The human motor cortex and action sequence learning by observation

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Abstract

How do people learn to perform new actions through observation? Does it involve the immediate formation of a new motor representation of the action, or is more abstract thought, such as mentally rehearsing spoken instructions, involved in learning the new action? This study aims to answer these questions by examining how the rolandic Mu rhythm (8-14 Hz), found in the human electro-encephalogram, is influenced by action sequence learning by observation. The Mu rhythm, found over the human motor cortex, is known to be suppressed by arm and hand movements, as well as by the observation of others performing similar movements. Electro-encephalograms were measured to determine Mu rhythm power in two conditions. During an imitation condition participants observed sequences of button presses presented on a computer, with each sequence presented four times. Participants were required to reproduce each sequence immediately after the fourth presentation. During the detection condition participants observed action sequences similar to the ones used during the imitation condition, but only had to detect rare deviant button presses, where buttons on screen were pressed with a thumb instead of an index finger. The detection condition served as a control condition where the Mu rhythm might already have been somewhat inhibited by action observation, which allowed the full effect of learning by observation from the imitation condition to be examined. Relative to the observation of sequences in the detection condition, Mu power was reduced during the observation of sequences in the imitation condition, indicating an increased processing load in the motor cortex. This suggests that action sequence learning by observation involves the formation of new motor representations of such action sequences. Furthermore, Mu power was reduced the most during observation of the second, third and fourth presentations of each sequence in the imitation condition, with a stronger Mu rhythm visible during the initial presentation. This indicates an additional processing load in the motor cortex after the initial presentation, which could mean that motor representations are rehearsed after the initial formation, suggesting that a certain amount of abstract thought might also be present while learning to perform new actions.

1. Introduction

The learning of action sequences by observation is a well-studied subject in cognitive psychology. It has been used in a wide variety of fields, including the study of amnesia (Adlam, Vargha-Khadem, Mishkin, & De Haan, 2005), schizophrenia (Delevoye-Turrell, Giersch, Wing, & Danion, 2007), the development of motor skills such as tool use (Järveläinen, Schürmann, & Hari, 2004) and theories about the evolution of language (Molnar-Szakacs, Kaplan, Greenfield, & Iacoboni, 2006; Muthukumaraswamy, Johnson, & McNair, 2004). However, opinions are still divided on the exact way in which action sequence learning by observation works.

Baddeley's (2003) model of working memory states that the working memory consists of four components: a visuospatial sketchpad, used for storing visual imagery; a phonological loop, which is a short-term storage based on sound and language; an episodic buffer which binds together information to created integrated episodes; and a central executive which divides attention between all these components, and can not only recall old memories, but can turn the information contained within into new representations. Applied to learning a new action sequence by observation, this model

would suggest a rather abstract way of learning. An observed action sequence could be stored in the visuospatial sketchpad, perhaps converted into language using the phonological loop, before being recombined into an episodic representation which can be rehearsed in order to learn how to perform the new action sequence. As an example, a sequence of button presses could first be observed, with each button press being converted into mentally spoken text, before these are mentally combined ("first press the middle button, then the right, then the left") in order to learn how to perform the complete action sequence. This type of abstract thought would generally be accompanied by increased activity in the frontal cortex of the brain (e.g. Miller & Cohen, 2001).

Another possibility is that observed action sequences are more directly mapped onto motor representations of those sequences, using available pathways in the motor areas of the brain. In their magnetoencephalography (MEG) experiment, Van Schie, Koelewijn, Jensen, Oostenveld, Maris and Bekkering (2007) found near immediate activation of the motor cortex after observation of a hand pushing a button from an egocentric perspective. Their findings suggest the existence of a process linking observed hand movements directly to the motor cortex. The this process could possibly be further facilitated through the use of mirror neurons, which are neurons which fire both when people observe an action being carried out by another and when they carry out the action themselves (Cochin, Barthelemy, Roux, Martineau, 1999; Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999; Falck-Ytter, Gredebäck, & Von Hofsten, 2006). It is possible that learning how to reproduce an action sequence after observing it works in a similar way, evoking increased activity in areas such as the motor cortex as well. Activity in this area can be indexed by measuring the amplitude of the *Mu rhythm*, present in the human scalp electro-encephalogram (EEG). The present study will attempt to reveal the mechanisms behind action sequence learning by observation through analyzing this Mu rhythm.

