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Behavioural and neural mechanisms of motor sequence learning by observation

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MINISTRY OF DEFENCE
[dstl]

SoBA Lab
SOCIAL BRAIN IN ACTION

To Peter Wendorff

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Summary

Learning by observation is a natural way of acquiring new skills. Previous research suggests that physical and observational training share a similar neural basis. However, it remains poorly understood to what extent observational training affects neural representations of the acquired skill and what factors influence the training effect. Employing a keypress sequence learning paradigm and brain imaging, brain stimulation, and behavioural methods we investigated three parallel questions to help to provide a more comprehensive and integrative perspective on motor skill learning through observation and how it compares to previous findings on learning by doing. In Study 1 (Chapter 2) we investigated whether action observation establishes movement-sequence-specific neural representations that become more distinct with observational practice as reported in a previous physical practice study. In Study 2 (Chapter 3) we investigated whether non-invasive brain stimulation could facilitate observational practice effects, as stated for learning through physical practice. Finally, in Study 3 (Chapter 4) we examined whether individual differences in learning through observation could be explained by the same cognitive abilities and personality characteristics as in learning by physical practice. Overall, across the three studies, we found that same as physical practice, the observational practice provides behavioural benefits on motor skill acquisition. Furthermore, same as physical performance, action observation establishes distinct sequence-specific activity patterns in premotor and parietal brain areas. However, unlike following the physical practice, the sequence-specific activity patterns did not become more specialised following observational practice. Moreover, unlike with physical practice, anodal transcranial direct current stimulation over primary motor cortex during observational practice provided no benefits for motor skill acquisition through observation. Also, it appears that cognitive processes play a different role in learning by observation than in learning by doing. Perhaps although deliberate cognitive processes are involved in observational learning, the limited aspect of hypothesis-testing makes observational learning itself more implicit than explicit in its nature.

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List of Abbreviations

aIPL	anterior inferior parietal lobule
ANCOVA	analysis of covariance
BIC	Bayesian information criterion
BOLD	blood-oxygenation-level-dependent
CI	confidence interval
ET	execution time
fMRI	functional magnetic resonance imaging
FWE	familywise error
FWHM	full width at half maximum
GLM	general linear model
HRF	haemodynamic response function
IRI	Interpersonal reactivity index questionnaire
LDA	linear discriminant analysis
LDC	linear discriminant contrast
LTP	long-term potentiation
M1	primary motor cortex
MNI	Montreal Neurological Institute
MRI	magnetic resonance imaging
MVPA	multivariate pattern analysis
NPI	Narcissistic personality inventory
OP	observational practice
PP	physical practice
PPI	psycho-physiological interaction
ROI	region of interest
SPM	statistical parametric mapping
tDCS	transcranial direct current stimulation
TMS	transcranial magnetic stimulation

CHAPTER 1

General introduction

If you happen to be in Cambridge on a lovely sunny day, what could be better than punting[1] on the river Cam? So I thought, and for the first time hired a punt to take my visiting family on a punting tour. This cannot be difficult, I thought and grabbed the long punting pole, just to discover how heavy and difficult to handle it is, and that I am utterly unable to navigate the boat in a straight line. Seeing another novice punter fall into the river ended my illusion that this would be an easy task. *"Punting is not as easy as it looks . . . it takes long practice before you can do this with dignity"*, wrote Jerome K. Jerome in his novel *Three Men in a Boat* (1889). I could not agree more. Slightly ashamed, I was determined to put in some serious practice before leading a punting tour again.

A good way to start was to watch expert punters: how smoothly they handle the pole and navigate the boat with ease. I had watched punters before, prior to my own embarrassing punting attempt. However, now that I had first-hand experience and understanding of the basic movements and challenges involved in this deceptively difficult task, I could much better relate to the actions I watched the expert punters perform. And, importantly, now my intention was not just to appreciate the experts' skill, but to watch and learn the skill myself. Instead of watching expert punters, I surely could have just carried on with a trial and error approach to improve my boat navigation skills. However, although it was clear I would not

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[1] A punt is a flat-bottomed boat used in shallow waters. The punter propels the punt by pushing against the river bed with a 4-5 m long and about 5 kg heavy pole. Originally used as cargo boats, nowadays pleasure punting is one of the most popular tourist attractions in Cambridge.

reach an expert level of punting performance by watching alone, this observational experience definitely accelerated my learning. With an action plan in mind and knowing what to expect if, for example, I put the pole too far from the boat or push it too hard into the riverbed, I was well prepared for my next punting tour.

What this example illustrates, and what human beings have discovered on their own terms throughout history is that throughout our lives, we learn by watching others. Without this ability, skill development would be vastly tedious and often harmful. Learning by observation is a natural and powerful way of knowledge transfer (Bandura, 2004). It provides more effective and efficient means of skill acquisition than learning by doing alone (Gog, Paas, Marcus, Ayres, & Sweller, 2008; van Merriënboer & Sweller, 2005; Paas, Renkl, & Sweller, 2003) and works better than verbal instructions only (Al-Abood, Davids, & Bennett, 2001; Annett, 1996), as words cannot describe precisely enough essential aspects of human behaviour. Overall, observation accelerates skill learning, reducing the time needed to learn by doing.

Although extensively studied, the exact mechanisms of the ability to learn by observation are still to be established. In the context of motor skill learning, prior research suggests that action observation generates internal representations of the motor programs required to perform the action (for reviews, see Gentsch, Weber, Synofzik, Vosgerau, & Schütz-Bosbach, 2016; Rizzolatti & Sinigaglia, 2010). Such representations enable us to learn new motor skills by just watching others, without overt physical practice (Mattar & Gribble, 2005). However, it remains poorly understood how specialised the established representations are and what factors influence observational practice effects.

