The neural correlates of skill transmission: An fMRI study

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Abstract

Studies on cumulative cultural evolution and cultural transmission typically focus on the changes in performance or potential improvements as a result of skill learning. Although there is great interest in the human brain and the evolution of technology, the neural foundation of the cultural transmission of these technologies remains largely unexplored. The aim of this study was to investigate the neural networks for skill transmission from a neuroarcheological perspective. This study combined a transmission chain paradigm with functional fMRI to investigate how an acquired skill, in this case knot tying, was passed along chains to mimic the process of cumulative cultural evolution using cultural transmission. Results show that learning and tying knots were associated with several sensorimotor systems. Across subjects, knot tying compared to control condition was associated with activation in left, superior parietal lobule, left superior occipital gyrus and left intraparietal sulcus. When comparing activation associated with learning and tying the first knot and the last knot, shifts in activation attributed to the effects of learning were demonstrated. It was concluded that the human capacities for sensorimotor adaptation are important factors in the evolution of human technologies.

Keywords: cumulative culture, fMRI, cultural transmission, toolmaking, knot tying

Sammendrag

Studier av kumulativ kulturell evolusjon og kulturell transmisjon fokuserer typisk på endringer i prestasjon eller potensielle forbedringer som et resultat av ferdighetslæring. Selv om det er stor interesse for menneskehjernen og evolusjonen av teknologi, forblir det nevrale grunnlaget for kulturell transmisjon av disse teknologiene stort sett uutforsket. Hensikten med denne studien var å undersøke de nevrale nettverkene for overføring av ferdigheter fra et nevroarkeologisk perspektiv. Studien kombinerte et transmisjonkjede paradigme med funksjonell MR for å undersøke hvordan en tilegnet ferdighet, i dette tilfellet knuteknyting, ble ført videre gjennom kjeder for å etterligne kumulativ kulturell evolusjonsprosessen ved bruk av kulturell transmisjon. Resultat avdekket at læring og knyting av knuter var assosiert med flere sensomotoriske systemer. På tvers av deltakere, var knuteknyting sammenlignet med kontroll betingelsen assosiert med aktivering i venstre superior parietal lapp, venstre superior oksipitale gyrus og venstre intraparietal sulcus. Ved sammenligning av aktivering assosiert med læring og knyting av den første knuten og den siste knuten, ble det demonstrert skift i aktivering attribuert til effekten av læring. Det ble konkludert at menneskelig kapasitet for sensomotorisk adaptasjon er viktige faktorer for evolusjonen av menneskelig teknologi.

Nøkkelord: kumulativ kultur, fMRI, kulturell transmisjon, redskapslaging, knuteknyting

Preface

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1. Introduction

The first stone tools modified with intention appear in the archeological record over 2.5 million years ago (Stout & Chaminade, 2007). The tools were made by striking one stone (the core) with another (a hammerstone), chipping of flakes, making acute edge angles on the core stone. Starting with these simple stone tools used for cutting and hammering, it advanced to more precise tools such as spears and axes. This set of skills were then passed on from generation to generation, enabling prehistoric humans to hunt and transport with great efficiency and accuracy, making everyday tasks easier.

The improvements in toolmaking skills are central to the study of human culture (Sasaki & Biro, 2017). Tennie et al. (2009) argue that human culture is a unique evolutionary phenomenon, and that the reason for this is that the practices and products that humans produce are cumulative (Tennie et al., 2009). The specific way one generation does things, is passed on to the next generation, with slight improvements or modifications. These modifications will continue across generations with several changes and cultural novelties along the line. This is called the "ratchet effect» because these modifications will stay in the population until changes "ratchet things up" (Tennie et al., 2009). Cultural transmission is the process by which these modifications or behaviors are passed on and spread to individuals and groups (Taylor & Thoth, 2011). This includes the attitudes, beliefs, values, and behavioral scripts that become somewhat stable traditions.

It is argued that a key difference between humans and non-humans in regards to cumulative culture lies in the structure and complexity of our social life (Muthukrishna et al., 2014). Our ability to construct useful tools and develop skills is considered a result of the fact that us as humans have access to large social networks that enable us to learn from multiple teachers. It is therefore proposed that this level of advancement in technology may be depended on the size, sociality, and interconnectedness of a population (Muthukrishna et al., 2014).

Research on the field of cultural transmission so far has mainly focused on the changes in performance as a results of the transmission, exploring the mechanisms involved and the products that come of it. The neural foundation of cultural transmission has remained largely in the dark, as well as potential changes in the activation over generations as the skill evolves. The understanding of the neural aspects of toolmaking emerges as a key-issue for neuroarcheology. By combining functional magnetic resonance imaging and a transmission chain design, we investigated the neural networks and brain areas involved in learning to tie different knots.

To provide context to the study, I first explain how toolmaking progressed in prehistory and how language might prove beneficial in facilitating toolmaking. As cultural transmission is considered the important process for passing on cultural elements, in this case toolmaking, the role of cultural transmission in the cultural evolution of our species will be explored and its relation with learning processes more generally. Using knot tying as an example of toolmaking, brain areas involved in toolmaking and learning will be explained that could be compared to the findings of our study. Lastly, I will briefly address the potential relevance of handedness as it involves hand movements.. The study purpose of this study was to provide more evidence for the neural foundation of human tool skill and its evolutionary antecedents.

1.1 Toolmaking in Human Prehistory

Stone tools, like sharpened rocks and axes from early Stone Age, show signs of intention in making tools with a specific purpose (Stout et al., 2008). When comparing tools from different periods of the Stone Age, there is a clear change in the shape and design of the tools as time passes. The Paleolithic Age, also called the Old Stone Age, is a time period spanning from to ca. 3.3 million years ago (Myr) to ca. 12 thousand years ago (ka), and is divided into Lower, Middle, and Upper periods. In the Lower Paleolithic emerged a simple stone tool industry (style), Oldowan, that dates back over 2.5 Myr and is the first evidence of humans using a tool to make another tool (Stout & Chaminade, 2007). They were made by hitting a rock against another one, removing flakes from the stone and making it more angled. The result is an angled, relatively round stone. Later, a more advanced toolmaking method evolved, making the stone even sharper. With the Acheulean stone tool industry in the Lower Paleolithic era (1.75 to 0.125 Myr), the tools became narrower and longer, and showed signs of symmetry. The skills were becoming more refined, which require a certain intention and planning (Stout et al., 2008). The development of these skills may indicate a cumulative evolvement, where humans from generation to generation have changed their methods and ways as a result of learning from their ancestors.

In addition to stone tools, twisted fibers have been found in the Paleolithic site, Abri du Maras (Hardy et al., 2020). These fibers are the oldest direct evidence of fiber technology that we know of, dating back to 41+- 2 ka. The fibers were plied together to form a 3-ply chord, which is a chord consisting of three strands of rope that have been twisted together to form a single rope. These fibers were found attached to tools and flakes, but whether the fibers were related to the use of the tools remain unclear. This fiber technology still indicates an established tradition amongst the Neanderthals with a possibility of a larger repetoire and area of usage (Hardy et al., 2020).

At Blombos Cave in South Africa, 68 shells were found where 24 of these were assumed to belong to a single beadwork (Vanhaeren et al., 2013). The shells were recovered from four Middle Stone Age levels in the cave. When studying the perforation, size, and pattern of the bead collection, we can see changes in how the beads were strung over time. Beads are seen as an early form of communication in humans, where the beads were worn with a specific symbolic meaning which the other members of the same culture could interpret (Vanhaeren et al., 2013). The meaning of the beads could be displayed in several ways, through the arrangement, number, size, color, and bead type (Vanhaeren et al., 2013). The change revealed in the arrangement of the beads from Blombos Cave could be argued to be a reflection of new norms within the culture and the symbolic meaning attached to them and may be the earliest documented behavior of changes in symbolic cultural norms (Vanhaeren et al., 2013). The wear patterns on the shell beads indicate that prehistoric humans were tying beads on strings at least 70 ka.

The ability to tie the cordage together to form knots could be considered an important tool for prehistoric humans, making everyday tasks and hunting remarkably easier. Previous findings on the site Abri du Maras, suggest the use of hafting which indicate that some sort of cord tying must have been applied (Hardy et al., 2013). With this kind of technology, Neanderthals would have been able to manufacture baskets, nets, snares, and fabric that would prove useful transport and storage and aid them in hunting. The fibers used to make the cordage were made of bast, which is the inner bark of the tree, and was likely harvested from conifers (Hardy et al., 2020). Bast is softer and easier to manipulate before it hardens and becomes bark. This implies that the Neanderthals had the sufficient knowledge to separate the bast from the bark and apply the most appropriate materials to twist together to form a cordage.

Toolmaking skills has been shown to be of high value for prehistoric humans, enabling them to make use of efficient tools for different purposes e.g., hunting, clothes, and transportation. Through thousands of years, these tools have changed and become more refined and precise than before. This suggests that cumulative cultural evolution has occurred in the skill of toolmaking, in which the modifications of the skill have been passed on through generations.

1.1.1 The effects of language on toolmaking.

Studies on language and toolmaking skills suggest that there is a link between toolmaking and the use of language (Putt et al., 2014). Putt and colleagues (2014) conducted an experiment to investigate the effects of language on learning how to make stone tools. Participants with no prior experience with flintknapping were taught how to make bifacial cutting tools, where one group were instructed using spoken language and the other were taught non-verbal with observation and imitation. Results showed that verbal instruction had no significant effect on the quality, symmetry, or shape of the bifacial tools. However, there were large differences in the analysis of the debitage (the waste produced from making the tools) that was left after flintknapping. The verbal group had set up both significantly larger striking platforms and produced significantly larger flakes than those in the non-verbal group. On the other hand, the non-verbal group produced overall a larger number of flakes and did so more efficiently. The flakes were also large and thin, indicating more control over platform size. Even though there were no significant differences between the two conditions, verbal communication did appear to have an effect on the debitage output.

The same neural structures have demonstrated to be active during language and toolmaking, suggesting that the two might be connected (Putt et al., 2014). Therefore, it has been theorized that language may have emerged at the same time as the ability for making tools and continued to co-evolve with this technology. It was also pointed out that language plays a large role in the learning process of making bifacial tools, and that without language, the transmission of these skills may prove very difficult. Findings by Morgan et al. (2015) suggest that teaching and language facilitate the learning of making Oldowan stone stools more than just imitation or emulation. Imitation is the process where individuals copy the actions of another individual and match their movements, and is considered the direct result of observation (Hodges et al., 2007). With emulation, the end goal is copied, but the steps that are required to achieve it are not necessarily copied. The focus is on the goal, and the attempts to reproduce it may be a result of prior knowledge or individual learning (Tomasello, 1998). The findings support the gene-culture co-evolution account of human evolution that explain how improvements in the transmission of actions increase with complexity of communication forms. It was therefore argued that if the emergence of language did not facilitate learning, and the simpler forms of learning were sufficient enough to continue the evolutionary process, then verbal teaching would not have evolved (Morgan et al., 2015). While it is not documented that prehistoric humans either had or needed language to manufacture tools, does not rule out that they had some sort of ways to communicate about making them.

1.2 What is Cultural Transmission?

Cultural transmission is a form of social learning that is estimated to have originated 2,6 to 1,8 Myr (Hillesund, 2021). Early humans discovered that teaching their methods and knowledge to the next generations through simple communication secured more accurate transfer of skills. This includes the skills, beliefs, institutions, values, and norms that a given community has developed and is a product of a cumulative evolution. Humans were able to extract valuable and beneficial information from the all the social information that was transmitted. The accumulation of skills eventually resulted in a pool of knowledge that no single human or generation alone could accomplish by themselves. This process initially started slowly, but has only gotten faster and faster with time (Hillesund, 2021).

It has been theorized that our capacity for social learning, specifically cultural transmission, has evolved as a result of natural selection for its ability to separate adaptive from maladaptive information from the surrounding environment (Henrich, 2004). Maladaptive information can include changes that make individuals less likely to survive and reproduce, or cases where the costs outweigh the benefits. Henrich and Gil-White (2001) explain that humans have a psychological tendency to direct their attention to individuals that are considered skillful and will try to imitate them. As well as try to interact and socialize themselves with their skillful models. These models are regarded as reliable sources of information and are said to have *prestige*, in the sense of being someone that has earned the right to be heard and to have their opinions considered more closely than other of their group (Henrich & Gil-White, 2001). By preferentially seeking these skillful models, the time costs of individual learning are saved, and it becomes an adaptive cultural transmission that natural selection favors.

1.2.1 The role of sociality in cultural transmission.

To test the assumption of sociality on skill development, Muthukrishna and colleagues (2014) conducted two laboratory experiments using transmission chain design. One experiment to test the effects of having multiple models on cumulative cultural change, with the first generation being untrained. The second experiment tested the effects of having multiple models on the loss of cultural complexity, with the first generation being trained. Each generation consisted of five participants, in a total of 10 generations in both experiments. Participants were randomly assigned to either a one-model or a five-model treatment. In the one-model treatment, participant only had access to information given to them from a single participant from the previous generation, whereas in the five-model treatment, the participants had access to information from all five participants in the previous treatment. In experiment 1, participants were given the task of recreating a target image. They were provided with written information which the previous generation had written for their assistance, as well as the target image (with and without measurements), and a screenshot from the previous generation. In experiment 2, the participants were instructed to tie a knot system commonly used in rock-climbing. Unlike in the first experiment, generation 1 was trained to become "experts" in the knot system before teaching the next generation through an instructional video.

Results showed that in experiment 1, the five-model chain showed a significant improvement of skills, whereas the one-model chain showed no improvement, rather a slight decline in skill level. In experiment 2, both conditions showed a decline along the chains. The knot tying skills of the one-model chain declined faster over the three first generations, compared to the five-model chain and ended up at a higher average performance score. These findings were consistent with the assumption that access to multiple teachers or models facilitates learning and enhances performance. Muthukrishna and colleagues (2014) conclude that populations that are more sociable will develop more complex skills compared to populations with less sociable member, and that with less sociality these skill will gradually decline over generations.

It is important to note that the effects of number of models is dependent on how much time the participants have to evaluate and integrate the information presented to them. A large number of models and input does not necessarily generate better outcome if the time frame is limited. Caldwell and Millen (2010) ran a transmission chain study with 20 chains and 10 participants in each that consisted of a *microculture* or *microsociety*, which regards the chain as a mini population. The three conditions were divided into a one-model, two-model, and three-model chain, where the longest-observing participant was replaced with a new participant at regular intervals. Half of the participants were instructed to build paper planes to fly as far as possible, and the other half had to build a tower of spaghetti and modeling clay as high as possible. Results from the paper plane group showed that both the one-model and the two-model generated cumulative learning across generations, but the three-model condition showed no significant effect of cumulative learning. It was expected that the threemodel condition would show an increase in flight distance due to a greater number of models. Rather, the condition had overall lower test scores on the flight distances of the paper planes compared to the two-model condition. The authors speculate whether the time frame may not have been sufficient for learning from a larger number of models, and that this might be the reason for overall lower performance level (Caldwell & Millen, 2010). It has also been

pointed out that increasing the number of teachers or models might have little impact on performance if the task is too easy. This could explain why the three-model condition in the Caldwell and Millen (2010) study did not show significant effects for better performance level nor cumulative learning (Muthukrishna et al., 2014).