The rolandic Mu rhythm, usually encompassed in the Alpha and low Beta ranges (8-14 Hz), originates from the human sensorimotor cortex. Originally thought to occur infrequently, more recent studies have shown that it is present in the scalp EEG of most adults (Makeig, Westerfield, Jung, Enghoff, Townsend, Courchesne, & Sejnowski, 2002). It is typically observed when the motor cortex is in a state of rest. If the motor cortex becomes desynchronized, such as when hand or arm movements are made, or even just imagined (Nair, Purcott, Fuchs, Steinberg, & Kelso, 2003), the typical result is diminished power along the Mu rhythm band (Pfurtscheller, Neuper, Andrew, & Edlinger, 1997; Pfurtscheller, Neuper, & Krausz, 2000).

The motor cortex is also known to be engaged by the observation of actions performed by others (Hari, Forss, Avikainen, Kirveskari, Salenius, & Rizzolatti, 1998). This in turn results in a decrease in Mu rhythm power similar to, but to a lesser degree than actual movement execution (Muthukumaraswamy & Johnson, 2004). For example, in their experiment, Muthukumaraswamy and Johnson let participants watch an experimenter who made various hand movements in front of them, which caused a decline in Mu rhythm power. Furthermore, observation of a precision grip caused a statistically significant change in power compared to observation of a simple hand extension, demonstrating that the Mu rhythm is sensitive to subtle changes in observed actions. These results are further strengthened by the finding that goal-directed actions cause a greater desynchronization of neuron populations in the motor cortex than observation of nongoal-directed actions (Järveläinen et al., 2004). This is reflected in a greater Mu rhythm power decrease during goal-directed action observation than during nongoal-directed action observation (Muthukumaraswamy et al., 2004).

These previous findings allow us to form a baseline for examining the influence of sequence learning by action sequence observation on the human Mu rhythm. The present study sets this baseline by recording Mu rhythm power during passive action sequence observation with the help of EEG. These data are compared with Mu recordings obtained from an experimental condition where participants are required to observe the same type of action sequences, only with the intention to memorize them and reproduce them afterwards. If action sequence learning by observation works by mapping action sequences onto motor representations of those sequences, the increased motor cortex activity should cause a significantly inhibited Mu rhythm in the latter condition when compared to the former.

2. Methods

2.1 Subjects

Fifteen participants (six males, nine females) participated in the experiment. Two females were removed during data analysis for methodological reasons. The remaining participants were between 18 and 26 years of age, with a mean age of 20.5 years and a standard deviation of two years. All were right handed as assessed by the Annet Handedness Inventory (Annet, 1970). All participants were university students, gave informed consent to participate and were given course credit as a reward.

2.2 Apparatus

A custom response box was constructed for this experiment, consisting of four buttons arranged in a square shape, with a fifth in the middle of this square (see Figure 1a). Each button had a built-in orange LED which could light up. The response box was connected to and positioned in front of a Pentium IV computer with a 17 inch monitor. The experiment itself was programmed and carried out in E-prime (Psychology Software Tools, Inc., http://www.pstnet.com/).

2.3 Stimuli and procedure

Participants sat approximately 70 cm (28 inches) in front of the computer screen. Prior to the start of the experiment, participants were administered a computerized Corsi Block Task (Berch, Krikorian, & Huha, 1998) to assess their visuospatial working memory capacities. This task has often been used as an index for learning at the motor level. As such, a positive correlation of the Corsi Block Task with performance on the current experiment would be a theoretical indication that action sequence learning by observation makes use of motor representations. The Corsi task works by tapping a sequence of blocks in a specific order, which participants were supposed to imitate. In the computerized version these blocks appeared on screen, and participants tapped them by clicking on them with the mouse. Sequence length increased until performance broke down. The final score on the task represents the highest sequence length which was successfully imitated.

After completion of the Corsi Block Task the response box was placed in front of participants at a distance which they found comfortable. The experiment then started, which consisted of an *imitation* and a *detection* (control) condition, each containing 40

trials. Each participant carried out the imitation condition first and the detection condition last. The entire experiment, including the application of the electrodes and both conditions, lasted approximately three hours.