This thesis aims to investigate the behavioural and neural mechanisms of motor skill learning by observation, specifically focusing on motor sequence acquisition. The thesis examines three parallel questions: how specialised the internal representations of the observed actions are and how they change with observational practice (Chapter 2), what the potential is to use non-invasive brain stimulation to facilitate observational practice effects (Chapter 3), and whether individual differences in learning by observation are explained by the same cognitive abilities and personality characteristics as in learning by physical practice (Chapter 4). Answering these questions will help to provide a more comprehensive and integrative view on motor skill learning by observation and how it compares to learning by doing.

Before moving on to the main research questions, the rest of this chapter will provide an overview of the evidence for positive effects of motor skill learning by observation, summarise the current understanding of the mechanisms underlying the ability to learn by observation, detail the motor sequence learning paradigm employed in the thesis, and conclude with a thesis outline.

1.1 Behavioural evidence for motor skill learning by observation

Performance benefits of motor skill learning by observation have been reported in a wide variety of areas, such as sports (for reviews, see Lago-Rodríguez & Cheeran, 2014; Maslovat, Hayes, Horn, & Hodges, 2010a), guitar playing (Gardner, Aglinskas, & Cross, 2017; Higuchi, Holle, Roberts, Eickhoff, & Vogt, 2012), dancing (Kirsch & Cross, 2015; Kirsch, Drommelschmidt, & Cross, 2013), medicine (for a review see, Cordovani & Cordovani, 2015), and physical rehabilitation (for reviews, see Buccino, 2014; Caligiore, Mustile, Spalletta, & Baldassarre, 2017; Nakano & Kodama, 2017; Yutaka, 2013). Furthermore, various aspects of motor skills can be learned by observation, including temporal (Blandin, Lhuisset, & Proteau, 1999; Rohbanfard & Proteau, 2013) and spatio-temporal (Vogt, 1995) dynamics, force dynamics (Mattar & Gribble, 2005), coordination (Hayes, Hodges, Scott, Horn, & Williams, 2006; Maslovat, Hodges, Krigolson, & Handy, 2010b), and sequencing (Bird & Heyes, 2005; Boutin, Fries, Panzer, Shea, & Blandin, 2010; Frey & Gerry, 2006; Heyes & Foster, 2002).

In a meta-analysis study Ashford, Bennett, and Davids (2006) concluded that learning by observation is the most beneficial for skills that involve serial movements, but less so for skills with continuous or discrete movements. According to skill classification (Schmidt & Lee, 2011), discrete movements have a defined beginning and end (e.g., kicking a ball), continuous movements continue until stopped arbitrarily (e.g., swimming), serial movements contain a series of different discrete movements chained together in a defined order (and sometimes timing; e.g., gymnastics routine). Serial movement skills involve both performance of a single movement and coordination between multiple movements and are more complex and novel for a novice learner compared to discrete or continuous movements. Consequently, observing a model performer improves the familiarity with the serial task providing considerable improvements in skill performance, especially at early stages of learning (Ashford et al., 2006).

The early stage of learning corresponds to the cognitive stage of skill acquisition, according to the classic three-stage model by Fitts and Postner (1967). Within this stage, task goals are established, and an appropriate sequence of actions for meeting these goals is determined. As learning progresses, reliance on conscious cognitive processes transits through an associative, partly cognitive, stage to an autonomous stage which relies on automatic motor processing with little cognitive involvement. It is suggested that learning by observation primarily supports the cognitive stage of learning and therefore is more efficient for tasks involving strategic knowledge (Blandin & Proteau, 2000; Blandin et al., 1999; Hodges, 2017), explaining the more beneficial effects for serial movement tasks. Nevertheless, although likely to a smaller extent, evidence shows that learning by observation engages not only cognitive, but also motor processes of the observer and skill learning can extend beyond just the cognitive stage.

For example, in three observational training studies, observers showed a positive effect of a keypress sequence learning only if in the post-training test they performed the sequence with the same fingers as they had seen the model performing it (Bird & Heyes, 2005; Heyes & Foster, 2002; Osman, Bird, & Heyes, 2005). This effect indicates that observers did not merely learn the sequence structure, but learning was effector-specific. Effector-specific learning is regarded as evidence for motor process involvement and true motor learning (as opposed to cognitive learning; Hikosaka, Nakamura, Sakai, & Nakahara, 2002). More evidence of motor learning by observation was provided by Mattar and Gribble (2005). In their study participants performed a mental arithmetic task and simultaneously observed another person learning accurate arm movements in a novel force environment. Observers successfully learned to move in the novel environment despite their attention being engaged with the cognitively demanding arithmetic task during observational practice. The authors argued that the positive effect of observation was not due to the conscious formation of movement strategies, but due to implicit engagement of motor systems during observational practice. These studies suggest that learning by observation engages (or can engage) not only cognitive but also motor processes leading to true motor learning.

Overall, there is ample evidence for positive effects of motor skill learning by observation (for reviews, see also Hodges, 2017; Lago-Rodríguez & Cheeran, 2014; Vogt & Thomaschke, 2007), however exact mechanisms underlying these effects are still to be established. The next section provides an overview of some of the current theories aiming to explain the mechanisms that make learning by observation possible.