1.2.2 How to investigate cultural transmission.

When investigating whether cultural transmission occur in either humans or nonhumans, observational studies can give valuable insight into how species behave and interact with each other. But it does not give enough information to be able to draw conclusions based on the behaviors that are observed. Therefore, it is more beneficial using experimental design, in which variables can be manipulated and controlled for in order to discover the correlations between the inputs and outputs in the study. An example of an experimental design is a transmission chain design, which is when one participant watches a trained model performing a behavior and then tries to recreate it. The participant will then become the model for the next participant in line, and so on. Another design is open diffusion, where the model or models are either trained or spontaneous innovators of a skill that is presented to a population. The spread of this skill is left open, and diffuses across social networks (Whiten, 2021). An example is a study introducing new foraging techniques into a wild sub-population of great tits (Parus major), using two trained birds that were seeded into each of the five subpopulations (Aplin et al., 2015). The new technique spread rapidly, reaching an average of 75 percent of the individuals. Despite a high turnover in the population, the foraging technique became an established local tradition and stayed stable over two generations. Effects of social conformity also arose, demonstrating that individuals in the populations adopted the variant

that was the most frequent when first acquiring the behavior. This showed that the birds preferred social information over personal information. The study serves as an example of how socially transmitted behavior might spread in natural settings among animal populations and suggests that the cultural behavior of animals might be more complex than originally theorized.

A third design option is replacement design, where the longest standing individual is replaced by a new individual after each transmission. Using homing pigeons, Sasaki and Biro (2017) tested to see if repeated removal and replacement of birds in groups increased the efficiency over generations. The generations started with a single pigeon flying the same route twelve times, where a second pigeon was added for the next generation. The first pigeon was then replaced with a naïve one in the following generation, and this procedure continued down the chain. Birds in the replacement condition were compared to a solo bird and a fixed pair and measured on the same route. Results showed that the pairs in the experimental groups significantly outperformed the two control groups and did so by the fourth generation of the twelve generations in total. The authors conclude that their study fulfills the criteria for cumulative cultural evolution by; showing that the pigeons performance improved over consecutive generations, the pairs outperformed the solo pigeons at the end of the generations, and the similarity of the homing routes were larger within the same chain than between the chains. Even though the study did not show an increase in complexity or have an openendedness to it, it still showed important aspect of cumulative cultural evolution and how collective intelligence can become a drive for the cumulative process (Sasaki & Biro, 2017).

When studying and investigating the effects of cumulative evolution, it is important to keep in mind that it cannot be studied in real time. The improvements or other effects of

cumulative culture have happened over years and several generations; therefore, a true recreation will be unrealistic. The timeframe has to be scaled down, which can bring limitations to the study.

1.2.3 Cultural differences in teaching and learning strategies.

Teaching is a social learning process that can be dated back to hunter-gatherer societies and appears in many forms (Boyette & Hewlett, 2018). In modern western countries, teaching through formal education is considered the standard learning strategy. Formal education is based on a curriculum and the teacher is responsible for the learning of the student. The involvement of the students in their own learning experience can vary between cultures and educational level. In active learning, students are encouraged to participate in the learning process, by for instance discussing or role-playing. With passive learning, the students are expected to listen, learn, and internalize the information given to them from the teacher.

In some hunter-gatherer groups, teaching through lessons and evaluation is not as highly prioritized as it is in today's society. Storytelling, observational learning, and trial and error are acknowledged as important ways of learning as well (Boyette & Hewlett, 2018). Storytelling is used to convey information about generalizable knowledge, using direct eye contact, singing, and body language to add to the experience. Recurrent topics of storytelling include problems in the forager life, such as information about topography and ecology. The stories also serve the purpose of norm teaching and learning about instrumental techniques (Biesele, 1986). Observation of and participation in "wrong behavior" is also partly considered a way of learning the right behavior (Biesele, 1986). Autonomy is another highly valued strategy in the hunter-gatherer societies and is reflected in their teaching. For Inuit hunter-gatherers, children's autonomy is respected through encouraging them to learn by themselves through collaboration and observation. This can be done through "teasing", which is when the teacher wants to help the child to learn values that are considered important for their culture, and states or asks ambiguous questions over which the children must reflect and resonate. This will lead up to more questions and serve as a motivation for individual learning in the child (Boyette & Hewlett, 2018).

Manual skills such, as toolmaking, were an important part in past human societies and have likely been passed on through observational learning (Michel & Harkins, 1985). Through observing other's values, attitudes, and ways of behaving and thinking, we are often influenced to do the same (Bandura, 2008). Observational learning and imitation are seen in very young children, in the way they mimic the movements and actions of their relatives (Kurzban & Barrett, 2012). It is assumed that the observer's behavior is a direct product of the demonstrator (Hodges et al., 2007). This kind of behavior requires that children have the ability to make inferences about the goals and intentions of the behavior through watching the movements. Since this ability emerges early in life, it may indicate that we are born with the mechanisms required for social learning. These special learning mechanisms may have developed as a result of the necessity for specific knowledge and behaviors for survival in different conditions (Kurzban & Barrett, 2012). An example is the importance of separating edible foods from poisonous foods.

In a learning setting, there is a risk of either overimitation or emulation. Overimitation is when both the relevant and irrelevant actions that have been observed are copied. Behavior that is believed to be important to achieve the end goal is continuously copied without serving a function. In a recent study investigating the effects of verbal instruction versus modelling on imitation found that there was no difference in transmission fidelity between the verbal instruction and demonstration conditions (Papa et al., 2021). There was also no significant difference between children and adults in the demonstration condition. However, emulation was greater in the verbal condition, compared to the demonstration condition. This may be due to language underspecification or lack of visuals of the model presented in the audio. In the verbal condition, the adults showed a significantly decline in irrelevant action over generations compared to the children. The casually irrelevant actions are related to overimitation, where in this case the children showed a greater tendency to overimitate. The prediction of a more pronounced loss of irrelevant actions in children versus adults was therefore not supported in the verbal condition. The reason for children being more overimitative may be due to the task itself. The box which the participants had to manipulate may have been perceived as more playful, and consequently lead to more irrelevant actions. The findings of Papa et al. (2021) are in contrast to a study on overimitation in children and adults that demonstrated that overimitation increases with age, where adults typically coping more irrelevant actions than children (McGuigan et al., 2011). It was argued that overimitation can secure high fidelity transmission and may be a drive for cumulative cultural evolution, but the efficiency of the transmission will be reduced. It seems that overimitation behavior depend on a number of factors, such as the specific task, context, and the modeled actions, suggesting that overimitation is flexible in terms of contextual factors (Hoehl et al., 2019). In terms of cumulative cultural evolution and social learning, it could be concluded that both verbal and non-verbal communication are considered efficient in transmitting information.

1.2.4 Is teaching and imitation necessary for cumulative culture?

If we look at learning in conjunction with cumulative cultural evolution, we run into a "chicken or egg"-problem. It is argued that learning is a prerequisite for a cumulative cultural evolution. Humans had the mechanisms and capabilities for social learning, such as imitation and teaching, which contributed to the accurate transmission of behaviors. These mechanisms existed before and were the cause of cumulative culture (Caldwell et al., 2017). It could also be argued that learning is a consequence of cumulative cultural evolution (Caldwell et al., 2017). If the cause or intention of a behavior is unclear or ambiguous to the observer, then the person conveying the information must adjust their ways. It was proposed that social learning and teaching have evolved as a response to this problem. The person observing has had the intention of learning this information, and give it meaning (Caldwell et al., 2017).

Tennie, Call and Tomasello (2009) describe the cumulative cultural evolution as a process where a skill or a certain way of doing things is modified or improved over generations, where the next generation learns from the previous one. They argue that the products of human evolution such as tools and artefacts, could only be a result of modifications that have accumulated over time. And that this process is supposedly due to transmission and social learning (Tennie et al., 2009). With emulation learning, the focus is on the effect the action has on the surrounding and the environment. Instead of copying the process leading to a product, the focus is on the end product and how to re-construct it. This type of learning can be seen in chimpanzees. When demonstrated how to use a tool, the attention is on the effect being produced in the environments, and not on the actions by the person using the tool (Tennie et al., 2009). Even though emulation can facilitate learning,

they argue that cumulative culture requires higher fidelity behavior, and that social learning and imitation drive this process.

Others argue that even though teaching and imitation contribute to cumulative culture, it is not necessarily crucial for cumulative cultural evolution (Caldwell & Millen, 2009). To test this assumption, a study using transmission chains tested which learning mechanisms that were necessary for cumulative cultural evolution (Caldwell & Millen, 2009). Participants were asked to build paper planes and get them to fly as far as possible. They were divided into seven groups, and got access to different types of information, such as observing others build their plane, hearing and viewing their results, and receive teaching from the person before them in the chain. Results showed that there was a significant improvement in performance along all of the chains, and that none of the conditions showed complete loss of cumulative learning (Caldwell & Millen, 2009). In addition, none of the conditions were overall better than the other, and each source of information was an effective strategy. This study demonstrated that emulation, that is copying the end product, was sufficient enough in demonstrating cumulative culture, and that teaching and imitation were not the only learning strategies necessary for driving this process. Cumulative cultural evolution is according to this study possible in the absence of social learning.

In a study of cumulative cultural evolution, improvements in tool manufacturing were investigated by the creating baskets (Zwirner & Thornton, 2015). A transmission chain design was used to determine whether emulation was sufficient in generating cumulative improvements. Baskets were evaluated to see if they could carry more rice than previous baskets in the chain and the durability of the basket. Participants were divided into groups of asocial, emulation, imitation, and teaching. All four groups showed improvements in the mass of rice the baskets could carry along the chains, and there were no significant differences between the conditions. In all conditions except for Teaching, there were no significant differences in the durability of the basket. Teaching showed a greater durability than the other conditions. From this study, it could be argued that emulation is sufficient in generating cumulative improvements, and that high-fidelity learning mechanisms are not the only mechanisms responsible for cumulative cultural evolution (Zwirner & Thornton, 2015). These findings are in line with Caldwell and Millen's (2009) paper plane study. Even though all conditions showed improvements along the chain, Teaching stood out as the most effective learning strategy in the durability test of the baskets. With Teaching, the participants were given verbal instructions and they were able to communicate about aspects of construction that may not be as apparent with observation only. It seemed that the participants in the Teaching condition benefitted the most from the knowledge the participants before them had collected. This reflects the core of what cumulative cultural evolution is. It may be that emulation is not a sufficient strategy in every learning situation but is has been shown to be effective in several cases. Both the study by Zwirner and Thornton (2015), and Caldwell and Millen (2009) show that imitation and teaching are not the only strategies responsible for the drive of cumulative culture, and that emulation could in fact produce similar results.

Studies on cumulative culture are often set in laboratories, such as Caldwell and Millen's (2009) paper planes study and are not always generalizable. In the real world, the process of evolution is much more complex and is a result of several strategies and developments that may be difficult to reproduce in experimental settings. Even though some behaviors could be accumulated with emulation only, does not mean that teaching and imitation are not crucial for other behaviors and are necessary for the transmission to the next generation. An interplay between different forms of learning dependent on circumstances and the environment is likely the driving force behind cumulative culture.

1.2.5 Cumulative culture in non-humans.

Culture in animals such as birds, chimpanzees, whales, and dolphins have been claimed (Tennie et al., 2009; Whiten et al., 2003). Examples of animal culture have been shown in for instance regional dialects in birdsong and the development of a certain technique for feeding on pinecones by black rats (Whiten et al., 2003). Culture in this sense could be described as "the phenomenon whereby features of behavior pass by learning from one individual to another" (Whiten et al., 2003). Chimpanzee culture has been well documented, with studies showing for instance how Tai Forest chimpanzees manage to use twenty different tools, or how central and East African chimpanzees use different tools for harvesting food (Whiten et al., 2003). This method for harvesting and feeding was about four times more efficient that other techniques used by chimpanzees in other parts of the world (Whiten et al., 2003).

Several findings suggest that culture can be found in animals, but are there signs of the "rachet effect" that can be found in humans and of cumulative cultural evolution? Whiten et al. (2003) argue that there is little evidence of cumulative culture in chimpanzees, and that the behavior observed in them has not advanced beyond the behavior of its original creator. In order for the culture to be cumulative, the behavior has to persist over several generations. Chimpanzee behavior has only been studied for decades, and it is therefore difficult to say for certain that there has not been a cumulative evolution in their behavior. Even though a few findings may suggest that there is evidence for some cumulation among animals (e.g.,

harvesting in Tai chimpanzees), there is still an ongoing debate on whether or not the culture or traditions could be labeled as cumulative culture. Human cumulative culture is much more complex, and it is hypothesized that the psychological mechanisms required for transmission of culture is more limited in animals compared to humans (Whiten et al., 2003). The prevalence of cumulative cultural evolution in humans may therefore be not only dependent on the learning mechanisms, but also on unique cognitive and behavioral capabilities (Caldwell & Millen, 2009).

1.3 Brain Areas and Activities involved in Toolmaking and Learning

Identifying the neural basis of toolmaking is important for a broader and deeper understanding of the processes involved. Previous studies have identified areas such as the cerebellum (Seidler, 2010), basal ganglia (Doya, 2000), and intraparietal sulcus (IPS) (Cross et al., 2017) related to skill learning. The areas are involved in the action observation and execution of a skill. As we know of, no study has investigated and compared the neural activation of the different stages of skill acquisition. Therefore, more research on this field is necessary for the understanding of the complex processes and activation of toolmaking. In the section below, the different aspects and brain areas involved in toolmaking and learning will be further explained.

1.3.1 Motor learning.

Toolmaking is a motor skill that requires the use of coordinated movements that involve the processes for *motor learning*. Motor learning can be defined as "a set of processes associated with practice or experience leading to relatively permanent changes in the capability for skilled movement" (Schmidt et al., 2018). Examples of motor learning can be learning to play an instrument or a sport. The learning consists of several processes, for instance if you want to learn how to play the guitar, you have to learn how to hold the guitar correctly, how the strings work, what they sound together, and so on. These processes have to be learned over a time course, and through consistent rehearsal for the movements to become permanent. Only then can you say that you have mastered to play the instrument. These motor movements are then stored as a pattern in the brain and can be retrieved and used when it is convenient. This type of motor learning is called de-novo motor learning or sequence learning (Bastian, 2008).

Another variant of motor learning is sensorimotor adaptation. The ability for sensorimotor adaptation allows us humans to act and change according to new demands in our society, which has been important for our ancestors, e.g., in terms of hunting, toolmaking, and the manipulation of tools. Sensorimotor adaptation can be defined as the during which a person modifies their "movements in response to changes in sensory inputs or motor outputs" (Seidler, 2010). The process can be viewed as trial-to-trial based, with the brain predicting how the body will move and evaluating the situation with regards to the task's demands (Bastian, 2008). The brain will want to reduce the costs of each trial, such as preserving energy, reducing fatigue and inaccuracy. Martin et al. (1996) have set the following three criteria for the definition of *adaptation:* (1) the movement is identifiable as the same, but a change in some sort of parameter occurs (e.g., direction or force); (2) the change occurs as a result of repetition of the movement which happens gradually and continuously; (3) the previous behavior cannot be retrieved once the new behavior has been adapted; instead the newly adapted behavior must be changed, following the same course, back to the previous

behavior (Martin et al., 1996). By investigating sensorimotor adaptation, we gain a better understanding of how the human body interacts with the surrounding environment, through both planning and production of movement.