In the imitation condition the participants were asked to observe sequences of button presses presented on the monitor, and to reproduce them from memory using the physical response box immediately after they had been presented on the screen for a total of four times. Each trial from the imitation condition consisted of a single sequence repeated on screen four times, followed by the subsequent execution of this sequence by the participant. Sequences were predetermined, but were shown in random order to each participant. Each sequence consisted of six movements and always started with both hands placed in the starting position, meaning that both lower buttons on the response box were depressed using the index fingers. Each movement in a sequence consisted of using one index finger to push one of the upper two buttons, then returning to the starting position. The middle button was never pushed during sequences and was only used as a warning light during sequence presentation, indicating when each individual sequence started and ended. As such, there were four possibilities for each movement in a sequence: moving the left hand to the upper left button and back, moving the left hand to the upper right button and back, moving the right hand to the upper left button and back, and moving the right hand to the upper right button and back.

The exact sequence timing and presentation, as shown on the computer screen, is illustrated in Figure 3. The monitor showed photos of the response box with two virtual hands from an egocentric perspective. Sequence presentation always started with a five second warning signal, so that participants knew that the sequence was about to be shown to them. The warning signal showed the virtual hands in the starting position, with the middle light on the response box shown on the monitor turned on (see the first frame of each sequence in Figure 3). After the on-screen warning signal extinguished, the monitor showed the hands executing all six movements of the current sequence. Each movement was represented by two photos. The first photo showed one of the hands pushing one of the two target buttons, giving the impression that the hand moved to press the button. The second picture showed both hands back in the starting position, resulting in the apparent motion of the hand moving back to the starting position. Each photo was displayed for 500 ms. The entire sequence was repeated three more times (for a total of four sequence presentations) immediately after the previous sequence ended. Each repetition again started with a warning signal, providing a demarcation between the end of one presentation and the start of the next, and a final warning signal was displayed immediately after the last repetition. At this point an instruction screen was displayed, containing text which prompted participants to put both fingers in the starting position, pressing both lower buttons on the response box. This instruction screen also contained a picture showing participants how to place their fingers in the starting position. Pressing the lower buttons caused the warning light in the middle of the physical response box to turn on. The instruction screen told participants to execute the observed sequence from memory as soon as the warning light on the response box extinguished, which it did after keeping both lower buttons depressed for five seconds. At this point participants reproduced the sequence. Before the experiment started they were instructed to execute the sequences as quickly and accurately as possible, but to give priority to accuracy. At the end of each trial, participants received feedback on accuracy, speed and overall progress through the imitation condition. The imitation condition lasted for 40 trials. Participants were also presented with three practice trials at the start of the condition for familiarization purposes, which were not recorded for statistical analysis. The structure itself (six movements per sequence, four sequence presentations and the stimulus timing) was determined in a brief pilot experiment carried out before the present study. During the pilot experiment, participants made one or more mistakes in roughly half of the reproduced sequences, showing that actively learning a sequence is necessary in order to reproduce it correctly.

After completing the imitation condition, participants moved on to the *detection* condition. During the detection condition participants observed another 40 predetermined sequences, different from the ones used in the imitation condition, but this time they were instructed not to memorize the sequences, but to detect deviant movements where buttons were pressed with a thumb instead of an index finger (see Figure 1b). This condition served as a control condition for the experiment, where participants were actively engaged in action observation, but were not learning any action sequences. Each trial in the detection condition consisted of the presentation of one of the sequences using the exact same timing as was used in the imitation condition previously. Again each sequence consisted of six movements and was presented four times. However, this time there was a one in five chance for each sequence presentation that one of the buttons would be pressed with a thumb instead of an index finger. Participants were not informed about the exact odds of deviant movements occurring, only that they would occur. They were instructed that if they spotted a deviant movement, they were to press any button on the response box during the standard warning signal that followed the sequence presentation. If a mistake was made, the word "FOUT!", which is Dutch for "WRONG!", was displayed for the rest of the duration of this warning signal, after which a new, neutral warning signal was displayed, and the experiment continued. At the end of each trial participants received feedback on overall progress and accuracy in the detection condition up to that point. Again, participants were offered three practice trials at the beginning of the condition so that they could become familiarized with the task, but performance on these trials was not recorded for statistical analysis.



Figure 1. a) The response box used in the experiment. b) A deviant movement from the detection condition.