1.2 Mechanisms underlying the ability to learn by observation

An idea of an intrinsic link between perception and action dates back already to the very first psychology textbook. There William James, describing his ideomotor theory of action wrote: *“every mental representation of a movement awakens to some degree the actual movement which is its object”* (James, 1890, p. 526). Then speculation, nowadays the notion of shared mechanisms between perception and action is receiving increasing empirical support. While there is an ongoing debate about the exact nature of the perception-action link and which aspects of the motor hierarchy action perception involves (Giese & Rizzolatti, 2015; Grafton & Hamilton, 2007; Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014), a general consensus is that perception and action are intrinsically related (Gentsch et al., 2016). When perceiving an action (e.g., by observing, imagining, or hearing), an internal representation of the action is formed similar to the one instrumental in its execution (Jeannerod, 1994; Prinz, 1997). It is believed that because of such representations, new motor skills can be learned just by watching others, without overt physical practice (Mattar & Gribble, 2005). Various theories have been proposed to explain the nature of the internal action representations and how they support motor skill learning.

1.2.1 Internal action representations

Early explanations of how the observed visual information transforms into motor behaviour (visuo-motor transformation) were based on the ideas of cognitive representations (Carroll & Bandura, 1982; Sheffield, 1961). It was suggested that the perceived information is mentally rehearsed providing a “blueprint” to guide novel behaviour and that the formed cognitive representation serves as a mediator between perception and action. The cognitive representation theories, specifically Albert Bandura’s social learning theory and social cognitive theory (Bandura, 1977, 1986), dominated the observational learning literature from the 1970s through to the 1990s. However, these theories were more focused on the aspects of social learning and lacked specificity in their attempts to explain how the observed movement features are encoded in the brain to support motor skill learning.

In the 1990s, a discovery of so-called “mirror neurons” started a new era in theories of the perception-action link. The name “mirror neurons” was used to describe a newly discovered class of neurons that fire both when an action is performed and when the same or similar action is observed. They were first discovered in the ventral premotor (area F5) and inferior parietal (area PFG) brain areas of macaque monkeys (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Mirror neurons, for the first time, provided direct evidence of shared neural mechanisms between action perception and performance.

Similar perception-action mirroring mechanisms have also been confirmed in humans, however mainly by indirect measures. To our knowledge, only one study has reported direct evidence of human mirror neurons. Single-neuron responses were recorded in patients undergoing surgical treatment of epilepsy (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Neuronal extracellular activity was acquired from medial frontal, anterior cingulate, amygdala, and medial temporal lobe regions (defined by clinical criteria) while patients watched or performed grasping actions and facial expressions. Populations of neurons in the supplementary motor area and medial temporal lobe regions responded both during action observation and execution conditions, likely reflecting mirroring mechanisms related to movement planning and memory of the action.

Nevertheless, in human studies, there is growing indirect evidence from neurophysiology and brain imaging studies that action perception and performance share common neural networks and mechanisms (for reviews, see Iacoboni & Dapretto, 2006; Kilner & Lemon, 2013; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). A meta-analysis of brain imaging studies have uncovered widespread brain areas that are activated both during action perception and performance (Hardwick, Caspers, Eickhoff, & Swinnen, 2017; Molenberghs, Cunnington, & Mattingley, 2012), including inferior frontal gyrus and inferior parietal lobule (likely homologous to macaque areas F5 and PFG where the mirror neurons were first discovered; Rizzolatti & Craighero, 2004).

The discovery of mirror neurons encouraged ideas of a direct motor system activation during action observation. The so-called “direct matching hypothesis” (Iacoboni et al., 1999) suggested that motor representations of perceived actions can be formed directly, without a cognitive representation as a mediator. In other words, it was proposed that action observation evoke direct internal simulation (motor resonance) of the observed action without conceptual reasoning about it (Gallese, Keysers, & Rizzolatti, 2004). However, although, motor systems are indeed activated during action observation, their activations are likely not as direct as initially thought. It is postulated that action, perception, and cognition are closely interrelated processes that work together to form action-perception circuits (Pulvermüller, Moseley, Egorova, Shebani, & Boulenger, 2013). Furthermore, the internal representations of perceived actions span across different levels of the motor hierarchy, from a highly abstract level of action intentions to action kinematics (Grafton & Hamilton, 2007; Preston & de Waal, 2001).

Importantly, motor representations of the perceived actions are evoked only if the particular action is in the observer’s own motor repertoire (Giese & Rizzolatti, 2015). Brain imaging studies support this view showing that activity in the sensorimotor brain regions is positively related to the familiarity with the observed action (Buccino et al., 2004; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006; Gardner, Goulden, & Cross, 2015; Kirsch & Cross, 2015). Related to this is the idea that mirror neurons (and mirroring mechanisms more generally) are the product of learned sensorimotor associations (Burgess, Lum, Hohwy, & Enticott, 2017; Catmur, Press, & Heyes, 2016; Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2010; Keysers & Gazzola, 2014; Press, Heyes, & Kilner, 2011). Such associations are developed, for example, when we see our own actions or when we are imitated. Subsequently, the correlated activation of sensory and motor neurons bind them together through a Hebbian-like learning mechanism (stronger synaptic connection between neurons that fire at approximately the same time) producing a mirror neuron system in the brain (Keysers & Perrett, 2004).

The learned sensory-motor associations enable us to understand the actions of others (Press et al., 2011). Specifically, when perceiving an action, the prior action experience generates a prediction of the action goals, the subsequent movement patterns and their sensory consequences (predictive coding account; Friston, Mattout, & Kilner, 2011; Kilner, Friston, & Frith, 2007; for reviews on other theories see Gentsch et al., 2016; Giese & Rizzolatti, 2015). Thus, the motor representations of the observed actions (the mirroring mechanisms) reflect the hypothesised (predicted) proprioceptive and exteroceptive consequences of those actions. Such predictions are a natural way of preventing surprising events, understanding others’ intentions, and being prepared for adequate responses to the changing environment.

