub-technique * Session * Group	0.1658	1	0.1658	0.2659	.611
Residual	15.5874	25	0.6235		

Note. Type 3 Sums of Squares. Significant results are written in bold.

3.2 Results Regarding the Second Time-Window: Error Monitoring

The second time window is the period of time during which participants witnessed an action was carried out whether correctly or incorrectly. Additionally, The TMS pulse that participants received as a part of the whole experimental design also falls within this time interval. Since the TMS pulse was only present for half of the experiment's trials, we separately displayed topographic maps for TMS and non-TMS trials. As mentioned before, the analysis in this time window was limited to the TMS trials since there was no evident activity in the GFP for non-TMS trials (see Figure 2). For this reason, we did not go further and stopped analyses for non-TMS trials. Here, we will report the results only relevant to the trials with TMS.

Figure 8 shows the topographic maps for experimental and control groups, specified with incorrect and correct trials both for flintknapping and pottery techniques. It can be clearly noticed that there is a difference between topographic maps of flintknapping and pottery without considering the groups or correct/incorrect actions.

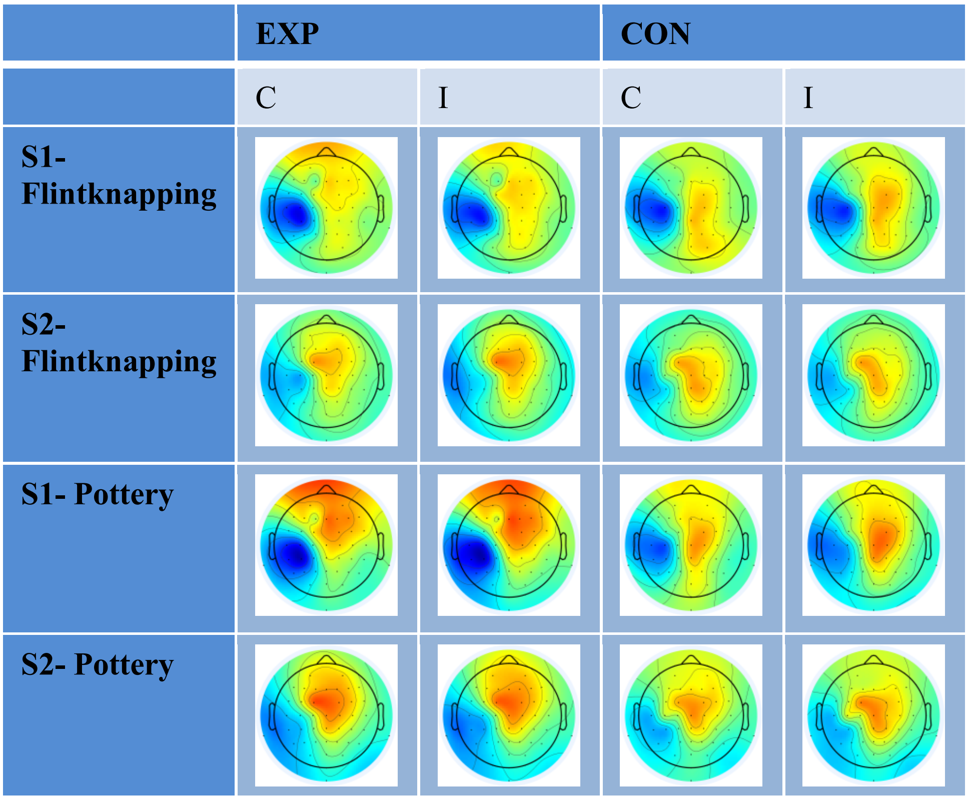


Figure 8. Topographic maps for only trials with TMS. C: Correct action, I: Incorrect action.

Table 5 and 6 shows the results of 2 x 2 x 2 x 2 ANOVA. As can be expected from the differences in topographic maps, analysis revealed a significant difference between techniques ($p<.001$). We did not observe any significant main effects of the session or error variables however there was a significant interaction effect between session and error ($p=.028$).