2.4 Electrophysiological recording

Sixty-one-channel EEG (F_{PZ} , F_{P1} , F_{P2} , AF_Z , AF_3 , AF_4 , AF_7 , AF_8 , F_Z , F_1 , F_2 , F_3 , F_4 , F_5 , F_6 , F_7 , F_8 , FT_7 , FT_8 , FC_Z , FC_1 , FC_2 , FC_3 , FC_4 , FC_5 , FC_6 , T_7 , T_8 , C_Z , C_1 , C_2 , C_3 , C_4 , C_5 , C_6 , TP_7 , TP_8 , CP_Z , CP_1 , CP_2 , CP_3 , CP_4 , CP_5 , CP_6 , P_Z , P_1 , P_2 , P_3 , P_4 , P_5 , P_6 , P_7 , P_8 , PO_Z , PO_3 , PO_4 , PO_7 , PO_8 , O_Z , O_1 and O_2 ; see Figure 2a for locations) was recorded according to the International 10-20 System of Electrode Placement (Pivik, Broughton, Coppola, Davidson, Fox, & Nuwer, 1993), using a BrainVision QuickAmp amplifier (Brain Products GmbH) in combination with shielded Ag/AgCl electrodes. Electrode impedances were kept below 10 k Ω . EEG was sampled at 500 Hz with a 140 Hz low pass filter and a 50 Hz notch filter. The average reference was used during acquisition of the EEG signal.

Because arm and hand movements could influence the Mu rhythm, electromyograms (EMG) were recorded using bipolar electrodes placed over flexor carpi radialis and extensor pollicis longus on both forearms, so that covert movements made by participants could be detected (Muthukumaraswamy & Johnson, 2004). To this end, participants were instructed to move as little as possible during sequence observation in both conditions. Furthermore, vertical and horizontal electro-oculograms (EOG) were recorded. The vertical EOG bipolar electrodes were located at the supraorbital and infraorbital ridge of the right eye. The horizontal EOG bipolar electrodes were placed lateral to the outer canthus of each eye. This was done to ensure that participants did not move their eyes too much during observation, which would allow them to learn sequences of movements by moving their eyes along with the sequence presentation. To avoid this, participants were also instructed to fixate on the middle button of the response box presented on the monitor during sequence observation in both conditions. Offline EEG, EMG and EOG signal processing was performed by using BrainVision Analyzer (Brain Products GmbH).

2.5 Analysis

In the offline analysis, the signal was segmented into epochs, starting at the onset of the warning signal before each sequence presentation, and ending 15 seconds later. This was done separately for the imitation and detection conditions. EEG and EMG segments where the voltage increased by more than 150 μ V between sampling points were discarded, as well as EEG and EMG segments which contained values more than 400 μ V apart. Furthermore, segments where the EOG signal contained values which were more than 500 μ V apart were also discarded. Fast Fourier Transforms (FFT) were performed on the remaining EEG segments (512 points, Hanning window, 10%), and the results were averaged, resulting in frequency spectra for observation during both the imitation and detection conditions.

Individual Mu rhythm bands were determined by subtracting the frequency spectrum of the sequence execution phase during the imitation condition (which represents the lowest Mu activation due to hand movements) from the frequency spectrum of observation during the detection phase (which represents the highest Mu activation). The frequency spectrum for sequence execution was obtained in the same manner as detailed above, skipping artifact rejection for EOG en EMG electrodes. The difference was topographically mapped, after which a 2 Hz frequency band best representing Mu activation was manually determined for each participant.

A cluster of 14 electrodes was created which covered most of the area typically associated with Mu activation (C_1 , C_3 , C_5 , CP_3 , CP_5 , FC_3 and FC_5 on the left side, C_2 , C_4 , C_6 , CP_4 , CP_6 , FC_4 and FC_6 on the right side; see Figure 2b for locations). The average Mu power within this cluster was calculated for observation during the first, second, third and fourth sequence presentations for the detection and imitation conditions separately.

A task (imitation, detection) x presentation (first, second, third and fourth) repeated measures ANOVA was performed to analyze the difference in Mu activation between stimulus observation during the imitation and detection conditions. Greenhouse-Geisser corrections were always employed where possible. Gender and age were used as between-subjects variables. Contrasts were used to further analyze the difference in Mu activation between presentations during the imitation condition only. Lastly, scores on the Corsi Block Task were correlated with errors made during the imitation condition.

All statistical tests were performed in SPSS 15.0 for Windows (SPSS, Inc., http://www.spss.com/).



Figure 2. a) All EEG electrode locations which signals were recorded from during the experiment. **b)** Electrode clusters used for analysis of the Mu rhythm.