The internal representations of the observed actions enable us to relate to other persons’ actions not just through conceptual reasoning but also through sensorimotor resonance which is based on our own motor experience. Moreover, the internal action representations (both cognitive and motor) may support new motor skill acquisition by observation in a similar way as when learning by physical practice.

1.2.2 Building new action representations through practice

A popular view is that the central nervous system uses internal inverse (sensory-to-motor) and forward (motor-to-sensory) models for motor planning, control, and learning (Wolpert, Ghahramani, & Jordan, 1995; Wolpert, Ghahramani, & Flanagan, 2001). The inverse model (the controller) creates a motor plan for achieving a desired sensory state (e.g., ride a bike), while the forward model (the predictor) predicts potential sensory consequences of the actual motor behaviour (e.g., falling off the bike). The actual sensory consequences are then compared with the predicted ones, as a form of hypothesis testing, and the prediction error is used to update the motor commands for the next sensory-motor-sensory feedback loop. As learning progresses, less corrective action is necessary resulting in more accurate, smoother and faster movements.

Brain imaging studies demonstrate that motor-skill learning lead to changes in brain activity both regarding the expansion and the strength of cortical activation (for reviews, see Dayan & Cohen, 2011; Hardwick, Rottschy, Miall, & Eickhoff, 2013; Kelly & Garavan, 2005; Penhune & Steele, 2012; Poldrack, 2000). Depending on the task domain, the involvement of cognitive processes, learning stage and number of other factors, studies report both increase and decrease in brain activity. A general consensus is that motor skill acquisition leads to more specialised and more efficient neural processing (Bassett, Yang, Wymbs, & Grafton, 2015; Diedrichsen & Kornysheva, 2015; Kelly & Garavan, 2005) with individual movement elements bound together in a unified representation (Diedrichsen & Kornysheva, 2015; Wiestler & Diedrichsen, 2013). Processing individual action elements as a single action unit (chunk) reduces the cognitive demand and facilitates fast action initiation and smooth execution (Diedrichsen & Kornysheva, 2015; Rhodes, Bullock, Verwey, Averbeck, & Page, 2004; Sakai, Hikosaka, & Nakamura, 2004; Solopchuk, Alamia, Olivier, & Zénon, 2016; Verwey & Abrahamse, 2012).

It is proposed that motor skill learning by observation is similarly supported by the internal inverse and forward models like learning through physical practice (Flanagan, Vetter, Johansson, & Wolpert, 2003; Friston et al., 2011; Iacoboni, 2005; Oztop, Kawato, & Arbib, 2006). If none of the movements that constitute the observed action is in the observer's motor repertoire, then action perception would be based solely on visual analysis of the action elements (Buccino et al., 2004). However, in many cases, new motor skills are a novel combination of some basic movements that already are in an observer's motor repertoire but require novel sequencing, timing, and coordination. If the basic movements are in the observer's motor repertoire, then action observation can evoke motor resonance thus activating processes based on internal inverse and forward models of motor learning (Flanagan & Johansson, 2003). The internal action representations provide a 'raw material' for higher order supervisory processes needed for the development of new action representations through observation (Hamilton, 2015; Sakreida et al., 2017).

When observing a novel action performed by an actor, the observer's internal inverse model generates representations of the motor commands that would be used to perform the observed action (the motor resonance of the observed action). The internal forward model then is used to predict the forthcoming movements of the actor. Subsequently, the predicted movements are compared with the actual movements of the actor, updating the corresponding motor representations of the seen action (Oztop et al., 2006).

It is plausible to think that, learning by observation would generate increasingly accurate and specialised neural representation of the action like in learning through physical practice. To our knowledge, no reports yet exist of more specialised action representations following observational practice (we address this question in Study 1). Nevertheless, brain imaging studies show that as in motor skill learning through physical practice, observational practice too leads to similar changes in brain activity (e.g., Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Frey & Gerry, 2006; Higuchi et al., 2012) and connectivity (e,g., van der Helden, van Schie, & Rombouts, 2010; Higuchi et al., 2012) indicating higher neural efficiency following observational practice.

Overall, previous research shows that mechanisms that underlie the ability to learn by observation are supposedly similar to the mechanisms of learning through physical practice. Action observation and action execution share common neural representations both at the cognitive and at the motor levels. Internal representations of the observed actions enable us to learn by watching as if we were doing the action ourselves, by continuously updating the motor plans to meet the desired sensory states.

1.3 Outstanding questions and thesis overview

The presumption that learning through observation and physical practice involves similar mechanisms and processes raises several unexplored questions. This thesis addresses three of them attempting to provide a more comprehensive and integrative perspective on motor skill learning through observation and how it compares to learning by doing.

1.3.1 Specificity of the 'inner representations' of observed actions (Study 1)

An essential aspect of many motor skills is movement sequencing, and skilled performance is characterised by a smooth execution of distinct actions. Think of a piano performance, for example. As learning progresses, initial distinct key-presses transform into a smooth well-coordinated melody. Evidence shows that, at a neuronal level, sequential movements group into unified action representations that become more specialised with physical practice (Wiestler & Diedrichsen, 2013). The emergence of such skilled action representations enables more efficient neuronal processing and production of the desired behaviour (Diedrichsen & Kornysheva, 2015).