In the field of motor learning, a novel hypothesis proposes an ability of "learning to learn". It suggests that learning is not necessarily specific to a context or a task, but rather that learning can be generalized and transferred to different situations (Seidler, 2010). This means that your experience with playing the guitar will be beneficial when learning to play another instrument, but it does come with a cost. Although the movement becomes more adaptable through several learning experiences, the newly learned movement becomes less resistant to outside disturbances (Seidler, 2004).

1.3.2 Neural correlates of motor learning.

When investigating the brain areas involved in the learning process, disentangling the areas is challenging. Many of the same brain areas are involved in the different aspects of learning, such as when learning the specific skill and executing it. Seidler (2010) highlights that variables, such as the rate, force, and errors of the movements, change through the acquisition of a skill. It then proves difficult to determine whether these changes reflect the effects of practice, with the different performance levels that occur during this process, or whether the changes represent "true contributions to the learning process" (Seidler, 2010).

There is evidence for the involvement of the cerebellum in motor learning, specifically sensorimotor adaptation (Seidler, 2010). The cerebellum is known to be involved in motor control and for fine-tuning movements, and is specialized in supervising learning (Doya, 2000). The area is error-driven, which means that the cerebellum has an error-signal system

for adjusting and improving motor performance. Studies have also shown that the cerebellum is involved in movements driven by external cues, such as visually guided movements. This is in contrast to basal ganglia, which is involved in internally generated movements, such as movements retrieved from memory (Doya, 2000). It is argued that the reason for the differential involvement of brain areas is because both areas have their specialized functions for selecting the appropriate computation and action. Cerebellum is as mentioned involved in computing motor output from the visual input it has received, and the basal ganglia is responsible for selecting the appropriate action drawn from memory and for stopping action that is not appropriate for this particular situation (Doya, 2000). This has to do with the fact that basal ganglia is involved in predicting reward value, whereas the cerebellum predicts sensory consequences of actions (Seidler, 2010).

A study by Imamizu and colleagues (2000) challenges the previous view that the cerebellum is only involved in the early learning phases, and that the memory of the newly learned task is not stored in the area. Their work showed that two types of cerebellar activation occurred when human subjects learned to use a new tool; one was activation of a large area in the lateral cerebellum related to error signals for acquiring internal models during learning, and the second was an area near posterior superior fissure which reflects that an internal model for newly learned task has been acquired. This was also the area that was active during adaptation of movements to visually different distortions (Imamizu et al., 2000). This showed that the cerebellum was both active during and after learning, and that cerebellar activity could be linked to sensorimotor adaptation.

Damage to the cerebellum impairs sensorimotor adaptation. The improvements in performance that usually happen trial-by-trial decreases, and the stored effects of the motor

adaptation is diminished (Bastian, 2008). This damage may affect several movements, such as arm movements, eye movements, balancing and walking. Damage to other brain areas involved in movement, e.g., basal ganglia and the cerebral cortex, has not shown any severe impairment to this process. Even though the sensorimotor adaptation is still largely intact, the function of choosing of motor strategy and reaching for objects seem to be slowed down or altered in some ways (Bastian, 2008).

1.3.3 Neural activation during object interaction and manipulation.

Everyday objects belong to different categories (e.g., a hammer to the category of *tools*, a dog to *animals*), and this influences how we interact with these objects. We would not treat a tool and an animal the same way. When studying the brain while viewing different objects, it is important to be able to differentiate which category the object falls into. In a study investigating how the brain constructs representations of objects, participants learn to either name or tie different knots (Cross et al., 2012). Using an fMRI scanner, brain activity was measured before and after learning the name or tying the knot. The participants showed better naming performance for knots they had learned to name only, than for knots they had learned to both name and tie. In addition, participants showed better tying performance for knots they had learned both to tie and name. Cross et al. (2012) argued that these results may indicate that the systems for perceptual-motor and linguistic learning are not fully independent of each other (Cross et al., 2012). The study showed a greater response in bilateral regions of the intraparietal sulcus (IPS) when

naming condition did not show activations in areas that were expected to be associated with language, such as middle temporal gyri and inferior frontal gyri.

Several studies have found that visual experience with novel objects can cause activation in sensorimotor areas associated with object manipulation (Cross et al., 2017). Additionally, observing another person interacting with an object can cause activation in the areas associated with manipulating the object, as if they were manipulating it themselves. In an fMRI study, participants were divided into two experimental categories: one where participants learned to tie knots by physically practicing, and one category where they observed their partner learning to tie knots (Cross et al., 2017). Results showed a significant larger activation of the left superior parietal lobe when comparing the before knot practice and the after knot practice scans for both the physical and observed group (Cross et al., 2017). After a week of training, the right dorsal premotor cortex and right IPS were activated when the participants were shown images of knots they learned to tie themselves, and images of knots they had seen their partner tie, compared to knots that were untrained (Cross et al., 2017). No significant difference in IPS parameter estimates were found when comparing the tied and the observed conditions. Both conditions, tied and observed, showed responses in the right IPS and the right dorsal premotor cortex (Cross et al., 2017). IPS is a part of the parietal lobe and receives sensory and motor signals for controlling and guiding action in space (Grefkes & Fink, 2005). The area encodes information such as the shape, size and orientation of objects, and the position of body parts (Grefkes & Fink, 2005). The different areas of the IPS have more specific functional purposes. Specifically, the anterior IPS has been linked to object manipulation and grasping movements, whereas lateral IPS has been shown to be

involved in the control of eye movements and attention and has a higher sensitivity to salient sensory input.

When learning a new skill, it requires a sequence of actions that often follows a specific pattern. In the processing of these repetitive patterns, the early visual cortex plays an important role (Hodgson, 2006). It is responsible for the construction of the images and objects being processed, and the information goes from here to temporal areas for recognition of the images/objects (Hodgson, 2006). The neurovisual resonance theory postulates how an organism is at any given time is set to perceive patterns that are considered important to them. The early visual cortex becomes especially responsive when these patterns are repeated, because the patterns may be of importance to the organism when managing the visual world (Hodgson, 2006).

1.3.4 Learning and handedness.

Handedness is a general characteristic of mammals, where humans show a distinct uneven distribution (Michel & Harkins, 1985). It is estimated that about 85 percent of the human population is right-handed and use the right hand for fine manipulations and the left hand for support and stabilization (Uomini & Lawson, 2017). Prehistoric bones and fossils show a clear right-handed bias, and thus handedness may be a result of early evolution (Uomini & Lawson, 2017). Since toolmaking is a skill that requires the use of hand movements, it is natural to assume that handedness may play a role in tool use and manufacture.

A study on handedness and learning showed that participants were able to tie more knots when their handedness corresponded with their teachers', in addition to faster learning times (Michel & Harkins, 1985). This was the case for both groups of right-handed observers and teacher, and for left-handed observers and teacher. There were no significant sex differences in learning time. The study concluded that when the observer' and teacher' handedness is concordant, the learning of a skill becomes more efficient. Their reason for less efficiency for concordant handedness was that the observer has to transform the information given to them, in order to match that of their teacher, or that additional steps were required to perform the task (Michel & Harkins, 1985). Therefore, it would be advantageous for the observer to match their handedness to their learner, and this may be the reason for the righthanded bias that has emerged through human evolution.

1.4 The Current Study

In this project, we aim to investigate how cultural transmission has contributed to the development of a toolmaking, in this case knot tying. The neural networks involved in teaching and learning of this skill were investigated, using a functional magnetic resonance imaging (FMRI) combined with a transmission chain paradigm. The study was a simulation of cumulative culture where the acquired skills was passed down the chain, mimicking the acquisition of a trait through the course of evolution. In addition, we investigated what differences there were in neural activity in the different stages of the transmission chain. The present project is a pilot study a part of a larger study involving both knot tying and symbol production.

The gender of the participants has been controlled for, with separate chains of male or female only. It was not expected to see any major sex differences, and if there were, the differences are likely to be small. Mental rotation is the largest observed sex difference, where

men show better performances. Whereas women perform better in tasks involving spatial visualization (Hirnstein et al., 2019). The two sexes have their strengths and weaknesses, but in general their presentations are rather equal.

Participants were divided into three chains of either right-or lefthanded only or an alternating handedness chain. While inside the fMRI scanner, participants were instructed to learn a total of five knots, which they had to reproduce. Their demonstration of the different knots was recorded and used as the instruction video for the next participant in their assigned chain. The current study aims to characterize the brain regions involved in the acquisition of knot tying skills. This research complements recent attempts to utilize neuroimaging to test hypothesis on the evolution of human cognitive functions. Using knot tying as an example of toolmaking, we attempted to compare the neural foundation of knot tying with prior research on the neural foundation of toolmaking. Mapping the brain regions involved in knot tying could prove useful in shedding light on the cognitive functions of prehistoric humans.

2. Method and materials

2.1 Choosing a Design

Both naturalistic observation and experimental design can be used to investigate human evolution. Naturalistic observations give insight into how different behaviors and phenomenon occur without interference from outside, in a way that does not affect or change the behavior or phenomenon under observation. Nevertheless, it has its disadvantages when it comes to investigating human evolution. The behavior or phenomenon to be studied has evolved and changed over the course of hundreds and thousands of years, and it becomes challenging to interpret and draw conclusions about the correlations and causations without using an experimental design. With experimental design, variables can be manipulated in a way that makes it possible for us to draw conclusions that can be generalized on a population level. Even so, we have to be careful when making these generalizations. Laboratory experiments are simplifications of reality, and it is therefore easy to exclude variables that may be important for the phenomenon being investigated (Caldwell et al., 2017).

The design of this study is based on studies of Caldwell & Millen (2008), investigating learning through generations in an experimental setting with use of transmission chains. Transmission chain studies show how participants from earlier generations pass on their experiences to the next generation, and how this may result in better performances. The experience passed on from previous generations can give useful information on how to improve and become more efficient (Caldwell et al., 2017).

The study was set up as a block design, with a learning phase, a reproduction phase, and a resting phase. This was repeated 6 x 6 times to get sufficient measurements for the analyses. The knot videos and the reproduction phase had a duration of 30 seconds each, with a 15 second rest phase. Measurements were taken every 2 seconds during every phase of the scanning period. The order was as following: the instruction video (30s), reproduction phase (30s), and then a resting phase (15s). In total, the sequence lasted for 7,5 minutes per knot. This was repeated 6 times for each of the knots, including the control condition in the study. Participants were not able to pause or speed the program at any point during the scanning. The program was fixed and identical for all participants in the study, besides the randomization of the stimuli. Three chains were set up, with eight or seven participants in each of the chains. The chains were divided in right-handed males only (7), right-handed
females only (8), and alternating right-and left-handed males and females (8). Participants were randomized on the male and female only chains, but not completely randomized in the alternating chain due to ensuring that every other participant was left-handed.

The study was approved by Regional Committees for Medical and Health Research Ethics (REK) before experiment started (see Appendix A). It was also registered in the System for Risk and Compliance (RETTE), for data protection and privacy. The study was funded by the Center for Early Sapiens Behavior (SapienCE) at the University of Bergen (see Appendix B).

2.2 Participants

Participants were recruited through posters hung up on boards at different faculties at the University of Bergen in the period from August 2022 to December 2022. The recruitment poster (see Appendix C) briefly described the study and contained a QR-code, when scanned, lead to website for signing up for the study. On the website, they had read through the exclusion criteria and confirm that none of criteria applied to them. After signing up, they would receive an e-mail from a team member confirming that they could be a part of the study and schedule time for the fMRI scanner.

Twenty-three participants were in total recruited and completed all phases of the study. Out of 23 participants, 19 were right-handed, three were left-handed, and one participant reported that they were ambidextrous (uses both hands equally). There were 14 female (61%), and 9 (39%) male participants in this study. All participants were 18 years old or older, and consisted of mostly students at the University of Bergen.

Exclusion criteria for participating in the study included psychological, medical, or neurological illnesses, history of head trauma, and the usage of medications that effect brain function. These criteria were set to avoid any abnormal findings that could affect the interpretations of the results of this study. Due to the fact that metal could interfere with the magnetic field in the MRI when creating the images, causing a safety hazard, we had to make sure that none of the participants had any metal or implants in the body. Large tattoos on the head and/or neck had to be avoided due to previous reports on burning and irritation sensations during an MRI. Pregnancy was also excluded because of safety reasons for the fetus. Participants with knot experience from sailing, boy/girl scouts, or climbing had also been excluded from this study. This was to ensure that the participants had little to no knowledge of the chosen knots, and that they had the same starting point.

The study was piloted on a couple of team members and on one participant to test the procedure and participant experience before we started the main data collection. Data from the pilot runs were not included in the analyses. One participant was excluded from the study post-hoc. The participant was excluded due to lack of understanding of the procedures of the experiment, and failure to produce a sufficient amount of correct tied knots. Exclusion of this participant was done after the completion of the fMRI scanning.

2.3 Preparations

All participants had to fill out a form handed out by the radiographers with contact information, and other relevant information that was of importance before entering the fMRI scanner. Such information included whether the participants had: a pacemaker, any implants in the body, had an operation in their head or spine, any metal in the body, or had an injury in their eyes. In addition, all metal from the body, such as jewelry, watches, glasses, wired bras, had to be removed before entering the machine. Information about the experiment was then presented. First, the consent form (Appendix D) and a handedness questionnaire (Appendix E) had to be filled out. Participants were then informed about the practical aspects, such as adjusting the machine to their needs, and how the experiment works. They were shown images of the different phases of the experiment and told what they were supposed to do in those different phases. Each participant was told that they could at any time withdraw from the experiment without questions. Once they had filled out the necessary forms and confirmed that they understood the procedures, they were escorted to the fMRI scanner.

2.4 Stimuli and Material

Stimuli consisted of five knots that could be tied with a single rope and were classified as basic knots by the website that they were retrieved from <u>animatedknots.com</u>. These knots were chosen because they were easy to learn in a short period of time, required little to no experience, and could easily be reproduced with limited range of motion. The following knots were used: *figure 8 knot, sheet bend knot, slip knot, noose knot, and square knot*, in addition to a control stimulus (see Figure 1). The control stimulus was added to the study for filtering out variance due to factors that are not specific to the experimental condition. The control condition required that the participant pulled the rope between their hands from right to left, and back again. This required little learning and energy due to the simplicity of the task. Therefore, the activity during the control condition was subtracted from the experimental condition, revealing the true activity for knot tying. The knots had been tested beforehand by two team members of this study. Both the control stimulus and the knots were randomized for each person in every chain, using a researcher randomizer (<u>randomizer.org</u>).

The instruction videos were 30 seconds long and featured the hands of a demonstrator tying each individual knot. The knot tying techniques were identical to the techniques displayed on the <u>animatedknots.com</u> website. For the male chain, the instruction videos showed the hands of a male, and for the female chain the hands of a female. The instruction videos used for generation one for each chain were recordings of one of the team members' hands for the female chain and for the alternating chain, and for the male chain, the recordings were of a team member's partner's hands. The participants were told beforehand that they would be demonstrating the knots that they had been learning, and that their demonstration would be recorded and used as an instruction video for the next participant.

Figure 1



The knots used in the experiment.

Note. All images are outtakes from the instruction videos for the female chain, used for generation one, chain 1. The following knots are figure 8 knot (A), noose knot (B), control stimulus (C), sheet bend (D), slip knot (E), and square knot (F). The knots were retrieved from Animatedknots.com.