Table 5. 2 (sessions) x 2 (technique) x 2 (error) x 2 (group) ANOVA results.

	Sum of Squares	**df**	**Mean Square**	**F**	**p**
Session	15.5952	1	15.5952	0.4448	0.511
Session * Group	0.8832	1	0.8832	0.0252	0.875
Residual	841.5626	24	35.0651		
Technique	32.5905	1	32.5905	30.3207	**<.001**
Technique * Group	2.0104	1	2..0104	1.8704	0.184
Residual	25.7967	24	1.0749		
Error	3.7346	1	3.7346	3.9256	0.059
Error * Group	0.1309	1	0.1309	0.1376	0.714
Residual	22.8322	24	0.9513		
Session * Technique	1.0681	1	1.0681	0.6949	0.413
Session * Technique * Group	0.0542	1	0.0542	0.0353	0.853
Residual	36.8917	24	1.5372		
Session * Error	2.0595	1	2.0595	5.4757	**0.028**
Session * Error * Group	1.0419	1	1.0419	2.7702	0.109
Residual	9.0267	24	0.3761		
Technique * Error	0.0781	1	0.0781	0.0565	0.814
Technique * Error * Group	0.4101	1	0.4101	0.2964	0.591
Residual	33.2054	24	1.3836		
Session * Technique * Error	0.3619	1	0.3619	0.4248	0.521
Session * Technique * Error * Group	0.2486	1	0.2486	0.2918	0.594
Residual	20.4476	24	0.8520		

Note. Type 3 Sums of Squares. Significant results are written in bold.

Table 6. Main effect of Group.

	Sums of Squares	df	Mean Square	F	p
Group	7.34	1	7.34	0.164	0.689
Residual	1075.23	24	44.80		

Note. Type 3 Sums of Squares.

Table 7 presents the uncorrected t-test results. The analysis did not reveal any significant results for flintknapping or pottery. There was no evidence of different underlying cognitive processing for observed incorrect actions compared to observed correct actions. Moreover, given these results, we were not able to show that training had an impact on the monitoring of observed action errors. These findings were not in line with our expectations based on literature and possible reasons for these null findings will be further discussed later.

Table 7. Contrasts that a t-test performed and related p values for two techniques together and separately.

Technique	**Channels**	**Contrast**	***t*-value**	***p*-value**
Flintknapping	FC1, FC2, Cz, Fz	(Incorrect vs Correct) in S2 for EXP	1.2722	.230
		(Incorrect vs Correct) in S1 for EXP	0.7330	.479
		(Incorrect vs Correct) in S2 for CON	-0.1652	.871
		(Incorrect vs Correct) in S1 for CON	1.8695	.084
		(Incorrect-Correct) S2 vs (Incorrect-Correct) S1 for EXP	0.4786	.642
		(I-C_S2exp – I-C_S1exp) vs (I-C_S2con – I-C_S1con)	1.4236	.167

Technique	Channels	Contrast	*t*-value	*p*-value
Pottery	FC1, FC2, Cz, Fz	(Incorrect vs Correct) in S2 for EXP	-0.3133	.760
		(Incorrect vs Correct) in S1 for EXP	0.7651	.460
		(Incorrect vs Correct) in S2 for CON	0.0335	.974
		(Incorrect vs Correct) in S1 for CON	1.8056	.094
		(Incorrect-Correct) S2 vs (Incorrect-Correct) S1 for EXP	-0.9713	.352
		(Incorrect-Correct) S2 vs (Incorrect-Correct) S1 for CON	-1.5498	.145
		(I-C_S2exp – I-C_S1exp) vs (I-C_S2con – I-C_S1con)	0.4549	.653

Note. I: Incorrect action. C: Correct action. S1: Session 1, before training. S2: Session 2, after training. EXP, exp: Experimental group. CON, con: Control group. For the second time-window.