Regarding representations of observed actions, previous studies have discriminated between various action features. There are reports of effector-specific representations (with actions involving different body parts, e.g., hand, leg, mouth, showing roughly somatotopic activation; see, for a review, Fernandino & Iacoboni, 2010); goal-specific representations (e.g., lifting or punching an object; Jastorff *et al.*, 2010; Oosterhof *et al.*, 2010, 2012); viewpoint-specific representations (first-person or third-person; Oosterhof et al., 2012); action-specific representations (rock, paper, or scissors; Dinstein *et al.*, 2008); motor hierarchy-specific representations (showing different representations for kinematic, goal and outcome features, as summarised in Grafton & Hamilton, 2007). However, to our knowledge, no reports yet exist on whether observing actions that involve sequential movements evoke sequence-specific neuronal representations of the actions and whether the representations become more specialised with observational practice. We address this question in the Study 1 (Chapter 2). Specifically, we investigate whether keypress sequence observation establishes sequence-specific representations that become more specialised with observational practice, similar to physically performed and practised actions reported before (Wiestler & Diedrichsen, 2013).

1.3.2 Feasibility of brain stimulation to facilitate observational learning (Study 2)

It is acknowledged that motor learning increases excitability of the primary motor cortex (M1) and strengthens synaptic connections within M1 through long-term potentiation (LTP)-like mechanisms (Rioult-Pedotti, Friedman, & Donoghue, 2000; Sanes & Donoghue, 2000; Spampinato & Celnik, 2017). Non-invasive anodal transcranial direct current stimulation (tDCS) of the M1 is thought to induce similar effects on neuronal excitability (Nitsche & Paulus, 2000; Nitsche et al., 2008) and may facilitate motor practice effects. Indeed, several previous studies show that anodal tDCS of the M1 during physical practice promotes motor skill acquisition (for reviews, see Ammann, Spampinato, & Márquez-Ruiz, 2016; Buch et al., 2016; Hashemirad, Zoghi, Fitzgerald, & Jaberzadeh, 2016; Reis & Fritsch, 2011). Previous studies show that M1 is also engaged during action observation (Celnik et al., 2006; Stefan, 2005). However, an unexplored question is whether anodal tDCS of the M1 could promote motor skill acquisition through observation. Thus, in the thesis Study 2 (Chapter 3) we investigate whether anodal tDCS over M1 facilitates motor skill acquisition by observation, as previously reported for learning through physical practice.

1.3.3 Individual differences in learning by observation (Study 3)

People vary greatly in their ability to acquire new motor skills. For example, extensive evidence shows that motor skill acquisition through physical practice is related to working memory and fluid intelligence (Bo & Seidler, 2009; Christou, Miall, McNab, & Galea, 2016; Gebauer & Mackintosh, 2007; Janacsek & Nemeth, 2013; Maxwell, Masters, & Eves, 2003; Reber, Walkenfeld, & Hernstadt, 1991; Unsworth & Engle, 2005). However, little is known about individual differences in motor skill acquisition through observation. The involvement of shared mechanisms and processes in learning through physical or observational practice raises the question whether the same cognitive abilities can explain individual differences in both types of skill acquisition. We examine this question in the thesis Study 3 (Chapter 4) asking whether the same cognitive abilities and personality characteristics may explain individual differences in learning by observation and learning by doing.

1.3.4 Motor skill learning paradigm

Keypress sequencing is a commonly used task to study motor skill learning in experimental settings, and it is also used in the present thesis. In the three studies included in the thesis, we use a keypress sequence learning paradigm adapted from the physical practice study by Wiestler and Diedrichsen (2013). The paradigm requires participants to learn five-element continuous keypress sequences performed with a left (non-dominant) hand. Within each sequence, the five fingers of the left hand are pressed once but in a different order. Thus, the paradigm involves multi-finger movements and entails learning not only the sequence order but also transitions between sequential finger presses dynamically linking distinct movements into one continuous action.

Details of the paradigm used in the current work are described in Section 2.2. Overall, the physical performance (pre-test and post-test phases in all studies) and physical practice (in

Study 3) phases in our studies correspond closely to the original Wiestler and Diedrichsen paradigm. However, the observational practice phase (in all studies) differs from the physical practice in several aspects. First, during observational practice participants do not perform the sequences themselves, but watch videos of a model's hand performing them. Second, while during physical practice participants continuously receive feedback on their performance speed and accuracy, such feedback is not provided during observational practice. Third, during observational practice participants had to engage in an additional task – spotting errors in the model's performance.

1.3.5 Thesis overview

Employing a keypress sequence learning paradigm and brain imaging, brain stimulation, and behavioural methods we investigate three parallel questions to help to provide a more comprehensive and integrative perspective on motor skill learning through observation and how it compares to previous findings on learning by doing.

In the Study 1 (Chapter 2) we investigate how specialised the 'inner representations' of the observed actions are and how they change with observational practice.

In the Study 2 (Chapter 3) we examine the feasibility of non-invasive brain stimulation to facilitate observational practice effects.

In the Study 3 (Chapter 4) we ask whether individual differences in learning by observation can be explained by the same cognitive abilities and personality characteristics as in learning through physical practice.

Finally (Chapter 5) we summarise and integrate the findings from all three studies to provide an integrative perspective on motor skill learning by observation and how it compares to learning by doing.

CHAPTER 2

Movement-sequence-specific representations of observed actions and observational practice effects on brain activity and connectivity

2.1 Introduction

When learning a motor skill, we benefit from watching a skilled performer. Several theories suggest that action observation engages an observer's own motor system by establishing internal representations of the motor programs required to perform the action (for reviews, see Gentsch et al., 2016; Rizzolatti & Sinigaglia, 2010). Because of such representations, we can learn new motor skills by just watching others, without overt physical practice (Mattar & Gribble, 2005). Evidence shows that observational practice modulates brain activity, likely indicating increased neural efficiency that facilitates subsequent skill performance (Cross et al., 2009; Frey & Gerry, 2006; Higuchi et al., 2012). However, brain activity changes alone tell little about the internal representations of the observed actions. It remains poorly understood how specialised the action representations are and how they change with observational practice to further facilitate skilled performance.