The instructional videos were filmed on a neutral background, starting off with on a wooden table, as seen in figure 1. After getting feedback from some of the participants that there was too little contrast between the background and the hands tying the knot, we changed the background to a higher contrast. We switched to a black mat, measuring 30 x 45 cm, for the rest of the experiment (see Figure 2). The ropes used for knot tying were cut from the same polyester coil and burnt on each end to prevent the ropes from tearing. All ropes

measured between 58 cm to 60 cm in length, with a diameter of 5 mm. Videos were filmed from a first person perspective, where the camera placed 83 cm above the table (see figure 2). The camera was a Sony SLT-A65V, with a Sony SAL18552 zoom lens.

Figure 2

The set up used for recording of the instruction videos.



In the current study, fMRI scanning was used as an exploratory technique for identifying the brain regions of knot tying acquisition, where it detects changes in blood flow as a results of brain activity (Borthne & Tjelta, 2021). The processes in the brain that involve the production and transfer of nerve impulses, require energy which result in an increased need for oxygen supply. The blood flow and blood oxygenation in the nerve cells therefore increase, making these changes detectable for an MRI. The way the changes in the amount of oxygen in the blood is proven, is with the *Blood Oxygenation Level Dependent*- (BOLD) technique. Oxygenated and deoxygenated blood have different magnetic properties. When the hemoglobin in the blood in fully oxygenated, it becomes diamagnetic and is attracted to the magnetic field in the MRI through delivering radio frequency pulses. The changes in local magnetic field are then measured by coils that are placed within the fMRI scanner (Logothetis & Wandell, 2004).

All fMRI sessions were conducted at Haukeland University Hospital at the Radiology department. The T1- and T2 -weighted structural images and the functional images were acquired using a 3 Tesla GE-signa MRI 1.5T machine. The interscan interval was sat at 1.5 seconds, resulting in a total of 300 images per knot per participant. The whole brain was scanned, with a voxel size of 3 x 3 x 3 mm. Activa was used for programming the video sequence for the fMRI trials. Both the pre-recorded videos done by one of our team members and the participants instruction videos were recorded using the same camera and lens and was edited with DaVinci Resolve 18.1.17 to fit the format for Activa. The DICOM images were converted to NIfTI image format using MRIcroGL. The images were further pre-processed and analyzed using the Statistical Parametric Mapping (SPM 12) software package, running in MatLab version 9.10.

2.5 Procedure

Participants were placed in the fMRI scanner and told that they would be shown videos of knots that they had to learn. For each of the participants, the screen on which the instruction videos were shown was adjusted according to their needs, as well the mirror placed in the head coil that was used for viewing their hands while tying. A testing rope was given to each participant before the session for testing and adjusting the needed equipment. Resting pillows for their elbows and additional pillows and blankets were also provided. The participants were presented for one knot at the time.

Before the experiment could start, each of the participants went through pre-scanning, which took about six to seven minutes. Pre-scanning is used for highlighting physiological features of the brain that can be important for the study and was done through T1-weighted and T2-weighted images. These images show the contrast differences between types of tissue (University of Oslo, 2020). Radiologists went through these images and participants were notified if anything unusual that needed a follow-up was found.

The participants were given six ropes that were placed horizontally over their hip. They were instructed to use one rope per trial, and to place the used rope next to their left hip after use. Participants underwent six sessions of approximately 7,5 minutes, and each session comprised 6 trials. In one trial, there was the following three conditions:

- 1. Stimulus: a 30 second video clip of knot tying or control stimulus.
- 2. Task: reproduce the knot or control stimulus in 30 seconds.
- 3. Rest: 15 seconds of cross fixation.

Each trial started with the presentation of the stimulus, in which the participants had been told to lie completely still and focus on the video. After the stimulus, an image showing "Gjenta!" (repeat) appeared on the screen. Participants picked up one of the ropes placed over their hips and began tying a knot. This was followed by a rest period consisting of a fixation cross. The total trial duration was 45 seconds. The same stimulus was presented six times consecutively, comprising one session. Figure 3 illustrates the images that was shown on the screen during the experiment.

Figure 3

Images shown on screen during the fMRI sessions.



The rope was extracted from the scanner after each trial and untied by a person sitting next to the participant in the room during the whole experiment. A button was installed into the program for timing when participants finished tying after each trial. The assistant sitting beside the participant inside the scanner room was responsible for pressing the button after each finished trial. This was to make the data collection more accurate by eliminating noise in the sense of time without activity. After each sequence was completed, the participant was given six new ropes for the next trials. The fMRI part of the study lasts about 55 minutes.

Initially, it was planned to do the recording of the instruction video while the participant was still inside the fMRI scanner. Due to space issues and the inability to bring a

video camera inside the scanner room, the recording of the videos had to be done outside of the scanner. After the fMRI session, participants were led into another room for recording the instruction videos for the next participant in their chain. They were informed that they could only watch the initial instruction video once per knot, and that they had to reproduce each knot three times to secure good footage. Additionally, each participant was encouraged to do their best at reproducing, to avoid them giving up, leaving no footage for the next participant in the chain. They were sat at a desk with a black mat placed in front of them and were told to keep their hands in the middle of the mat at all times when tying the knots. A video camera was placed on a stand directly above the black mat, only recording the participants' hands. The rope used inside the fMRI scanner was the same used for recording the instruction video. The order of the knots they were reproducing was fixed, and sorted alphabetically in this order: control knot, figure 8 knot, noose knot, sheet bend knot, slip knot, and square knot. The video camera was recording nonstop from first to last trial, and the videos were edited and stretched/shortened to fit the 30-second time slot in the fMRI program. The videos were then incorporated into the program for the next fMRI run. After the completion of the experiment, the participants were debriefed and given a compensation of 300 kr in form of a gift card.

2.6 Handedness Questionnaire

A questionnaire by Raczkowski et al. (1974) was handed out and filled in by each participant (see Appendix E). The questionnaire was used to determine the participants' dominant hand and to see if the self-reported handedness matched with the scores of the form. The form consisted of 15 questions concerning which hand they use predominantly for several tasks, such as drawing, writing, throw a ball and so on. Participants could answer either of left, right or both for each of the questions. Next, the participants had to mark one of four drawings of hand position while writing that was most similar to their own. Two of the drawings were left-handed and two were right-handed. Lastly, they were asked whether they had any close left-handed relatives that they knew of. The questionnaire forms were anonymized and marked only with participant number.

2.7 Analysis

All data and information about participant were analyzed and stored in SAFE (Secure Access to Research data and E-infrastructure). Team members of this study were the only with access to these sensitive personal data and could only be accessed via log in to a safe desktop created for this project. Team members had to request access through the University IT-department and log in to their University of Bergen account. No identifiable personal data have been extracted and stored outside the SAFE desktop.

For pre-processing, the images were first realigned and unwarped, corrected for movement, improved for segmentation accuracy, normalized, and smoothed. Data analysis was then carried out in two steps, starting off with a first level analysis of the data from each individual subject. A first level analysis was used to look at the brain's response to a task, in this case the response to the different conditions of knot tying. Contrasts were created for the different conditions: "demonstration", "replication", and for "demonstration-replication". We changed the high pass filter from the default 128 to 158 to avoid potentially filtering out our true signal. No masking was applied because we wanted to examine all of the voxels in the brain, and do not wish to restrict our analysis. The uncorrected p-value was set to 0.001, which tested each voxel individually at the p-threshold of 0.001. The extent threshold for voxels was sat at 0. The resulting individual contrast images were used as input for the subsequent second level analysis.

Second level analysis combines the results for multiple subjects or groups. Both the first and second level analyses are based on the general linear model (GLM), which aims to estimate if, and to what extent, each predictor in the analysis contributes to the observed variability in the time-course of the voxels (Monti, 2011). The interest is in how the voxel intensity evolves over time. A one sample t-test was conducted to determine whether the knot tying condition was statistically different from the control condition. We were interested in finding the true activity of knot tying and identifying areas important for executing the skill. Therefore, the contrast "knot tying - control condition" for chain 1 was set. The contrast "knot tying" contained data for all tied knots from each participant. All three experimental conditions ("demonstration", "replication", "demonstration-replication") were explored in the analysis.

To explore potential differences in between the first knot and the last knot for each participant within the chain, we used a paired sample t-test. A paired sample t-test is used for comparing the mean scores for the same group of people at two different occasions (Pallant, 2013). The test was run to identify activation across fMRI sessions that occurred for knots as a result of learning, by comparing the first knot with the last knot within the chain. Pairs consisted of con-images of the first and last knot for each participant in chain 1. The following contrasts for knot order were specified: (Last knot – control condition) – (First knot – control condition) and (First knot – control condition) – (Last knot- control condition). This contrast would reveal activation significant in the last fMRI session relative to the first

session. All three conditions "demonstration", "replication", and "demonstration-replication" were investigated for both t-tests. For the second level analyses, no masking was applied, the p value adjustment was set to "none" using a threshold of 0.001, and the extent threshold for voxels was set to 0 for allowing to display all clusters.

2.7.1 Inspecting the data.

After pre-processing, all data was inspected to see if there were any artifacts or problems with them. First, the postscript files for each knot for all participants were screened for issues. Both the anatomical and functional images were checked, as well as the translation and rotation, indicating movement of the head. One participant's anatomical and functional images were crocked and off center and had to be further inspected and corrected. In addition, due to excessive movement, one knot from two participants each have been excluded from the analysis. Too much movement can degrade the image quality and cause misinterpretation of the data. The movement threshold was sat at 3 mm, or one voxel, and both of these knots exceeded the threshold.

Second, the anatomical images were checked for artifacts using SPM 12. This could include incorrect orientation, scanner spikes, poor contrast, and so on. Specifically, two artifacts were inspected for: Gibbs Ringing Artifacts and abnormal intensity differences in the white and grey matter. Gibbs Ringing Artifacts appears as ripples on the images and can cause failure in the brain extraction or normalization when pre-processing. The ripples may be an indication of an error occurring when the scanner reconstructs the MR signal or can be due to too much head movement. No such ripples were found on the participants' images. Abnormal intensity differences in the white or grey matter can be indications of pathologies

that need to be looked at by radiologists. No such differences were noticed by the any of the team members involved in this study. Third, the functional images were inspected for much of the same as the anatomical images, such as either extremely dark or bright spots in the white and grey matter, and for any ripples or other distortions. No such artifacts were found.

As an additional check, we inspected all images to see if the functional images coincided with the anatomical images. Due to a few of the participants having braces or retainers, some of the images came out cropped and imprecise. Therefore, Registration (the alignment between the anatomical and functional images) were checked for these participants, as well as a few other participants whose images needed a second look.

When inspecting the contrast and mask images for each participant, we noticed black and white stripes or lines in 14 of the participants. We had to perform additional first level analyses on each of the knots to single out which knots that had stripes and which did not. This had to be done for all 14 participants. We identified 19 con and mask images with stripes on them, which had to be excluded from the analyses. One of the striped images was also one of the images removed due to excessive movement. This left a total of 118 out of 138 knot images after excluding both the striped and excessive movement images.

The removal of striped images led to the exclusion of additional participants, due to having removed either the control, the first knot, or the last knot images. For chain 1, seven participants remained, with only one excluded participant. For chain 2, only three participants remained after having to exclude four of the participants, and for chain 3, four participants remained after excluding four of them. With nearly half of participants excluded from chain 2 and chain 3, it was decided not to use these chains for further analyses. The sample sizes were considered too small to include in the analyses and would likely increase the risk of type 1

and type 2 errors. There was no time for another data collection, therefore we had to make use of the remaining data. Therefore, the following results presented are from analyses based on chain 1 of the current study.

3. Results

3.1 Functional MRI Results

As the majority of the participants had to be excluded for reasons mentioned in the section above (see 2.6.1), only results from chain 1 are presented.

3.1.1 Knot tying – control.

To evaluate whether there were any differences in brain regions involved the knot tying and the control condition, we performed a one sample t-test. The following table (Table 1) presents brain regions that emerged from the knot tying sessions. There was a significant main effect of "demonstration-replication" (df= [1,0, 6,0], t=20.38, p <.001), with the knot tying condition being significantly different compared to the control condition. As seen in Table 1, one statistically significant cluster was identified for "demonstration-replication" in the left intraparietal sulcus (see Figure 4.)

In addition, a statistically significant effect was found for "demonstration" (df= [1,0, 6,0], t=18.53, p<.05). One significant cluster was identified in the left superior parietal lobule (see Table 1, and Figure 4). A statistically significant effect was also found for "replication" (df= [1,0, 6,0], t=21.48, p<.001). Here, one significant cluster was identified in the left superior occipital gyrus (see Table 1, and Figure 4).

Figure 4.

Brain activity associated with Knot tying – control in the conditions: *A*) "demonstrationreplication", *B*) "demonstration", and *C*) "replication".



Note. Images were rendered using a template from the built-in tool in SPM12.

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Table 1.

Brain regions associated with knot tying – control in the conditions: "demonstration", "replication", and "demonstration-replication".

Location	Demonstration						Replication					Demonstration - replication						
	X	У	Z	$k_{ m E}$	Т	Z	x	у	Z	k _E	Т	Z	X	у	Z	k _E	Т	Z
Knot - control																		
Left superior parietal lobule*	-26	-70	32	106	18.53	4.79												
Left superior occipital gyrus **							-28	-74	24	184	21.48	4.97						
Left intraparietal sulcus**													-26	-74	26	287	20.68	4.93

Note. Anatomical localization was performed using a brain atlas implemented in SPM12. Locations marked with * were significant using

Puncorrected 0.05, and locations marked with ** were significant using FWE-corrected 0.05.

3.1.2 Knot order.

To evaluate the potential differences in brain regions associated with the first knot and the last knot the participants learned and tied, we performed a paired sample t-test. We tested both "First knot - last knot" and "Last knot - first knot" in chain 1 to see if there were any differences in the direction of the analysis. By switching the direction of the analysis, the regions emerging as potentially significant may be different as a result of the order of which the conditions are subtracted. When conducting the analysis for "First knot - last knot", no main effect or other statistically significant results were found for "demonstration", "replication" or "demonstration-replication". Therefore, this direction was not further analyzed or investigated.

The following table (Table 2) presents the brain regions that emerged for the knot tying sessions for "Last knot – first knot". We found a significant main effect of "demonstration-replication", with the last knot being significantly different compared to the first knot. As seen in Table 2, "demonstration-replication" yielded statistically significant activity in a series of cortical regions, where seven clusters were identified (see also Figure 5). The areas of activation unique to "demonstration-replication" were the left middle frontal gyrus, left supramarginal gyrus, right supramarginal gyrus, and the right superior parietal lobule.

In addition, a significant difference was also found for "demonstration", in which five statistically significant clusters were identified (see Table 2 and Figure 5). Activations unique to "demonstration" for Last knot – first knot were the left superior frontal gyrus and the right precentral gyrus. Activation in the right precuneus, right middle frontal gyrus, and the left superior parietal lobule were common for both "demonstration-replication" and for "demonstration".

No statistically significant differences were found when inspecting the brain region of "replication".

Figure 5.

Brain activity associated with Last knot – first knot: A) Demonstration-replication, and B) Demonstration.



Note. Images were rendered using a template from the built-in tool in SPM12.

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Table 2.

Brain regions associated with knot tying for the Last knot – first knot during "demonstration" and "demonstration-replication".