CHAPTER 4: Discussion

The primary objective of this experimental study was to identify underlying cognitive processes related to action observation and error monitoring with electrophysiological measurements to understand how increasingly complex tools and human's interaction with them have shaped human cognition. For this objective, we examined how experience with the toolmaking skills affected the electrophysiological response of participants to the observation of actions related to these skills. The underlying idea posited that improvements in toolmaking caused functional changes in the human brain and these functional changes can be reflected while humans observe actions relevant to these tools. To gain insights into the functional changes associated with experience in toolmaking, we employed EEG recordings and conducted subsequent analyses. By examining the neural activity captured through EEG, we aimed to uncover the underlying mechanisms and detect any discernible alterations that may be attributed to the acquisition of toolmaking skills.

Upon examining the GFP, we identified an ERP which occurred 500 ms after the onset of video and lasted for 200 ms. Channels located on the occipital region of the brain were responsible for this increase in the activity. This ERP was likely associated with the processes of action observation. Further analysis revealed that there was an effect of training on this ERP which likely occurred with training's impact on the underlying cognitive mechanisms related to action observation. Experimental group participants who had training exhibited different activity patterns for the action observation time-window in the second session compared to the control group. This finding shows that the impact of training on the acquired skills can be revealed while observing the execution of relevant skills. Concerning error monitoring, there was no group difference, we were not able to identify any specific ERP irrespectively of participants having training on the toolmaking skills or not. Subsequent exploratory analysis revealed that the observation of flintknapping and pottery techniques caused significantly different activity patterns on the TMS evoked potential in this time-window, although we were not able to find any difference between correct and incorrect trials.

Overall, our study gave intricate results for action observation and results for the error monitoring part were not in line with the literature mentioned in Chapter 1. It is important to note that low statistical power in this pilot study may have caused this discrepancy.

4.1 Action Observation

We did not observe any main effect of the session, group or technique and there were no interactions between these variables. The absence of a significant interaction between session and group in our study was unexpected and did not align with our initial expectations. However, further uncorrected exploratory contrasts revealed that there was a significant difference between groups in the second session in the action observation time-window, especially for the pottery technique. Electrophysiological signals of participants in the experimental group who underwent training exhibited a difference compared to those of the control group. This result implies that training on toolmaking skills, which also served as experimental stimuli, might have had a significant effect on the observation of actions relevant to pottery making. There are several considerations that should be taken into account in interpreting our results. A first consideration is that we did not observe evident evoked activity in the channels located over motor scalp areas. The topographic maps for this time-window showed that the channels located over the occipital scalp region of the brain were identified as the key contributors to the observed increase in the GFP. The mirror neuron system has a key role for the understanding of actions, and it displays an enhanced activity pattern for observed actions, but this system is believed to operate within the motor regions of the brain, as previously discussed in Chapter 1. For this reason, the observed difference between sessions in our study does not seem to be mostly influenced by the enhanced activity of mirror neurons in the motor areas, although we could not infer anything related to brain generators of the observed signal in the scalp since we did not perform source analyses. Therefore, these results should be interpreted with great caution in terms of brain generators. Given the reciprocal interaction between the visual and motor systems in human action understanding suggested by *direct-matching hypothesis*, the observed increased activity in the occipital region in our study might indicate the coding and transmission of information from the visual to the motor region. Follow-up studies employing alternative methodologies could further explore the connectivity between occipital and motor regions in relation to action understanding.

A second consideration is that the difference between groups was mainly observed for the pottery technique. One possible explanation for this specific result is the unequal amount of time spent for training for the two types of techniques by the participants in this experiment, namely pottery and flintknapping. It is worth noting that the varying amounts of time dedicated to each technique may have influenced the observed results and contributed to the observed differences in electrophysiological responses. The majority of the participants in the experimental group (n=8) had longer duration of active practical training in pottery technique compared to flintknapping (see Table 1). Although a previous study (Marshall et al., 2009) reported the influence of limited experience on the underlying electrophysiological response associated with action observation, it is important to note that this study did not specifically investigate ERPs. Moreover, it is worth mentioning that, in the aforementioned study, the training was administered immediately following the initial exposure to the stimuli, and the second session of EEG recordings was conducted shortly after the training (i.e., imitation). In the current study, there was a longer time gap between the training and the second session EEG recording, especially for flintknapping technique, since participants had an additional refresh training for the pottery. The fact that the pottery training was divided into two separate rounds, especially that the second round was close to the second session of EEG recordings, may have contributed to a more profound acquisition of the pottery technique compared to flintknapping.