More research has investigated representations of physically performed and practised actions. Skilled actions, in general, are characterised by multiple movements linked into precise spatiotemporal arrangements to enable fast and fluent performance (Abrahamse, Ruitenberg, de Kleine, & Verwey, 2013; Lashley, 1951). Internal representations of the performed movement sequences involve multiple levels of motor hierarchy, from intentions to movement sequencing, to muscle commands (Diedrichsen & Kornysheva, 2015; Keele, Jennings, Jones, Caulton, & Cohen, 1995; Rizzolatti et al., 2014). Such representations are distributed throughout cortical and subcortical brain regions (Gallivan, Johnsrude, &

Flanagan, 2016; Grafton, Hazeltine, & Ivry, 1998; Kornysheva & Diedrichsen, 2014; Wiestler & Diedrichsen, 2013; Wiestler, Waters-Metenier, & Diedrichsen, 2014). Furthermore, internal representations of skilled actions are highly specialised. For example, execution of kinematically matched keypress sequences is associated with distinguishable, sequence-specific brain activity patterns in multiple frontoparietal brain areas (Wiestler & Diedrichsen, 2013). Moreover, the patterns become more distinct with physical practice, implying a more specialised neural representation of the learned sequence that enables its fast execution. To our knowledge, no reports yet exist of such highly specialised movement-sequence-specific representations of observed actions.

Thus, the main aims of the present study were to investigate whether a mere observation of kinematically matched actions evokes movement-sequence-specific neural representations and whether they become more distinct with observational practice. In addition, to provide a more comprehensive view of the observational learning effects, we investigated behavioural improvement, and brain activity and functional connectivity changes following observational practice. We seek to better understand the specificity of neural representations of observed actions and the neural processes underlying motor skill learning by observation.

The investigation was based on the physical practice study by Wiestler and Diedrichsen (2013). For four days, participants watched videos of a hand performing four different keypress sequences. Before and after the four-day training, participants were tested on their behavioural performance and underwent functional magnetic resonance imaging (fMRI). In the behavioural tests, participants performed the four trained (or to-be-trained) and four untrained sequences. During the fMRI sessions, participants watched videos of all eight (trained and untrained) sequences.

First, we assessed observational practice effects on behavioural performance, expecting better performance for the trained than for the untrained sequences. There is considerable evidence that motor skills can be learned by observation (for reviews, see Lago-Rodríguez & Cheeran, 2014; Vogt & Thomaschke, 2007). Second, we investigated differences in brain activity when watching trained compared to untrained sequences. The differences may indicate additional (activity increase) or more efficient (activity decrease) neural processing following practice (Poldrack, 2000). Processes underlying practice-related changes in brain activity further could be explained by interactions with functionally related regions, especially if the involved regions are subserving multiple functions (McIntosh, 1998). Thus, third, we used psycho-physiological interaction (PPI) analysis (Friston et al., 1997) to explore functional connectivity within the involved networks when watching trained compared to untrained sequences. For example, functional connectivity analysis could help explain the brain activity differences in relation to perceptual, attentional, and motor processes. Finally, and most importantly, we used multi-voxel-pattern analysis (MVPA; Kriegeskorte, Mur, & Bandettini, 2008; Nili et al., 2014), to investigate whether action observation evokes distinguishable movement-sequence-specific neural representations that become more distinct with observational practice, similar to physically performed and practiced actions reported before (Wiestler & Diedrichsen, 2013). Highly specialised representations of observed actions could further explain the practice-related brain activity and connectivity changes and the subsequent skill learning by observation.

To summarise, in the present study for four days participants learned four keypress sequences by watching videos of others perform them. Participants' behavioural performance was measured before and after the observational practice. In addition, during pre- and post-training fMRI sessions, participants watched the four observationally trained and four untrained sequences. The aims of the study were (1) to assess whether observational practice facilitates sequence acquisition; (2) to assess the brain activity changes following observational practice; (3) to explore whether the brain activity changes could be related to changes in functional connectivity within task-specific brain regions following observational practice; (4) to investigate whether action observation evokes distinguishable movement-sequence-specific neural representations; (5) and, most importantly, to investigate whether movement-sequence-specific neural representations become more distinct with observational practice potentially explaining the practice-related brain activity and connectivity changes and the subsequent skill learning by observation.

2.2 Method

2.2.1 Participants

Eighteen right-handed (based on self-report) Bangor University student volunteers participated in the study. Two participants were not included in the final sample: a pilot participant, who did not have the same testing parameters, and a participant who made excessive head movements (> 4 mm) in one of the scanning sessions. The final sample comprised 16 participants (8 males and 8 females), 20 to 40 years old (M = 24.31 years, SD = 5.06). All participants had normal or corrected-to-normal vision and no history of neurological disorders. Participants gave their written informed consent and were paid £45 for their participation. All procedures were approved by the Ethics Committee of the School of Psychology at Bangor University (approval number: 2014-11824) and the UK Ministry of Defence Research Ethics Committee.

2.2.2 Stimuli

A keypress sequence learning paradigm was implemented, based on the task used by Wiestler and Diedrichsen (2013). We used a standard QWERTY black computer keyboard with the Q 3 4 5 and Y keys covered with red tape and all surrounding keys removed. In pre- and post-training sessions, participants were required to press the red keys with the five fingers of their left hand in a specified order. During the observational training and fMRI sessions, participants watched videos of the experimenter performing the keypress task. For the video recordings, we used a similar keyboard with the only difference that the sides of the five keys were covered in yellow to improve the visibility of the key being pressed. Stimuli presentations and response recordings were performed using MATLAB 8.3.0 (The MathWorks, MA, USA) and Psychophysics Toolbox 3.0.12 (Brainard, 1997).