Location	Demonstration							Demonstration - replication							
-	X	у	Z	$k_{ m E}$	Т	Z	X	у	Z	$k_{ m E}$	Т	Z			
Last – first knot															
Right precuneus*	6	-68	50	78	11.99	4.26	10	-70	48	133	8.89	3.86			
Right middle frontal gyrus*	44	34	20	68	11.47	4.20	40	52	16	188	12.75	4.34			
Left superior frontal gyrus**	-26	-6	64	213	10.77	4.12									
Right precentral gyrus*	44	-4	44	55	8.55	3.80									
Left superior parietal lobule*	-24	-64	58	59	6.78	3.48	-34	-46	58	107	8.89	3.94			
Left middle frontal gyrus*							-54	18	30	52	10.16	4.04			
Left supramarginal gyrus*							-32	-48	38	64	7.99	3.71			
Right supramarginal gyrus*							46	-30	52	68	7.79	3.68			
Right superior parietal lobule*							34	-52	54	72	7.15	3.56			

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Note. Anatomical localization was performed using a brain atlas implemented in SPM12. Locations marked with * were significant using *P*uncorrected 0.05, and locations marked with ** were significant using FWE-corrected 0.05.

3.2 Behavioral Results

3.2.1 Chain 1.

For chain 1, the female only chain, we inspected and compared the knot tying videos produced by the last generation with the original instruction video for this chain. The videos showed that only the control condition and the noose knot were successfully transmitted and performed. All other knots had been altered in either technique or shape. The noose knot remained the same knot, but the knot tying method had been altered at some point over generations. Figure 8 knot, slip knot, and square knot turned out similar to the original knots in terms of shape, but with had either a reduction of steps or modified steps. Sheet bend knot had both been altered in shape and technique and ended up not resembling the original knots.

3.2.2 Chain 2.

For chain 2, the male only chain, we inspected and compared the knot tying videos from the last generation and compared each knot with the original instruction videos for this chain. The videos showed that two knots; the figure 8 knot and the square knot, as well as the control condition had been successfully reproduced by the last generation of chain 2. Both shape and technique were identical to the original instruction videos. The noose knot was not correctly tied but was tied in a similar manner and ended up resembling the original knot. Whereas the sheet bend knot and the slip knot turn out completely different, becoming two new knots.

3.2.3 Chain 3.

For chain 3, the alternating chain, knot tying videos from the last generation were compared to the original knot videos. When inspecting the videos, only the control condition ended up a true replication of the original demonstration. No other knots were successfully replicated for chain 3. The figure 8 knot was the only knot that had a resemblance to the original knot, whereas the other four knots turned out very different from how they were demonstrated in the instruction videos.

3.3 Handedness Questionnaire Results

Results from the handedness questionnaire showed that 83 percent of the participants classified as right-handers, and 17 percent classified as left-handers. The participant excluded from the analysis was also excluded from the results of the handedness questionnaire. Based on the questionnaire, the participants' self-reported handedness largely matched the results of the questionnaire. The handedness questionnaire by Raczkowski et al. (1974) has been adapted from two previous handedness questionnaires, by Hull (1936) and Oldfield (1971). When classifying results of the handedness of the questionnaire, we used the handedness assessment tool based on the Edinburgh Handedness Inventory by Oldfield (1971). Handedness score was calculated using this formula: 100*((Right-Left)/(Right+Left)) = score.

The number of left-, right-, and both-hands responses were counted, where answering both-hands counted as both one left and one right response. Table 3. shows the distribution of response scores for each of the participants in the study. The form (1971) was used to interpret the participants' scores calculated from the scoring form. These scores made it easier to classify the participants in categories of left-, right-, or ambidextrous. The participant that self-reported as ambidextrous was therefore classified as left-handed from the scores of this form. Additionally, one of the self-reported left-hander was classified as right-handed as a results of this handedness assessment tool. The left us with three left-handers and 20 right-handers.

Table 3.

Scores from the handedness assessment tool based on the Edinburgh Handedness Inventory (1971).

Handedness	Score	Male	Female		
-51 to -100	Pure Left-hander	1	1		
-1 to -50	Mixed Left-Hander	0	1		
0	Ambidextrous	0	0		
1 to 50	Mixed Right-Hander	2	1		
51 to 100	Pure Right-Hander	6	11		

4. Discussion

The main objective of this study was to characterize the brain regions involved in the acquisition of knot tying skills. Using a transmission chain study, a functional MRI was employed to investigate the neural aspects of learning a series of knots. The purpose of this study was to be able to map the brain regions involved in learning to tie knots, and ultimately compare the regions to previous studies on the neuroscience of toolmaking and possibly shed light on the mental capacities of our pre-historic ancestors.

4.1 Functional MRI Results

4.1.1 Knot tying – control.

To investigate the brain regions involved in the acquisition of knot tying skills, we performed an analysis to explore the differences between learning and tying the knots, and simply manipulating a rope. Results from the knot tying – control condition analysis showed significant activation for all three conditions: "demonstration", "replication", and "demonstration-replication". This implies that the activation for knot tying was significantly different from the control condition, which consisted of pulling the rope between their hands. The brain regions activated for knot tying are therefore most likely connected to the learning and tying of the knots, rather than merely manipulating the rope. For "demonstration-replication", activation was observed in the intraparietal sulcus (IPS) (Table 1; Figure 4), which is associated with action observation and understanding, temporal orientation, and controlling and guiding action in space (Davranche et al., 2011; Grefkes & Fink, 2005; Stout et al., 2011). A previous study has showed that activation in the IPS when participants discriminate between trained knots and knots they had no knowledge of, which suggests that

object knowledge is associated with neural systems for the manipulation of objects (Cross et al., 2012). In keeping with this, the observed activation of the IPS reflects the expected activation of learning to tie knots. This would explain the lack of activation of the IPS in the control condition, where no knots were either learned or tied.

For "demonstration", activation of the left superior parietal lobule (SPL) was observed (Table 1; Figure 4). Activation of the left SPL is associated with the reach-to-grasp network and to control goal-oriented limb movements (Gamberini et al., 2021). A study of the impact of physical experience with knot tying practice shaped a response of the left SPL, and that the activation became larger when discriminating learned vs. unlearned knots. This suggests that the area provides a description of objects associated with action (Cross et al., 2017). By relating previous findings to the findings of the current study, the activation of the left SPL suggests that during "demonstration", the description of objects and action, and guiding of action were important for learning how to tie the different knots. One cluster exclusive to the "replication" condition occurred in the left superior occipital gyrus (Table 1; Figure 4). The area was significantly activated for knot tying compared to the control condition, indicating a significant effect of the knot tying on the activation. The left superior occipital gyrus is an area associated with visual processing (Rehman & Al Khalili, 2019).

Findings from "demonstration-replication", "demonstration", and "replication" are in line with the results of the study by Stout et al. (2011). Their goal was to identify the brain regions involved in the observation of Paleolithic toolmaking and examined the contrasts of toolmaking observation with a control condition. Results showed activation of the left SPL and in the left IPS when comparing the response to observing toolmaking and the control stimuli. Similar activation of the left IPS and the left SPL were also found by Stout and Chaminade (2007) when teaching participants how to make Oldowan stone tools. Brain activation revealed from both mentioned studies and from the current study is primarily concerned with perceptual-motor adaptation, which suggest that the capacity for skill learning and executing are more dependent on sensorimotor capabilities, rather than executive capabilities (Stout & Chaminade, 2007).

4.1.2 Knot order.

To investigate the brain regions involved in the different stages of skill acquisition, we performed an analysis to explore the difference between learning and tying the first knot and the last knot. Results from the Last knot – first knot analysis showed significant activation for two of the three conditions: "demonstration" and "demonstration-replication". This revealed that the activation for the last knot differs significantly from the activation for the first knot, engaging different brain regions. By exploring how the activation of brain regions may shift from the first knot to the last knot, it could be possible to demonstrate the areas of activation specific to the learning stages of skill acquisition as opposed to simply the areas that are specific to physically tying the knot. The interest is in how the activation may change as a result of practice and learning.

The unique activations for "demonstration-replication" were observed in the left middle frontal gyrus (MFG), left supramarginal gyrus, right supramarginal gyrus (SMG), and right superior parietal lobule (Table 2; Figure 5). The different areas have been associated with literacy (left MFG) (Koyama et al., 2017), processing of phonological input and output (left and right SMG) (Hartwigsen et al., 2010; Oberhuber et al., 2016), and proprioception (right SMG)(Ben-Shabat et al., 2015). Proprioception refers to the knowledge of the location of where our limbs are in the absence of vision, and is important for motor control, coordination of movements and for motor skill acquisition (Ben-Shabat et al., 2015). The study by Stout et al. (2011) reported similar activation in the left and right SMG in response of the observation of toolmaking compared to control stimuli. Coordination of movements is important for knot tying and for skill acquisition in general. It requires that the person modifies their movements in response to the sensory input and motor output, in which the brain has to predict how the limbs move in response to the demands. It would therefore be expected that areas of the brain associated with movement coordination would be activated during knot tying.

Activation exclusive to the "demonstration" of the Last knot – first knot was observed in the right precentral gyrus (Table 2; Figure 5). The precentral gyrus is an area responsible for executing voluntary movements and is commonly recruited during action observation (Bookheimer, 2013; Stout et al., 2011). Also unique to the "demonstration" condition was left superior frontal gyrus (SFG) activation (Table 2; Figure 5). The area is probably best understood in terms of its role in working memory, executive and spatially oriented processing (Boisgueheneuc et al., 2006). The activations of the right precentral gyrus and the left SFG may reflect the processing of the knot tying stimuli.

Brain regions common for both "demonstration-replication" and "demonstration" are the right precuneus, right middle frontal gyrus (MFG), and left SPL. Activation of the precuneus is often found in episodic memory and memory retrieval, and could be related to visual imagery (Delazer et al., 2005). Activation of precuneus may indicate that the area plays a role in creating an episodic memory of procedure for knot tying. The right MFG has been proposed as a site for the convergence for attention networks, and to reorient the attention from exogenous to endogenous attentional control (Japee et al., 2015). This means that the right MFG is important for shifting attention for stimulus-driven attention that comes from external events in the environment, to attention driven by internal goals (MacLean et al., 2009). The suggestion of the role of left MFG in attention reorientation fits as well with the demands of skill learning, where the shift from watching the demonstration to replication the knots require different attention.

Activation of the right precuneus and left SPL have been associated with discriminating between trained knot and untrained knots (see section for more details 1.3.3) (Cross et al., 2017). Specifically, the response of left SPL was greater after several days of training, indicating an important role in learning and experience. The reason why only the demonstration showed significant activation compared to replication could be explained in the light of the findings of Cross et al. (2017). In their article, they argued that observing another person interacting with an object can cause activation in the same areas as when a person is physically manipulating the object. Activation of parietal and premotor cortices have also been demonstrated when viewing tools that is associated with a particular action (Cross et al., 2012). When participants watched the instruction videos, the areas related to physically tying the knots could be activated without actually tying them. Therefore, if the activation during demonstration of knot tying is partially the same as the activation occurring when replication the knots, then the common activation for both conditions would be cancelled out and only the significant activation that differs would remain. This would explain why only "demonstration" showed significant effect on knot tying, and not "replication".

An explanation for the involvement of different brain areas when tying the first knot compared to tying the last knot may be that as a results of learning or the use of different learning strategies during demonstration, a shift in the activated brain areas occurred. The acquisition of a new skill is characterized by an initial slow step-by-step processing, often involving trial and error. As learning progresses, the rate and effortlessness of the processing increases, and consequently the error rate decreases. The change in learning processing from slow to fast has been associated with learning-related decreases and increases of different brain regions. This provides evidence for the differential involvement of regions during early and advanced stages of learning (Debaere et al., 2004). In a study investigating whether different learning methods lead to differential modifications of brain activation, results showed that the use of different strategies on the same cognitive task as associated with a different brain activation reflecting the underlying learning method (Delazer et al., 2005). A shift or reorganization is also demonstrated by Stout et al. (2011) when investigating the effects of expertise on toolmaking observation. This revealed unique responses of each subject group (Naïve, Trained and Expert) to toolmaking observation. This suggests that the reorganization of activation between groups may be a reflection of shifts in cognitive strategy that is dependent on the level of expertise (Stout et al., 2011). Both a shift from slow to fast processing, and a change in learning strategy could serve as plausible explanations for the different brain areas involved in the first and last knot tying session.

The purpose of having one condition for "demonstration" and one for "replication" was to be able to separate the learning from the execution of the knots. However, when inspecting our results, it became difficult to separate the learning from execution. For Knot order, no significant results were found for "replication", only for "demonstration" and

"demonstration-replication". As mentioned, viewing tools, or viewing someone else manipulating a tool could activate the same area as when manipulating it ourselves. Therefore, we could only assume that the same neural structures activated during "replication" as in "demonstration" could be attributed to the execution of the knots, and that the unique activation for "demonstration" could be attributed to learning.

Knot tying is a complex skill that requires the coordination of hand movements and the ability for sensorimotor adaptation. It also requires the ability to perceive and explore multiple possibilities of action. The current study has uncovered the neural activation of different areas associated with learning and tying the knots. The results implicate that the areas of activation demonstrated are of importance for the different aspects knot tying. Activation is largely found in the parietal and frontal lobes of the brain, indicating that the sensorimotor systems play a key role in knot tying. By comparing these results with the results of previous studies on toolmaking and its relation to the toolmaking skills of prehistoric humans, we could infer that these brain regions and cognitive capacities that would have been essential for the development of toolmaking skills.

4.2 Explaining the Behavioral Aspects

Caldwell et al. (2017) explain how cumulative cultural evolution can result in improvements and increase in efficiency. In the current study, the majority of the knots do not end up identical to the original knots, but have all been altered in some way, either shape or technique. An interesting finding is that the noose knot from the last generation in chain 1 ends up identical to the original knot, but the technique has been altered along the chain. A possible explanation is that the original technique could have been considered more difficult, and for that reason, each generation has collectively contributed to the simplification of the knot tying technique. A simpler technique would be easier to learn and pass on to future generations, and ultimately become more time efficient. It is also possible that tying the knots while lying down instead of sitting, as demonstrated in the instruction videos, became a challenge for the participants. Movement of arms and head were restricted when inside the fMRI scanner, which could likely result in modification of tying technique.

Even though the knots did not turn out exactly how they were demonstrated, does not mean they cannot serve the same purpose. The original knots are commonly used for sailing or climbing, where the importance lies in their ability to sufficiently be able to carry or hold something together. The end products for each chain were not tested for their usability or for the purpose the knots originally serve. The knots might prove to be useful in some ways which we have not considered. When looking at the knot tying videos at the end of the three chains, the number of steps required for tying the knot is clearly reduced. As pointed out earlier, a result of cumulative cultural evolution can be efficiency (Caldwell et al., 2017). When the number of steps is reduced, the amount of time spent on tying the knot is reduced as well, making it more efficient. Therefore, it cannot be ruled out that the knots produced at the end of each chain may be an improvement in terms of efficiency from the original knots.

A closer look at the knot tying videos from the last generations of each chain reveal that many of the knots ended up similar to each other. For example, for chain 2, the slip knot ended up looking similar to the figure 8 knot at the end of the chain. This is speculated to be a result of the design, because participants were asked to repeat the knots numerous times, leading to potential confusion of which knot is which. Another important factor is that two of the knots, the noose knot and the slip knot look fairly similar despite their different techniques (for demonstration, see Figure 1 above). This could easily contribute to confusion for the participants when asked to replicate the knots when recording the instruction videos for the next generation in their chain.