In conclusion, participants may have exhibited different electrophysiological responses to pottery across sessions. In line with this argument, research showed that distributed practice has profound benefits for learning of different skills including motor skills over massed practice (Cepeda et al., 2006; Lee & Genovese, 1988).

As a minor side note, we found that activity patterns related to observation of sub-techniques of pottery significantly differed in the first time-window. Participants in our study displayed a significantly distinct electrophysiological signal when observing the coil building and spatula techniques. The observed differences in the signal may reflect variations in cognitive and motor processing associated with the specific actions. It seems that these two techniques' natural difference affected the action observation mechanism of participants rather than the training since there was not an interaction effect between the sub-techniques and the session. As depicted in Figure 1, the spatula technique in pottery making involves a grasping action, while the coil building technique does not require such a grasping action. This discrepancy between the two sub-techniques may have accounted for the observed significant difference in brain activity. Previous research has demonstrated that the observation of different hand actions can elicit distinct patterns of brain activation, with grasping actions showing relatively increased activation, particularly in the occipital regions (Pierno et al., 2009). Furthermore, the lack of significant differences within the sub-techniques of flintknapping may provide additional support for this argument, as both the hard and soft hammerstone techniques necessitate a grasping action. These findings collectively suggest that the variation in motor actions involved in sub-techniques can contribute to the distinct activity patterns. Furthermore, the absence of an interaction effect between the sub-techniques and groups provides further evidence to suggest that the observed difference in results between sub-techniques is not attributed to the training received by the participants. While it is important to be cautious in interpreting the results due to the statistical and methodological limitations of this pilot study, the presence of a significant difference at the second session regarding the action observation time-window suggests that further investigation in a larger sample and with improved methodological rigor could yield valuable insights.

4.2 Error Monitoring

Our findings indicate that the observed increase in activation within the GFP during this time-window was specifically associated with the application of TMS pulse. GFP of non-TMS trials exhibited a flat activity pattern. Hence, we were not able to find an ERP response related to error monitoring. These results might suggest that none of the participants was able to efficiently monitor errors since they were naive to the techniques, and they were not aware of the errors in the first session (or if they were able to monitor errors, this process was not detectable by the analyzed EEG signal). However, even after training we did not observe an ERP related to monitoring of errors. There was not a difference between groups in terms of error monitoring although there was a difference between groups for the action observation time-window in the second session. Training seems to have improved the action observation performance of the participants, but we were not able to observe any effect on the detection of errors. Analysis on motor evoked potential (MEP), which is not a part of this dissertation, showed that the experimental group displayed a difference in terms of error monitoring for pottery technique at the MEP level. The absence of an observed effect of training on our outcomes could potentially be attributed to the limited number of participants who received training on the toolmaking skills. With only 13 participants in the experimental group, the sample size might not have been sufficient to detect subtle or moderate effects of the training and to observe a relevant ERP. A small sample size poses a threat to statistical power and the replication of ERP studies (Clayson et al., 2019). Additionally, participants had training only on the coil building sub-technique of pottery and for each sub-technique there were only 16 trials which displayed an error during the experiment. Therefore, even if participants effectively monitored errors, we may not have been able to observe an ERP effect due to the limited number of trials.

To summarize this part of the results, it is challenging to determine whether the observed results can be attributed to the limited number of participants or to the possibility that the trained participants did not effectively detect errors during the task due to the absence of behavioral data on the detection of errors in this study.