Figure 3. Example of a sequence as it was displayed on the monitor. The first frame of each sequence presentation shows the warning signal with both hands in the starting position. Every sequence consisted of six movements, each depicted in two frames. Each trial of either the imitation or detection condition contained four presentations of the same sequence.

3. Results

No clearly definable Mu rhythm band could be found for two female participants, who were therefore excluded from further analysis. For the remaining thirteen participants the mean frequency band was 9.7-11.7 Hz, with a range of 8.7-13.7 Hz.

Figure 4 shows both left and right EMGs during the observation phase of the imitation condition. None of the EMGs deviate significantly from the baseline, showing that no covert hand movements were made during observation.





The task x presentation repeated measures ANOVA performed on the collected Mu power data revealed significant effects for task, with F(1,12) = 27.0, p < .001, and the interaction effect between task and presentation, with F(1.71, 20.46) = 4.4, p < .05. No significant effects were found for either gender (F(1,11) = 3.4, p < .1) or age (F(5,7) < 1, p < 1). Figure 5 shows that stimulus observation during the detection condition caused considerably higher Mu activation than stimulus observation during the imitation condition, which suggests increased motor cortex activity during observation when an action sequence is being learned with the intention to reproduce it. Since Mu activation during the detection condition is practically equal for each sequence presentation (F(1.81,21.75) < 1, p < .55), the interaction effect suggests that Mu activation during the imitation task is significantly different for at least one of the presentations. This was confirmed in the contrast analysis performed on the imitation condition. Polynomial contrasts indicated that there was a significant quadratic trend, with F(1,12) = 5.7, p < .05. Simple contrasts revealed a higher Mu power during the first presentation when compared to the second presentation, F(1,12) = 4.8, p < .05, which suggests increased motor cortex activity after the first stimulus presentation. The first presentation was not statistically different from the third and fourth presentations (F(1,12) = 3.1, p < .15 and F(1,12) = 2.1, p < .2, respectively). Furthermore, Mu power during the second presentation did not differ significantly from Mu power during the third presentation (F(1,12) < 1, p < .45), and Mu power during the third presentation did not differ from Mu power during the fourth presentation (F(1,12) < 1, p < .65).

As was mentioned before, a previous pilot study indicated that a sequence length of six movements and four sequence presentations per trial was difficult, but possible to reproduce for most subjects. Considering the amount of errors made by participants during the imitation condition in this experiment, this still holds true. On average, participants made 13.6 errors (sequence reproductions with one or more wrongly executed movements) during the imitation condition, with a standard deviation of 9.4 errors. This indicates that sequences were difficult to remember, and that participants had to be actively engaged while learning the sequences in order to be able to perform them correctly. Corsi Block Task scores showed a significant negative correlation with errors made during the imitation condition, Pearson Correlation -.75, p < .01 (two-tailed), meaning that better performance on the Corsi Block Task generally meant better performance when reproducing action sequences. A scatterplot demonstrating this correlation can be seen in Figure 6. Only three errors were made across all participants during the detection condition, which is too little for any further error analysis of this condition.



Figure 5. Mean Mu power for each sequence presentation during both conditions.



Figure 6. Scatterplot of errors made during the imitation condition, set out against Corsi Block Test scores.

4. Discussion

The main question posed in this paper is whether or not action sequence learning by observation makes use of available motor pathways to directly map an observed action sequence to a motor representation of that sequence. The results from the EEG data clearly indicate that there is a difference in Mu rhythm power between observation during the imitation condition and the detection condition, with the detection condition evoking a stronger Mu rhythm. Since diminished Mu power is generally caused by increased motor cortex activity (Pfurtscheller et al., 1997; Pfurtscheller et al., 2000), this suggests increased motor cortex activity during the imitation condition compared to the detection condition. Because the main difference between the imitation condition and the detection condition is that the imitation condition requires learning by observation, it can be concluded that learning by observation involves use of the motor cortex. This is in agreement with a recent functional magnetic resonance imaging (fMRI) study by Frey and Gerry (2006), which examined human brain activity during observational action sequence learning. They found that, compared to the resting baseline, passive action sequence observation increased activity in inferior frontal and parietal cortices typically implicated in action encoding, as well as areas involved in motor representation, such as the dorsal premotor cortex, pre-supplementary motor area, cerebellum, and basal ganglia. Importantly, these areas showed a further increase in activity when participants observed similar action sequences with the intention to reproduce component actions.