Another point to be made is that we did solely demonstrative tasks. Participants were shown videos of the knots, and asked to reproduce them as they were. The goal was not to achieve anything in particular with the tied knots nor to test their function or purpose. Participants were simply taught how to tie the knots, not how to use them. In real life, the reason for acquiring skills is to use them for a specific purpose. Toolmaking aided prehistoric humans in hunting and transportation, creating a drive for passing on these skills. With the skill of toolmaking, humans could more easily do tasks that previously could be considered difficult. An example is stone tools becoming narrower, longer and sharper, making them more precise for cutting (Stout et al., 2008). If the tied knots had a purpose, e.g., be able to carry something, there would be a drive for creating knots that would be favorable in carrying a certain weight. This favorable goal-directed behavior is considered a drive for cumulative cultural evolution. Beneficial behavior will replace the antecedent behavior and stay in the population until further modifications are made (Tennie et al., 2009).

4.3 The Influence of Handedness on Teaching

Previous studies have shown that the concordance of handedness between teacher and learner effects the efficiency of learning a skill (Michel & Harkins, 1985). In our study, the participants in the alternating chain learn knots from a previous participant with a different dominant hand, resulting in a mismatch in concordance of handedness. This could have had an effect on the results of the chain in terms of efficiency and transmission fidelity. A measure for efficiency could have been included to give an indicator of whether or not there were differences between the alternating chain and the right-handed chain in terms of knot tying efficiency.

However, with approximately 85 percent of the population being right-handed, it is inevitable that the majority of a left-hander's interactions have been with right-handers. This would include teachers, family, friends, and other social interactions one might encounter. Therefore, people with a dominant left hand preference would be accustomed to learning from people with a right-hand preference. By excluded chain 3, we do not have any results that could attest to any conclusion based on handedness in this study. Any speculation of the possible effects of concordance of handedness on teaching and the brain regions associated with these effects still remains unexplored.

4.4 Ethics

Conducting an fMRI study requires a lot of consideration to potential ethical concerns. These concerns include, safety, risk, confidentiality, informed consent, incidental findings etc. In terms of safety and risk, we had to evaluate and confer with one of the participants, including the radiographers, whether it was safe for the participant to go through with the procedure. One participant reported that they had diabetes and in order to go through with the scanning, they had to remove the sensor on their arm due to its magnetic properties. The sensor works as a monitoring system that connects to the cell phone which records the glucose levels. After conversations with the participant, it was considered safe for them to go through the procedure. The sensor was removed for the scanning session and put back right after the sessions had ended.

It could be discussed whether it was ethical to let this participant go through with the procedure. Even though it was conferred with two radiographers regarding the safety of removing the glucose sensor, we as team member did not have enough information about this topic. Therefore, we solely relied on information given by the participant themselves and the radiographers. More information about the safety and risks regarding removal of glucose sensors would have been beneficial for us when assessing the situation.

Another important consideration is the emotional and physical stress of lying still in a confined environment for some time. When inside the scanner, the head was secured in the head coil with limited space for movement. This limitation could be stressful and uncomfortable for a lot of participants. One participant reported that they were claustrophobic, and that they were nervous to go through with the procedure. Every step of the experiment was explained carefully and the participant was told that they would go through with the procedure but had to be extracted from the machine once for a break during the scanning session. Conversations with some of the participants after the completion of the study revealed that multiple of them experienced some discomfort during the fMRI scanning, but not to the extent that they did not want to complete the session.

It is important to have in mind when explaining procedure to people with claustrophobia that they do not feel compelled to go through with the procedure if they do not want to. Even though they voluntarily signed up for the study, they could withdraw at any time, before, during or after the scanning session. The procedure was also explained in great detail, the different phases of scanning, the sounds, duration etc. that could be considered essential for their comfort. This was done in hope that knowledge and comprehension about the procedure would minimize the fear and anxiety the participants experience. However, it is difficult to determine whether the participants force themselves to go through with the procedure due to a sense of obligation, or if they actually are comfortable enough to go through it.

We took every precaution of making the experiment safe for all participants and weighted the value of the research higher than potential risks. The knowledge derived from this research is important for the understanding of human behavior and how we acquire knowledge and pass it on to future generations. It also uncovers patterns of neural activation associated with skill acquisition that could prove useful for clinical research and diagnostics. A person's inability or difficulty with skill learning and performance could then be correlated with the brain areas identified in the current study.

4.5 Limitations and Future Directions

4.5.1 Experimental design.

During the knot tying condition, participants could only view the hands of the previous demonstrator. There were no other visual or auditory cues, leaving out body language and other gestures that may facilitate the learning process. Participants were given no indicators or feedback during any stages of the experiment. In real life, the learning settings are usually much more complex. We are mostly able to interact with our teacher and are given direct or indirect instructions of how to perform a task. We can rely on both language and demonstration to aid our learning and ask questions and receive feedback on our progress.
This is not easily implemented when using neuroimaging techniques, such as fMRI. Usually, when learning a new skill, it is not done in a sterile room with limited capacity for movement, with loud noises or in the absence of social dynamics. The fMRI scanner is an artificial environment for skill acquisition that could possibly affect the study's ecological validity. Ecological validity examines whether the findings of the study can be generalized to real-life setting (Andrade, 2018). In addition to the artificial environment, the controlled tasks and stimuli can also affect the ecological validity of the study (van Atteveldt et al., 2018). The tasks are highly controlled and simplified and have to be repeated a number of times because of neuroimaging signal noise, which can be exhausting for a lot of participants. This is a common limitation with fMRI studies and laboratory studies in general.

A known risk with performing this study was that combining fMRI with a knot tying task could potentially lead to poor data quality due to subject motion. Sligh movement of the head is common for all subjects and can corrected for during data processing. When movement exceeds the threshold sat at 3 mm, it can degrade the quality of the data and lead to data discarding. As reported earlier, we had to exclude two knots due to excessive movement of the head. The risk of pairing a movement sensitive device such as an fMRI with a physical task was carefully assessed before data collection. The task was accustomed to the scanner and tested for feasibility beforehand as a measure for limiting potential movement. Using fMRI for investigating skill acquisition also gives valuable insight into processes that other devices might not be suitable for. EEG (electroencephalography) is one of the most commonly used techniques for studying brain function. It is non-invasive, easy to use and is also portable, making it suitable for studies using physical tasks. However, EEG detects scalp signals, mainly reflecting cortical activity, whereas fMRI can measure brain activity of the

deeper structures of the brain (Abreu et al., 2018). Therefore, the benefits of combining fMRI with knot tying were considered greater than potential risks and other methods.

A central limitation in the current study is the small sample size. As previously mentioned, this is a pilot study and was used for testing out the design, procedure, and stimuli for the main study. In this case, using a small sample size is justifiable. However, due to excessive movement and striped images, the sample size was reduced to only 7 participants included in the analyses. Chain 2 and chain 3 were removed from the analyses due to having 50 % or more of the participants removed from each chain. To further examine and analyze chain 2 and chain 3 would likely yield results that could not be generalizable and the risk of type 1 and type 2 errors would increase. By excluding chain 3, no analyses were done to examine potential effects of handedness on learning and tying knots. It was originally planned to do analyses on all the right handed participants across chains, in addition to a comparison of the right-handed and the left-handed participants.

One should therefore be cautious about drawing conclusion from the results of this study. A study with a small sample size is at risk of having a low statistical power that declares no difference between groups or conditions, which increases the probability of making a type 2 error (false negative). Furthermore, low statistical power can also increase the probability of making a type 1 error, that is when concluding that results are statistically significant when they are not. In conclusion, low statistical power can negatively affect the likelihood that the statistically significant findings are actual reflections of true effects (Button et al., 2013). It is therefore possible that the activated brain regions this study has uncovered may be due to individual differences rather than a generalizable effect of the different conditions. The findings of the current study should therefore be considered preliminary.

4.5.2 Future research.

For future studies on the neural correlates of skill transmission, the use of portable devices such as fNIRS (functional near-infrared spectroscopy) would likely increase the ecological validity, optimizing the benefits of using neuroimaging for studies on learning. Experiments could be performed in more natural environments for learning, also allowing more movement and comfort. This could potentially eliminate some of the ethical issues regarding participants' safety, in terms of anxiety, phobia, medical conditions etc. Furthermore, the use of portable devices is more time efficient, which would make it possible for testing substantially more participants in one sitting. Future studies should also consider using a task that allows for more improvement and that has a specific purpose that could easily be tested. This could be knots used for carrying or tying something together. This would allow participants to learn and potentially improve function of the knots and have the opportunity to test the quality of the knots. Such potential findings would provide more insight into the foundation of cumulative cultural evolution and cultural transmission.

The relationship between handedness and learning in terms of skill acquisition still remains largely unexplored. Due to the current study's small sample size and the inability to run analyses on the possible effects of handedness, we were not able to draw any conclusions about the effects of lack of handedness concordance or about potential differences between left-and right-handers. Optimally, we should have had a whole chain of left-handed participants that would increase the sample size and statistical power, increasing the likelihood of statistically significant results (Button et al., 2013).

5. Conclusion

In conclusion, this current study has contributed to shed light on brain regions important for learning and tying different knots. The analyses conducted in this study has built a foundation for further research on brain regions involved in skill acquisition and transmission using neuroimaging techniques. Results show activation of several cortical areas associated specific to the different conditions in the study, which indicate the involvement of processes unique to each condition. The findings of the current study corroborate previous studies on toolmaking and skill acquisition that may prove important for the understanding of the cognitive abilities of prehistoric humans. Further research on the neural aspects of skill transmission, including effects of handedness and a more thorough examination of each generation within chains is needed.

References

- Abreu, R., Leal, A., & Figueiredo, P. (2018). EEG-informed fMRI: a review of data analysis methods. *Frontiers in human neuroscience*, *12*, 29.
- Andrade, C. (2018). Internal, External, and Ecological Validity in Research Design, Conduct, and Evaluation. *Indian J Psychol Med*, 40(5), 498-499. https://doi.org/10.4103/ijpsym.Jjpsym_334_18
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C.
 (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*(7540), 538-541.

- Bandura, A. (2008). Observational learning. *The international encyclopedia of communication*.
- Bastian, A. J. (2008). Understanding sensorimotor adaptation and learning for rehabilitation. *Curr Opin Neurol*, 21(6), 628-633. <u>https://doi.org/10.1097/WCO.0b013e328315a293</u>
- Ben-Shabat, E., Matyas, T. A., Pell, G. S., Brodtmann, A., & Carey, L. M. (2015). The right supramarginal gyrus is important for proprioception in healthy and stroke-affected participants: a functional MRI study. *Frontiers in neurology*, *6*, 248.
- Biesele, M. (1986). How Hunter-Gatherers' Stories "Make Sense": Semantics and Adaptation. *Cultural Anthropology*, 1(2), 157-170. <u>http://www.jstor.org/stable/656264</u>
- Boisgueheneuc, F. d., Levy, R., Volle, E., Seassau, M., Duffau, H., Kinkingnehun, S.,
 Samson, Y., Zhang, S., & Dubois, B. (2006). Functions of the left superior frontal gyrus in humans: a lesion study. *Brain*, *129*(12), 3315-3328.
 https://doi.org/10.1093/brain/awl244
- Bookheimer, S. Y. (2013). Precentral Gyrus. In F. R. Volkmar (Ed.), *Encyclopedia of Autism* Spectrum Disorders (pp. 2334-2335). Springer New York. https://doi.org/10.1007/978-1-4419-1698-3_203
- Boyette, A. H., & Hewlett, B. S. (2018). Teaching in hunter-gatherers. *Review of Philosophy* and Psychology, 9, 771-797.
- Button, K. S., Ioannidis, J. P., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S., & Munafò, M. R. (2013). Power failure: why small sample size undermines the reliability of neuroscience. *Nature reviews neuroscience*, 14(5), 365-376.

- Caldwell, C. A., & Millen, A. E. (2009). Social learning mechanisms and cumulative cultural evolution: is imitation necessary? *Psychological Science*, *20*(12), 1478-1483.
- Caldwell, C. A., & Millen, A. E. (2010). Human cumulative culture in the laboratory: effects of (micro) population size. *Learning & Behavior*, *38*(3), 310-318.
- Caldwell, C. A., Renner, E., & Atkinson, M. (2017). Human teaching and cumulative cultural evolution. *Review of Philosophy and Psychology*, *9*, 751-770.
- Cross, E. S., Cohen, N. R., Hamilton, A. F. d. C., Ramsey, R., Wolford, G., & Grafton, S. T. (2012). Physical experience leads to enhanced object perception in parietal cortex: insights from knot tying. *Neuropsychologia*, 50(14), 3207-3217.
- Cross, E. S., Hamilton, A. F. d. C., Cohen, N. R., & Grafton, S. T. (2017). Learning to tie the knot: The acquisition of functional object representations by physical and observational experience. *PloS one*, *12*(10), e0185044.
- Davranche, K., Nazarian, B., Vidal, F., & Coull, J. (2011). Orienting Attention in Time Activates Left Intraparietal Sulcus for Both Perceptual and Motor Task Goals. *Journal of cognitive neuroscience*, *23*(11), 3318-3330. <u>https://doi.org/10.1162/jocn_a_00030</u>
- Debaere, F., Wenderoth, N., Sunaert, S., Van Hecke, P., & Swinnen, S. (2004). Changes in brain activation during the acquisition of a new bimanual coordination task. *Neuropsychologia*, 42(7), 855-867.
- Delazer, M., Ischebeck, A., Domahs, F., Zamarian, L., Koppelstaetter, F., Siedentopf, C. M., Kaufmann, L., Benke, T., & Felber, S. (2005). Learning by strategies and learning by drill—evidence from an fMRI study. *Neuroimage*, 25(3), 838-849.

- Doya, K. (2000). Complementary roles of basal ganglia and cerebellum in learning and motor control. *Current opinion in neurobiology*, *10*(6), 732-739.
- Gamberini, M., Passarelli, L., Filippini, M., Fattori, P., & Galletti, C. (2021). Vision for action: thalamic and cortical inputs to the macaque superior parietal lobule. *Brain Struct Funct*, 226(9), 2951-2966. <u>https://doi.org/10.1007/s00429-021-02377-7</u>
- Grefkes, C., & Fink, G. R. (2005). The functional organization of the intraparietal sulcus in humans and monkeys. *Journal of anatomy*, 207(1), 3-17.
- Hardy, B. L., Moncel, M.-H., Daujeard, C., Fernandes, P., Béarez, P., Desclaux, E., Navarro, M. G. C., Puaud, S., & Gallotti, R. (2013). Impossible Neanderthals? Making string, throwing projectiles and catching small game during Marine Isotope Stage 4 (Abri du Maras, France). *Quaternary Science Reviews*, 82, 23-40.
- Hardy, B. L., Moncel, M. H., Kerfant, C., Lebon, M., Bellot-Gurlet, L., & Mélard, N. (2020).
 Direct evidence of Neanderthal fibre technology and its cognitive and behavioral implications. *Sci Rep*, *10*(1), 4889-4889. <u>https://doi.org/10.1038/s41598-020-61839-w</u>
- Hartwigsen, G., Baumgaertner, A., Price, C. J., Koehnke, M., Ulmer, S., & Siebner, H. R.
 (2010). Phonological decisions require both the left and right supramarginal gyri. *Proceedings of the National Academy of Sciences*, 107(38), 16494-16499.
- Henrich, J. (2004). Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses—the Tasmanian case. *American antiquity*, *69*(2), 197-214.

- Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and human behavior*, 22(3), 165-196.
- Hillesund, T. (2021). Kulturens rolle i evolusjonen: teorien om genetisk-kulturell koevolusjon utfordrer samfunnsvitenskapene. *Tidsskrift for samfunnsforskning*, *62*(3), 293-304.
- Hirnstein, M., Hugdahl, K., & Hausmann, M. (2019). Cognitive sex differences and hemispheric asymmetry: A critical review of 40 years of research. *Laterality*, 24(2), 204-252. <u>https://doi.org/10.1080/1357650X.2018.1497044</u>
- Hodges, N. J., Williams, A. M., Hayes, S. J., & Breslin, G. (2007). What is modelled during observational learning? *Journal of sports sciences*, 25(5), 531-545.
- Hodgson, D. (2006). Understanding the origins of paleoart: The neurovisual resonance theory and brain functioning. *Paleoanthropology*, 2006, 54-67.
- Hoehl, S., Keupp, S., Schleihauf, H., McGuigan, N., Buttelmann, D., & Whiten, A. (2019).
 'Over-imitation': A review and appraisal of a decade of research. *Developmental Review*, *51*, 90-108.
- Hull, C. J. (1936). A Study of Laterality Test Items. *The Journal of Experimental Education*, 4(3), 287-290. http://www.jstor.org/stable/20150404
- Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takino, R., PuÈtz, B., Yoshioka, T., & Kawato, M. (2000). Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature*, 403(6766), 192-195.

- Japee, S., Holiday, K., Satyshur, M. D., Mukai, I., & Ungerleider, L. G. (2015). A role of right middle frontal gyrus in reorienting of attention: a case study. *Frontiers in systems neuroscience*, 9, 23.
- Koyama, M. S., O'Connor, D., Shehzad, Z., & Milham, M. P. (2017). Differential contributions of the middle frontal gyrus functional connectivity to literacy and numeracy. *Scientific reports*, 7(1), 17548. <u>https://doi.org/10.1038/s41598-017-17702-6</u>
- Kurzban, R., & Barrett, H. C. (2012). Origins of Cumulative Culture. Science (American Association for the Advancement of Science), 335(6072), 1056-1057. <u>https://doi.org/10.1126/science.1219232</u>
- Logothetis, N. K., & Wandell, B. A. (2004). Interpreting the BOLD signal. Annu. Rev. Physiol., 66, 735-769.
- MacLean, K. A., Aichele, S. R., Bridwell, D. A., Mangun, G. R., Wojciulik, E., & Saron, C.
 D. (2009). Interactions between endogenous and exogenous attention during vigilance. *Atten Percept Psychophys*, 71(5), 1042-1058. <u>https://doi.org/10.3758/app.71.5.1042</u>
- Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J., & Thach, W. (1996). Throwing while looking through prisms: II. Specificity and storage of multiple gaze—throw calibrations. *Brain*, 119(4), 1199-1211.
- McGuigan, N., Makinson, J., & Whiten, A. (2011). From over-imitation to super-copying: Adults imitate causally irrelevant aspects of tool use with higher fidelity than young children. *British Journal of Psychology*, 102(1), 1-18.

- Michel, G. F., & Harkins, D. A. (1985). Concordance of handedness between teacher and student facilitates learning manual skills. *Journal of Human Evolution*, 14(6), 597-601.
- Monti, M. M. (2011). Statistical analysis of fMRI time-series: a critical review of the GLM approach. *Frontiers in human neuroscience*, *5*, 28.
- Morgan, T. J., Uomini, N. T., Rendell, L. E., Chouinard-Thuly, L., Street, S. E., Lewis, H. M., Cross, C. P., Evans, C., Kearney, R., & de la Torre, I. (2015). Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nature communications*, 6(1), 6029.
- Muthukrishna, M., Shulman, B. W., Vasilescu, V., & Henrich, J. (2014). Sociality influences cultural complexity. *Proceedings of the Royal Society B: Biological Sciences*, 281(1774), 20132511.
- Oberhuber, M., Hope, T. M. H., Seghier, M. L., Parker Jones, O., Prejawa, S., Green, D. W.,
 & Price, C. J. (2016). Four Functionally Distinct Regions in the Left Supramarginal
 Gyrus Support Word Processing. *Cerebral Cortex*, 26(11), 4212-4226.
 https://doi.org/10.1093/cercor/bhw251
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97-113. <u>https://doi.org/10.1016/0028-3932(71)90067-4</u>
- Pallant, J. (2013). SPSS survival manual : a step by step guide to data analysis using IBM SPSS (5th ed.). McGraw-Hill.

- Papa, A., Cristea, M., McGuigan, N., & Tamariz, M. (2021). Effects of verbal instruction vs. modelling on imitation and overimitation. *Humanities & social sciences communications*, 8(1), 1-12. <u>https://doi.org/10.1057/s41599-021-00925-4</u>
- Putt, S. S., Woods, A. D., & Franciscus, R. G. (2014). The role of verbal interaction during experimental bifacial stone tool manufacture. *Lithic Technology*, 39(2), 96-112.
- Raczkowski, D., Kalat, J. W., & Nebes, R. (1974). Reliability and validity of some handedness questionnaire items. *Neuropsychologia*, *12*(1), 43-47.

Rehman, A., & Al Khalili, Y. (2019). Neuroanatomy, occipital lobe.

- Sasaki, T., & Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature communications*, *8*(1), 15049.
- Schmidt, R. A., Lee, T. D., Winstein, C., Wulf, G., & Zelaznik, H. N. (2018). *Motor control* and learning: A behavioral emphasis. Human kinetics.
- Seidler, R. D. (2004). Multiple motor learning experiences enhance motor adaptability. *Journal of cognitive neuroscience*, *16*(1), 65-73.
- Seidler, R. D. (2010). Neural correlates of motor learning, transfer of learning, and learning to learn. *Exerc Sport Sci Rev*, 38(1), 3-9. <u>https://doi.org/10.1097/JES.0b013e3181c5cce7</u>
- Stout, D., & Chaminade, T. (2007). The evolutionary neuroscience of tool making. *Neuropsychologia*, 45(5), 1091-1100.

https://doi.org/10.1016/j.neuropsychologia.2006.09.014

- Stout, D., Passingham, R., Frith, C., Apel, J., & Chaminade, T. (2011). Technology, expertise and social cognition in human evolution. *European Journal of Neuroscience*, 33(7), 1328-1338.
- Stout, D., Toth, N., Schick, K., & Chaminade, T. (2008). Neural correlates of Early Stone
 Age toolmaking: technology, language and cognition in human evolution. *PHIL TRANS R SOC B*, 363(1499), 1939-1949. <u>https://doi.org/10.1098/rstb.2008.0001</u>
- Taylor, M. J., & Thoth, C. A. (2011). Cultural Transmission. In S. Goldstein & J. A. Naglieri (Eds.), *Encyclopedia of Child Behavior and Development* (pp. 448-451). Springer US. https://doi.org/10.1007/978-0-387-79061-9_755
- Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Phil. Trans. R. Soc. B*, 364(1528), 2405-2415. <u>https://doi.org/10.1098/rstb.2009.0052</u>
- Tomasello, M. (1998). Emulation learning and cultural learning. *Behavioral and Brain Sciences*, *21*(5), 703-704.
- Uomini, N., & Lawson, R. (2017). Effects of handedness and viewpoint on the imitation of origami-making. *Symmetry*, 9(9), 182.
- van Atteveldt, N., van Kesteren, M. T. R., Braams, B., & Krabbendam, L. (2018). Neuroimaging of learning and development: improving ecological validity. *Frontline Learn Res*, 6(3), 186-203. <u>https://doi.org/10.14786/flr.v6i3.366</u>

Whiten, A. (2021). The burgeoning reach of animal culture. Science, 372(6537), eabe6514.

- Whiten, A., Horner, V., & Marshall-Pescini, S. (2003). Cultural panthropology. *Evol. Anthropol*, *12*(2), 92-105. <u>https://doi.org/10.1002/evan.10107</u>
- Zwirner, E., & Thornton, A. (2015). Cognitive requirements of cumulative culture: teaching is useful but not essential. *Scientific reports*, *5*(1), 16781.

Appendix A – REK approval



Region: REK vest

Fredrik Kolstad Rongved

 Telefon:
 Vår dato:

 55589715
 20.12.2021

Vår referanse: 351425

Andrea Bender

Prosjektsøknad: Nevrale nettverk i kulturell evolusjon Søknadsnummer: 351425 Forskningsansvarlig institusjon: Universitetet i Bergen

Prosjektsøknad godkjennes med vilkår

Søkers beskrivelse

Funn fra de arkeologiske utgravningene Blombos og Klipdrift i Sør-Afrika indikerer at det i midten av steinalderen var et vendepunkt i menneskelig evolusjon, spesielt med tanke på kulturell akkumulasjon. Kumulativ kultur er en av de evolusjonelle prosessene som har bidratt til å skille menneske fra andre dyrearter, og bygger på en predisposisjon vi har til å lære og lære bort. Prosessen går ut på at nye generasjoner bygger videre på de kulturelle innovasjonene fra foregående generasjoner. Dette er prosesser som virker over store tidsintervaller, og ikke lar seg undersøke i sanntid. Laboratoriestudier har imidlertid vist at man kan simulere slike prosesser ved bruk av et "transmission chain" design. Her vil første deltager i rekken tilegne seg en evne for deretter å lære bort denne evnen til neste person i rekken. Person nummer to i rekken lærer deretter evnen videre til person nummer tre osv. Hittil har slik forskning fokusert på endringer i prestasjon som resultat av den sosiale overføringen, det vil si, produktet av kulturell evolusjon, og mekanismene som påvirker denne prosessen. Den nevrale aktiveringen involvert i prosessen er foreløpig ukjent, samt de potensielle endringene i denne aktiveringen etter hvert som man kommer nedover i rekken som konsekvens av hvordan evnen utvikler seg.

Målet for dette prosjektet er å undersøke hvilke nevrale nettverk som er involvert i det å tilegne seg nye evner og lære disse videre over simulerte mini-generasjoner for å få bedre innsikt i de evolusjonelle prosessene som har formet mennesket til det vi er i dag. Spesielt ønsker vi å undersøke hvorvidt nevral aktivering for redskap-produksjon skiller seg fra aktiveringen for symbol-produksjon, hvorvidt det å ha noen som aktivt førsøker å lære bort evnen skiller seg fra det å ikke ha noen som aktivt prøver å lære bort, og om aktiveringen endrer seg etter hvert som man kommer nedover i rekken. Vi ønsker også å finne ut ved hvilket punkt og i hvilken grad språk-relaterte nettverk kobles inn, og hvordan hånd preferanse påvirker overføringsprosessen.

For å finne svar på disse spørsmålene vil vi benytte oss av et transmission chain design kombinert med fMRI teknologi. Deltagerne vil få en redskapsproduksjons oppgave, bestående av å knyte en knute de får demonstrert, og en symbolproduksjons oppgave, bestående av å reprodusere en gravering hentet fra Blombos, som skal utføres inne i MR maskinen. Alle deltagerne vil få tildelt en plass i en av flere rekker. Den første personen i hver rekke vil bli vist originalstimuliet for begge oppgavene og gitt tid til å øve inn

REK vest

Besøksadresse: Armauer Hansens Hus, nordre fløy, 2. etasje, Haukelandsveien 28, Bergen | E-post: rek-vest@uib.no Web: https://rekportalen.no løsningen. I aktiv lærings-betingelsen (teaching condition) vil deltageren bli bedt om å demonstrere for neste deltager hvordan de løste oppgaven. I passiv læring-betingelsen (asocial learning condition) vil deltageren kun bli bedt om å demonstrere at de klarer å løse oppgaven. I begge betingelsene vil deltagerens demonstrasjon bli filmet og brukt som stimuli for neste deltager i rekken. Denne prosessen gjentas til alle deltagere i rekken har demonstrert løsningen.

Vi planlegger å rekruttere deltagere fra studentmassen ved universitetet i Bergen da det ikke er krav til noen forkunnskaper hos deltagerne.

Hjerneaktivitet under både aktiv og passiv læring-betingelsen vil bli avbildet og analysert for signifikante mønstre. Lignende studier som bruker slike rekker har et 10X10 oppsett hvor man bruker 10 kjeder à 10 deltagere. Dette for å få statistisk kraft til å se mønster både innad i rekkene og på tvers av rekker.

Den største verdien av dette prosjektet er for vitenskapen. Denne studien vil kunne gi et første, indirekte innblikk i de kognitive og nevrale prosesser som var nødvendige for overføringen av de evner som har lagt grunnlag for den teknologiske kompleksiteten vi ser rundt oss i dag.

Vi viser til søknad mottatt 27.10.2021 for ovennevnte forskningsprosjekt. Søknaden ble behandlet av Regional komité for medisinsk og helsefaglig forskningsetikk (REK) i møtet 01.12.2021. Vurderingen er gjort med hjemmel i helseforskningsloven § 10.

REKs vurdering

Ingen av komiteens medlemmer var inhabile, og saken ble behandlet i full komité.

Om søknadsplikten:

Dette prosjektet har ikke som sitt primære formål å skaffe til veie ny kunnskap om helse og sykdom. Prosjektet søker å skaffe til veie ny kunnskap om menneskets evolusjon og om grunnleggende psykologiske funksjoner.

NEM har imidlertid vurdert i tidligere saker, de såkalte Doeller-sakene i NEM 2017/313, -/312, -/311, at prosjekter hvor det skal erverves kunnskap som kan anvendes for fremtidig forskning på helse og sykdom, evt. for å hjelpe oss å forstå god eller dårlig helse, kan tas inn og behandles under helseforskningsloven. REK vest vurderer at dette prosjektet har et formål som likner på disse sakene som ble behandlet av NEM. Av den grunn har komiteen valgt å ta saken til behandling. Prosjektet er søknadspliktig, jf. helseforskningsloven §§ 2 og 4 bokstav a.

Forsvarlighet:

Målet for dette prosjektet er å undersøke hvilke nevrale nettverk som er involvert i det å tilegne seg nye evner og lære disse videre over simulerte mini-generasjoner for å få bedre innsikt i de evolusjonelle prosessene som har formet mennesket til det vi er i dag.

124 studenter skal rekrutteres ved Universitetet i Bergen til å gå gjennom noen tester i en MR-skanner. Undersøkelsen vil ta omtrent 1 times tid. Komiteen vurderer at prosjektet er forsvarlig organisert så lenge REKs vilkår tas til følge.

Beredskap:

Det beskrives som en fordel i studien at hver enkelt deltager vil få en fri undersøkelse for hjernepatologi da alle bilder rutinemessig undersøkes for patologi av en nevroradiolog. Komiteen ønsker å gjøre prosjektgruppen oppmerksom på at dette kan oppleves som en ulempe, ettersom det er presumptivt friske studenter som skal rekrutteres. Derfor er det viktig med god informasjon til studentene i rekrutteringsfasen. De må forberedes på at det er mulig å oppdage sykdom ved denne undersøkelsen, og deltakerne må informeres om hvilke tiltak som blir satt inn dersom man mistenker sykdom.

Organisering:

Det er en MR-maskin på Helse Bergen som vil bli brukt for undersøkelsene. Det er også nevnt at en nevroradiolog vil gjennomføre undersøkelsene. REK vest setter vilkår om at også Helse Bergen HF legges til som forskningsansvarlig institusjon.