4.3 Limitations

This study had several limitations. Since the training required long durations of dedication it was difficult to find participants, and this affected the statistical power of the study to find significant results and replicate findings from literature. Additionally, methodological constraints may have contributed to this issue. Participants in the experimental group had training on two distinct types of skills and there was a high variability in the amount of time participants spend on techniques. The time passed between the training and the second EEG recording session was not well-controlled for participants, since time-slots for recording sessions were decided mostly according to availability of the participants which were university students. Moreover, participants in the control group did not perform any control training which is not related to the aforementioned toolmaking skills to see if the change in underlying brain activity was specific to training which participants in the experimental group performed. Assignment of participants to the experimental and control groups was not randomized. Participants who accepted to do the training were assigned to the experimental group. This caused a bias of selection between motivated and less motivated students in participating in the study. Hence, it was challenging to understand if the observed differences between groups (when detected) were caused by the training or by the interaction between training and motivation. Participants' behavioral motor performance was recorded only for one of the techniques (i.e., coil building). This may have biased the EEG signal differences between techniques since participants practiced on this technique just before the EEG recording. Furthermore, the interaction between TMS and EEG can be complex, and the observed effects are highly contingent on various experimental parameters including TMS intensity, timing, and precise stimulation site. Hence, co-registration of TMS and EEG can pose challenges in replicating findings and drawing consistent conclusions across different studies. It is important to remember that all these mentioned constraints may have prevented us from obtaining more reliable and optimal results.

4.4 Significance of the Current Study and Future Directions

Despite all these limitations, this study revealed valuable findings which can help build more complete studies to shed light on the process of co-evolution of cognition and toolmaking strategies. We showed how human cognition may have evolved in relationship with the increased complexity of the toolmaking repertoire by showing that acquired skills modulated the underlying cognitive processing. Moreover, we showed that the action observation network can be regulated by the experience. This study can be thought of as a preliminary example of a relatively new discipline of neuroarchaeology. Further studies should give importance to collecting data from a higher number of participants and try to better control the variability in the training durations and the subtle but important differences in the stimuli used. In this experimental study, participants were not given explicit instructions to focus on the hand movements of the experts throughout the trials and they were instructed to maintain a fixation in a central fixation cross between trials. However, it is worth considering whether explicitly instructing participants to specifically track the hand movements of the expert would yield more optimal results. Previous research by D'Innocenzo et al. (2017) demonstrated that when participants were directed to focus their gaze on specific locations, their ability to accurately track hand motions during action observation was enhanced, leading to increased underlying neural activity. A further study in which participants will be explicitly instructed to focus on the hand of the person who is performing the action can shed light on this issue.

Another effective strategy, along with action observation for learning motor actions is motor imagery in which participants mentally simulate performing an action and it has been argued that both strategies employ similar neural networks, mirror neuron system (Gatti et al., 2013). Research shows that motor imagery is associated with the activation of motor areas such as supplementary motor area (SMA) and premotor area (PM) (Dechent et al., 2004) which are also activated during action observation. Moreover, the combination of action observation and motor imagery has been shown to elicit higher patterns of neural activity compared to action observation alone (Vogt et al., 2013). Considering these findings, incorporating motor imagery as a component of training can be advantageous in achieving heightened brain activity levels especially in motor regions which we were not able to show in our study.

Conclusion

In this study we showed that training on the toolmaking skills which were a common technological repertoire for our ancestors for long times throughout evolutionary history can modulate the underlying cognitive mechanisms. Novice individuals who had the chance to have an experience with those skills observed somewhat different electrophysiological signals which may underline the ongoing cognitive processing. Moreover, the current study has demonstrated that a combination of various neuroscience techniques, such as EEG, TMS, and kinematic recordings, can be employed together to address more complex inquiries about the human mind. Although our findings should be considered as exploratory, promising results from the intersection of archaeology and neuroscience suggest that collaboration between these two fields should be further encouraged. Neuroarchaeology offers important answers to questions about the human mind that are challenging for archaeology and neuroscience to answer alone.

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