However, there are at least two potential confounding variables. The first involves participants performing small hand movements during the imitation condition in order to better memorize sequences, thereby activating the sensorimotor cortex and inhibiting the Mu rhythm (Muthukumaraswamy et al., 2004). This has been controlled for by measuring EMGs for both hands and discarding segments where movements by either hand were detected, ensuring that this would not influence Mu power.

The second possibility is a difference in attention between the two conditions. It is possible that participants were less attentive during the relatively passive detection condition compared to the imitation condition, where they were required to execute the presented sequence observation. In another experiment, Pfurtscheller, Brunner, Schlögel and Lopes da Silva (2006) demonstrated an increase in hand area Mu activity during imagined foot or tongue movements. This opens up the possibility that a lack of attention on the task at hand could cause in increase in Mu rhythm power. A quick look at errors made during the detection condition suggests that participants were indeed paying attention to the sequences presented on the monitor: among all the participants, only three sequence presentations were wrongly identified as containing a thumb press or not. However, this is not sufficient to rule out the possibility that the difference in Mu power was due to attentional differences between conditions. When asked to comment on the experiment after completing both conditions, a number of participants expressed dislike for the detection condition because of boredom experienced during performance. A comparison of Alpha band frequency power over occipital areas between the imitation and detection conditions could provide more insight into general levels of arousal experienced by participants during both conditions. This analysis fall outside of the scope of this paper, but is being carried out at the time of writing.

Further contrast analysis of the imitation condition, where sequences needed to be learned and reproduced, shows that the initial presentation of a sequence evoked a stronger Mu rhythm than the second presentation, but no stronger than the third and fourth. Interestingly, tentative results from a study using data of the present study, linking the severity of errors made during sequence execution with Mu power during the observation of these sequences (Van der Helden, Van Schie, & Rombouts, in progress), indicates that sequences where more severe errors were made (such as not reproducing a single correct movement during sequence execution) generated higher Mu power during the final two presentations than sequences where a simple error was made (such as only making a single mistake while reproducing the sequence). This suggests that Mu power across the second, third and fourth sequence presentations could all be lower than Mu power during the first presentation, as long as sequences were learned correctly. Suppression of the Mu rhythm generally signifies the desynchronization of the underlying neuron populations, which reflects an increased processing load in the motor cortex (Pfurtscheller et al., 1997). These results therefore not only suggest that *learning* a sequence of actions by observation causes increased motor cortex desynchronization when compared to only action sequence observation, but causes additional motor cortex desynchronization during subsequent sequence presentations. A possible explanation for this finding is that the motor representation of an action sequence is formed during the first sequence observation, and that it is rehearsed and reinforced each subsequent time it is shown. Action sequences which are not memorized accurately seem to be accompanied by less motor cortex activity. This means that a measure of abstract thought could also be involved in action sequence learning by observation. This is again in agreement with Frey and Gerry (2006), who also found activity in the inferior frontal cortex during action sequence learning, an area which is often implicated in cognitive and executive control of other cortical brain functions (Miller & Cohen, 2001; Aron, Robbins, & Poldrack, 2004).

Since the Corsi Block Task is used as an index for motor learning, the negative correlation between errors made during the imitation condition and Corsi scores indicates that participants which are good at motor learning are also good at learning how to reproduce the type of action sequences used in this experiment after observing them, suggesting that motor learning occurs in the currect experiment. However, there are two issues with the scores achieved on the Corsi Block Task. The first is that the results are dichotomous; partcipants either succesfully completed a block sequence with a maximum length of five or a maximum length of seven. A greater variety in scores is necessary to be able to confidently state that there is a linear correlation between scores on the task and errors made during the imitation condition. The other issue is that the majority of participants attained a score of seven, with only four attaining a score of five. The only two outliers with regard to errors made during the imitation condition are among those receiving a low score on the Corsi Block Task, possibly skewing results. Therefore these results are not sufficient to confidently reach the conclusion that visuospatial working memory capacity predicts learning performance on this task.

In conclusion, the combination of these findings support the theory that action sequence learning by observation involves the motor cortex by directly mapping these action sequences onto motor representations of the same action sequences. It is possible, however, that more abstract thought is also involved in this process. This is suggested by the observation that motor cortex activity increased after the initial sequence observation, suggesting that motor representations are rehearsed after initial formation.

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