Data/materiale:

Kliniske undersøkelser: Opptak fra 3Tesla MR skanner.

<u>Spørreskjema</u>: Spørreskjema om foretrukken hånd (Raczkowski et al. (1974) handedness questionnaire oversatt til norsk).

Komiteen vurderer at opplysningene er relevante og nødvendige for å oppnå formålet med prosjektet, jf. helseforskningsloven § 32.

Informasjonsskriv og samtykkeskjema:

REK vest ber om at informasjonsskrivet revideres etter følgende merknader:

- Informasjonsskrivet mangler logo til forskningsansvarlig institusjon.
- Beskrivelsen av mulige fordeler og ulemper bør revideres: <u>Ikke fullt så relevant</u>: *«En risiko ved slike prosjekter er at resultatene er basert på simulering i en moderne hjerne av de prosesser som antas å ha vært tilstede i en forhistorisk hjerne. Hvorvidt disse prosessene er de samme eller ikke vil ikke helt kunne bevises».*

En mulig undervurdering: *«Det er ingen kjent risiko eller ulempe ved det å delta i prosjektet.»* Hva med muligheten for tilfeldige funn?

- Bør beskrive hva som blir gjort dersom man gjør et tilfeldig funn i undersøkelsen.
- Det står at undersøkelsen ikke medfører noe ubehag, men å ligge i MR-maskin i 1 times tid kan oppleves som ubehagelig for noen.
 - Informasjonsskrivet trenger en språkvask. Det er uklart hva som menes med *«behandlende instans».* Og følgende setning er tilsvarende uklar: *«informasjon om de etiske sikkerhetsmessige krav som gjelder for denne typen forsking, og vil bli etterfulgt denne studien.»*

Revidert informasjonsskriv med endringer markert kan sendes inn til REK gjennom en «Endring og/eller henvendelse» i portalen.

Deling av data:

Avidentifiserte opplysninger skal deles til land innenfor EØS (Tyskland). En av medarbeiderne i studien er tilknyttet Max-Planck-Institut für Menschheitsgeschichte i Tyskland. REK vest forutsetter at det foreligger en databehandleravtale mellom institusjonene som skal behandle data i dette prosjektet. Det gjelder også avidentifiserte opplysninger.

Behandling av data:

Data skal oppbevares i avidentifisert form med koblingsnøkkel. Koblingsnøkkelen oppbevares innelåst i en skuff på prosjektleders institutt. REK vest setter vilkår om at koblingsnøkkel lagres på forskningsserveren i en annen tilgangsstyrt mappe som er adskilt fra det øvrige datamaterialet.

Prosjektslutt og behandling av data:

Prosjektslutt er satt til 31.03.2023. Data oppbevares i fem år etter prosjektslutt til etterkontroll. Deretter blir opplysningene slettet eller anonymisert. REK vest har ingen merknader til dette.

Vilkår:

REK vest setter følgende vilkår:

- Helse Bergen HF skal legges til som forskningsansvarlig institusjon.
- Et revidert informasjonsskriv i tråd med REKs merknader skal sendes inn gjennom portalen.
- Koblingsnøkkelen skal lagres på forskningsserveren i tråd med institusjonens retningslinjer.

Vedtak

REK vest har gjort en helhetlig forskningsetisk vurdering av alle prosjektets sider. Prosjektet godkjennes med hjemmel i helseforskningsloven § 10 på betingelse av at ovennevnte vilkår tas til følge.

Sluttmelding

Prosjektleder skal sende sluttmelding til REK på eget skjema via REK-portalen senest 6 måneder etter sluttdato 31.03.2023, jf. helseforskningsloven § 12. Dersom prosjektet ikke starter opp eller gjennomføres meldes dette også via skjemaet for sluttmelding.

Søknad om endring

Dersom man ønsker å foreta vesentlige endringer i formål, metode, tidsløp eller organisering må prosjektleder sende søknad om endring via portalen på eget skjema til REK, jf. helseforskningsloven § 11.

Klageadgang

Du kan klage på REKs vedtak, jf. forvaltningsloven § 28 flg. Klagen sendes på eget skjema via REK portalen. Klagefristen er tre uker fra du mottar dette brevet. Dersom REK opprettholder vedtaket, sender REK klagen videre til Den nasjonale forskningsetiske komité for medisin og helsefag (NEM) for endelig vurdering, jf. forskningsetikkloven § 10 og helseforskningsloven § 10.

Med vennlig hilsen

Nina Langeland

Prof. dr. med.

Komiteleder

Fredrik Rongved

rådgiver

Kopi til:

Universitetet i Bergen Kenneth Hugdahl

Appendix B – Funding Application



Funding application form

1. Information about the applicant (s):

Applicant name:	Andrea Ber	nder				
Consortium partner/institut	tion: <u>SapienCE /</u>	UiB				
Research group: $(\boxtimes A)$	rchaeology)	Climate	Cognition			
Please tick all boxes that apply. Estimate main group where applicable.						
Sponsor/PI	Andrea Ber	nder				

Other participants

Name	Position	Consortium partner/institution
Kenneth Hugdahl	Prof.	SapienCE / UiB
Larissa Mendoza Straffon	PostDoc	SapienCE / UiB
Heidi Øhrn	PhD Candidate	SapienCE / UiB
Emilie Pettersen Sjursen	Master Student	SapienCE / UiB
Natalie Uomini	Senior Scientist	MPI–EVA, Leipzig (Germany)

2. Purpose of application

Research	Travel	Other (specify):
Short descripti	ion of purpos	e:
f	MRI study on	brain activations involved in teaching and learning of
t	ool-making an	d symbol production as part of a transmission chain
Project start da	ate: <u>Sept 1,</u>	2021 Project end date: <u>Nov 30, 2022</u>

Project description ... see pages 2-3

Please provide a project description as an attachment to this form. The description should be written in 12 pt font with 2,5 cm margins. The project description should not be longer than 2 A4 pages including references and figures. Suggested templates for different purposes are available below.

3. Project budget (for details, see page 4)

Please enter totals in this table. Please provide a separate detailed budget, see template table below. The budget justification and detailed budget can be up to 1 A4 page extra, 12 pt font, 2,5 cm margins.

Estimated total cost:	NOK 550,000
Co-financing (yes/no):	no
Name co-financer:	
Funds from co-financer:	
SapienCE total costs:	NOK 550,000

Page |1

Appendix C – Recruitment Poster



Vi gjennomfører et forskningsprosjekt som undersøker hjerneaktivitet under oppgaveløsning. Forsøket innebærer at du fyller ut et kort spørreskjema og gjennomfører en fMRI sesjon mens du knyter knuter.

Selve eksperimentet tar ca. 1,5 time og undersøkelsen vil finne sted på Haukeland Universitetssykehus.

Som deltaker vil du motta en kompensasjon på en verdi av 300 kr.

Scan QR-koden for å melde deg på:



Kontakt info: Har du spørsmål eller ønsker mer informasjon om studien kan du kontakte Heidi Øhrn på e-post: Heidi.Ohrn@uib.no

Prosjektansvarlig: Heidi Øhm, PhD stipendiat

Appendix D – Informed consent form

Forespørsel om deltagelse i forskningsprosjekt

Nevral aktivering for redskap- og symbol-produksjon

Dette prosjektet har som formål å forstå hva som skjer i hjernen når man lager enkle redskaper og symboler. Du er spurt om å delta i denne studien da du har vist interesse for å delta etter å ha sett annonsering eller blitt forespurt direkte.

Hva innebærer prosjektet?

Prosjektet har som formål å utvide vår kunnskap om de kognitive og nevrale prosesser som fantes hos våre hominide forfedre for ca. 70 000 år siden, ved å undersøke tilsvarende prosesser i hjernen hos det moderne menneske. Prosjektet kombinerer to velprøvde metoder som er brukt for å undersøke kulturell overføring av redskap- og symbol-produksjon tidligere.

For å undersøke hva som skjer i hjernen ved simulering av redskap- og symbol-produksjon benyttes funksjonell magnetresonansavbildning (fMRI) mens oppgavene utføres. Hele undersøkelsen vil ta ca. 1 time. Ansvarlig for prosjektet er Universitetet i Bergen, ved Professor Andrea Bender.

Du vil bli kontaktet for å avtale tidspunkt for gjennomføring av forsøket etter at du har akseptert deltagelse. Forsøket gjennomføres på Haukeland Universitetssykehus, hvor du plasseres i en MR-maskin og blir instruert i gjennomføringen av to ulike oppgaver som du utfører mens hjernen din avbildes. Hvordan du løser oppgavene vil bli filmet for senere koding av innholdet. Undersøkelsen krever at du kan ligge stille i opptil en time.

For å holde styr på hvilke responser som tilhører hvilken deltager vil det opprettes en koblingsnøkkel: en liste som kobler personopplysninger til forskningsdata. Koblingsnøkkelen vil bli oppbevart på en sikker server hos UiB. Kun ansvarlig personale vil kunne få adgang til koblede data, etter forespørsel og godkjenning fra prosjektleder. Forskningsdata registreres som lange rekker av tall og blir oppbevart på sikre dataservere ved Universitetet i Bergen og Haukeland Universitetssykehus. Forskningsdataene vil ikke inneholde koblingsnøkkelen.

Mulige fordeler og ulemper

Prosjektet driver grunnforskning og det forventes å gi ny og viktig kunnskap om hvordan hjernen og våre kognitive prosesser har utviklet seg over tid. Det er ingen kjent risiko eller ulempe forbundet med gjennomføringen av selve undersøkelsen. Undersøkelsen medfører heller ikke noe ubehag utover det å skulle ligge stille i en time. Alle deltagere vil få informasjon om de etiske sikkerhetsmessige krav som gjelder for denne typen forskning.

Alle bilder vil bli sett over av en nevroradiolog ved Haukeland Universitetssykehus for å avdekke eventuelle unormalheter i bildene. I tilfeller hvor det avdekkes noe unormalt vil du bli kontaktet av sykehuset for videre oppfølging.

Frivillig deltagelse og mulighet for å trekke sitt samtykke

Det er frivillig å delta i prosjektet. Dersom du ønsker å delta, undertegner du samtykkeerklæringen på siste side. Du kan når som helst, og uten å oppgi noe grunn trekke ditt samtykke. Dersom du trekker deg fra prosjektet, kan du kreve å få slettet innsamlede prøver og opplysninger, med mindre opplysningene allerede er inngått i analyser eller brukt i vitenskapelige publikasjoner. Dersom du senere ønsker å trekke deg eller har spørsmål til prosjektet kan du kontakte Heidi Øhm, Universitetet i Bergen, tlf: 55583224, epost: Heidi.Ohm@uib.no.



Hva skjer med opplysningene om deg?

Opplysningene som registreres om deg skal kun brukes slik som beskrevet i hensikten med prosjektet. Du har rett til innsyn i hvilke opplysninger som er registrert om deg, og rett til å få korrigert eventuelle feil i de opplysningene som er registrert. Du har også rett til å få innsyn i sikkerhetstiltakene ved behandling av opplysningene.

Alle opplysninger vil behandles uten tilknytning til ditt navn og andre direkte personidentifiserende informasjon. Kodingsnøkkelen som knytter deg til dine opplysninger vil oppbevares separat fra resultatene fra studien. Det er kun prosjektleder og de forskere som er direkte knyttet til studien som har tilgang til denne kodingsnøkkelen.

Opplysningene om deg vil bli anonymisert eller slettes senest fem år etter prosjektslutt. Videoopptakene vil slettes etter at innholdet har blitt kodet og anonymisert, senest et år etter gjennomført undersøkelse. Anonymiserte data kan bli gjenbrukt i senere forskningsprosjektet hvis det blir aktuelt.

Deling av data og overføringer til utlandet

Ved å delta i prosjektet samtykker du også til at opplysninger samlet inn kan overføres til utlandet som ledd i forskningssamarbeid og publisering, enten som avidentifiserte eller anonymiserte data. Overføring av data til utlandet skjer kun etter godkjenning fra REK. Prosjektleder vil sikre at dine opplysninger blir ivaretatt på en trygg måte. Koden som knytter deg til dine personidentifiserende opplysninger vil ikke bli utlevert.

Forsikring

Forsikring etter pasientskadeloven

Økonomi

Prosjektet finansieres av SapienCE. Det er ingen økonomiske interessekonflikter for forskerne i prosjektet. Du vil motta en godtgjørelse på 300,- for din deltagelse i studien.

Godkjenning

Regional komite for medisinsk og helsefaglig forskning har vurdert dette prosjektet, og har gitt forhåndsgodkjenning REK# 351425.

Etter ny personopplysningslov har behandlingsansvarlig institusjon Universitetet i Bergen og prosjektleder Andrea Bender et selvstendig ansvar for å sikre at behandlingen av dine opplysninger har et lovlig grunnlag. Behandling av personopplysningene i denne studien har rettslig grunnlag i EUs personvernforordning artikkel 6a og 9 nr. 2a. Det betyr at denne databehandling er tiltatt fordi du har gitt skriftlig informert samtykke til studien. Du har rett til å klage på behandlingen av dine opplysninger til datatilsynet.

Kontaktopplysninger

Dersom du har spørsmål til prosjektet, kan du ta kontakt med Heidi Øhrn.

Du kan også ta kontakt med institusjonens personvernombud Janecke Helene Veim, epost janecke.veim@uib.no, tlf. 55582029 dersom du har spørsmål om behandlingen av dine personopplysninger i prosjektet.

UNIVERSITETET I BERGEN []]



Jeg samtykker til å delta i prosjektet og til at mine personopplysninger brukes slik det er beskrevet i dette dokumentet

Sted og dato

Deltager signatur

Deltagers navn (blokbogstaver)



Appendix E – Handedness questionnaire

Fp nr

SPØRRESKJEMA FOR VENSTREHENDT-HENHOLDSVIS HØYREHENDTHET

Spørsmålene under gjelder hvilken hånd du bruker for å utføre ulike oppgaver. Sett en sirkel rundt (V) om du utfører en viss oppgave med <u>venstre</u> hånd, sett sirkelen rundt (H) om du utfører oppgaven med <u>høyre</u> hånd, og rundt (B) om du like gjerne utfører oppgaven med begge hendene. Hvis du aldri har utført noen av de oppgavene som listes opp nedenfor (og altså ikke vet hvilken hånd du foretrekker) skal du avstå fra å markere noe alternativ.

Svarene behandles konfidensielt.

Med hvilken hånd gjør du følgende:

1.	Tegner	v	8	F
2.	Skriver	v	в	F
3.	Deler ut kortene i en kortstokk når du gir	v	8	۲
4.	Bruker en brus-åpner	v	8	F
5.	Bruker en hammer	v	8	F
б.	Kaster en ball	v	8	H
7.	Bruker en tannbørste	v	8	F
8.	Skrur med et skrujern	v	8	H
9.	Bruker et viskelær for å viske	v	8	H
10.	Bruker en tennis- eller badmintonracket	v	8	н
11.	Klipper med en saks	v	5	H
12.	Holder i en fyrstikk når du tenner fyr på den	v	8	۲
13.	Rører om i en kaserolle/gryte	v	8	н
14.	Med hvilken fot sparker du til en ball	v	8	н
15.	Holder tråden når du trer den i en nål	V	8	н

Sett <u>ett kryss</u> (x) over de hånd og håndstilling som best viser din måte å holde i en penn når <u>du</u> skriver.