Keypress sequences

We used the same set of 12 five-element keypress sequences as previously by Wiestler and Diedrichsen (2013). Each sequence required the five fingers of the left hand to press once, but in a different order and with no more than three adjacent finger-presses in a row. All sequences were matched for difficulty, based on a pilot experiment (Wiestler & Diedrichsen, 2013). For each participant, from the set of 12 sequences, four sequences were randomly allocated to the Trained condition, and four others to the Untrained condition. The remaining four sequences were not used.

Videos

For observational training and both scanning sessions, 13-second videos were created showing the experimenter's left hand from a first-person perspective, slightly tilted to the right (see Figure 2.1A and http://ej.uz/gitHubE2stimuli). Each video showed the experimenter executing one sequence five times, with naturally varying breaks between each sequence repetition, to ensure a more authentic presentation of the performance. For the same reason, for each sequence, five different video versions were recorded, to allow closer to natural performance variation of the same sequence. An additional video version for each sequence was created where one of the five sequence executions was incorrect. This resulted in 72 videos in total.

Sequences were executed at an intermediate baseline performance level, determined by behavioural pilot test results, where the average correct sequence execution at baseline was 2.29 seconds (N = 17, M = 2.29 s, SE = 0.14). Each original video, showing five repetitions of the same sequence, was slightly speeded up or slowed down (±10%) to make it exactly 13 seconds long. Consequently, some authenticity was lost; however, the relative variability within the video remained intact, and the average single sequence execution in the videos was 2.3 seconds. The videos were presented on a computer monitor in full colour on a black background. The frame rate was 29 frames per second with a resolution of 600 x 526 pixels, showing approximately natural hand size.

Sequence execution trial

A sequence execution trial involved five continuous repetitions of the same sequence. Each trial started with a 5-digit cue (for 2.7 s), indicating the sequence of keypresses. The cue was then replaced with a cross, serving as a “go” signal to execute the given sequence five times as quickly and accurately as possible. After five executions of the same sequence, the trial ended, and the next sequence was cued.

Sequence observation trial

A sequence observation trial involved watching a video clip of an actor’s left hand performing five continuous repetitions of the same sequence. A trial started with a 5-digit cue (for 2.6 s), indicating the sequence to be executed, followed by a video (13 s) showing five executions of the cued sequence. Participants were instructed to watch whether the hand executed the correct (cued) sequence all five times. After some of the trials, participants were asked whether there was an error in any of the five executions – the error question.

2.2.3 Procedure

Participants underwent six testing days over a seven-day period (six testing days and one day off in between; Figure 2.1A). On the first day of testing, participants received task instructions and completed three single sequence execution trials to ensure they understood the task. The familiarisation procedure was followed by a pre-training session, which was immediately followed by the first scanning session. The next two consecutive days were observational training sessions, which were followed by a day off (usually Sunday). After the rest day came another two consecutive days of observational training sessions. The last day (day 6) started with the second scanning session, immediately followed by a post-training session. Each session is described in more detail below.

Pre- and post-training sessions

In the pre- and post-training sessions participants performed four Trained and four Untrained sequence execution trials in a random order with their left hand. Each trial consisted of five repetitions of the same sequence (Figure 2.1B). All trial-related information was presented centrally at the bottom of the screen against a grey background. A trial started with a black fixation cross (0.2 s), followed by the sequence cue presented as five digits (2.7 s) that indicated from right to left which key to press: “1” – the right-most key pressed with the thumb; “5” – the left-most key pressed with the little finger. After the cue, the digits were replaced by the fixation cross and five black asterisks above it. This served as a “go” signal to execute the memorised sequence five times as quickly and accurately as possible. If the correct key was pressed, the corresponding asterisk on the screen turned green, if a wrong key was pressed, the asterisk turned red.

After executing a single sequence, the central fixation cross changed colour giving feedback on the performance (0.8 s): green – correct sequence execution; red – incorrect sequence execution; blue – correct, but executed 20% slower than the median execution time (ET) in the previous trials; three green asterisks – correct and executed 20% faster than the median ET in the previous trials. After this short feedback, all asterisks turned black signalling the start of the next execution trial. After five executions of the same sequence, the trial ended, and the next sequence was cued.

Observational training sessions

In the observational training sessions, participants watched videos of the four Trained sequence executions. Participants were instructed to watch the videos and to pay close attention to whether the sequences were performed correctly. Occasionally they would be asked whether the performer in the video made an error in any of the five repetitions – the error question. They would respond by pressing a ‘b’ key (marked red) on a keyboard for ‘yes’ and an ‘m’ key (marked blue) for ‘no’. This task was included to ensure that participants paid attention to the videos. Participants were also informed that they will need to perform the watched sequences again at the end of the experiment.

All trial-related information was presented in the middle of the screen against a black background with a light grey font (Figure 2.1C). A trial started with a fixation cross (0.4 s), followed by the sequence cue presented as five digits (2.6 s), followed by the sequence video (13 s). After some of the trials, the error question was asked and participants had 2.6 seconds to respond.

A training session was divided into four blocks, separated by a rest period. Within each block, 20 videos were presented in a random order: each sequence video four times (randomly choosing one of the five video versions, described in *2.2.2 Stimuli-Videos*), and one 'error video' for each sequence (where at least one of the five repetitions of the sequence execution was incorrect). The error question was asked randomly 5-7 times per block. At the end of each block, participants received feedback on how accurately they spotted the incorrect sequence executions. The whole training session lasted approximately 25 minutes, and participants saw a correct execution of each sequence at least 80 times (4 blocks, 4 videos per block, 5 repetitions per video, plus some correct repetitions in the 'error video').

Scanning sessions

During identical pre- (day 1) and post-training (day 6) fMRI sessions, participants observed the four Trained and four Untrained sequence videos in a random order. The observation trials occurred in the same way as in the observational training sessions (see above and Figure 2.1C). In each scanning session participants completed 10 runs. Each run had 17 trials presented in a random order: eight sequence videos presented twice each, and one 'error video'. Same as in the observational training session, participants were instructed to watch whether all sequences are correctly executed and answer the error question when asked. The error question was asked twice within a run – always after the 'error video' and randomly after one of the correct videos. Each run also had five rest phases, one at the beginning of the run and four randomly interspersed, but not twice in a row. The rest phase was 13 seconds long and showed a fixation cross in the middle of the screen. Each run lasted approximately 6 minutes (2.6 s per whole-brain acquisition, with 138 acquisitions per run).

Stimuli were presented onto a screen located behind the magnetic resonance imaging (MRI) scanner and displayed to the participant via a mirror placed above the participants' eyes. The response to the error question was recorded using a scanner-safe fibre optic four-button response pad system (Current Designs, Philadelphia, PA) connected to the stimulus PC.

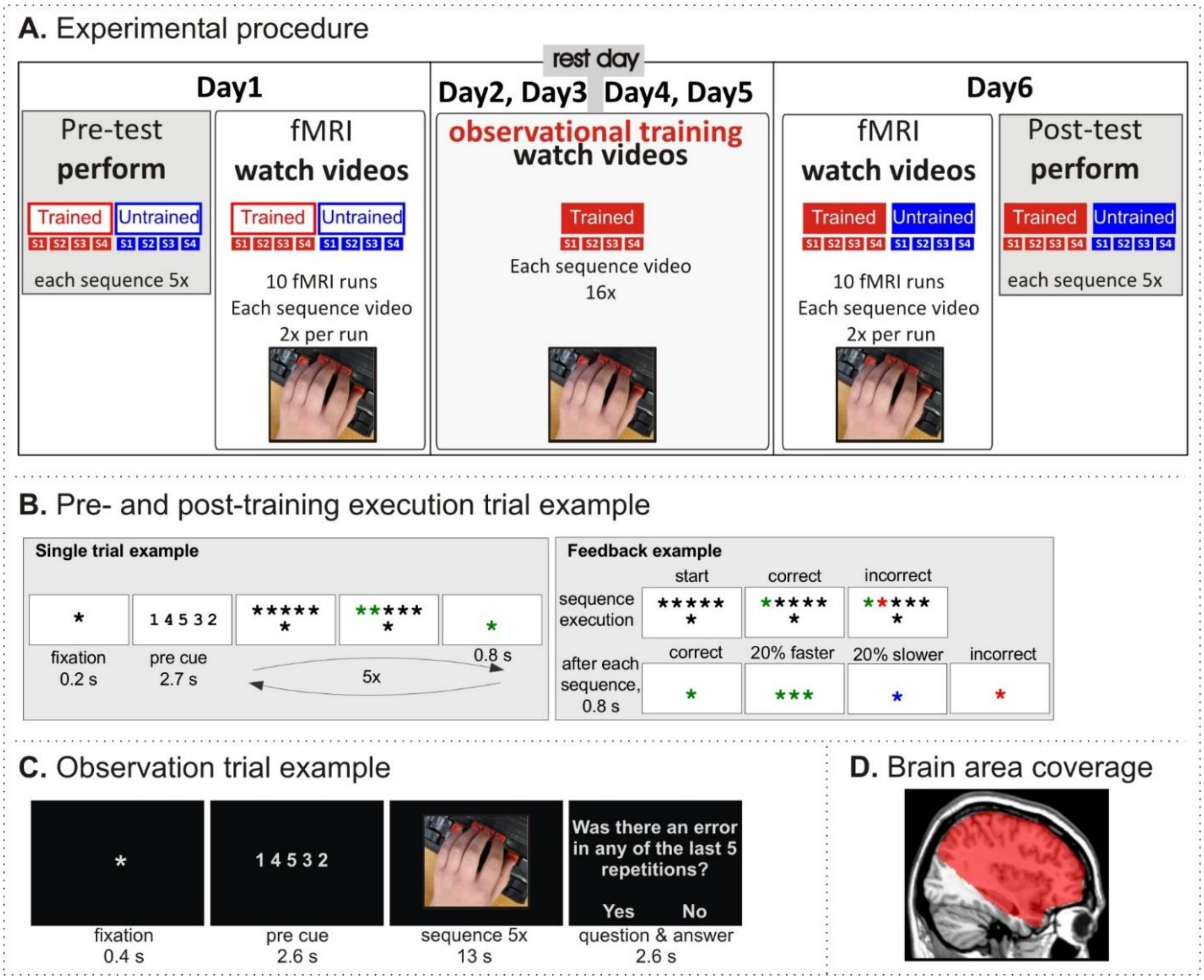


Figure 2.1. Experimental paradigm (adapted from Wiestler and Diedrichsen (2013)). **A.** Experimental procedure. The experiment involved pre-test and post-test, separated by four training days and two scanning (fMRI) sessions. In the pre- and post-test, participants performed eight keypress sequences (four of them to be trained, the other four untrained). In the scanning sessions, participants watched videos of a hand performing the same eight sequences. In the training sessions, participants watched videos of a hand performing four of the eight sequences. **B.** Execution trial example. A cued sequence had to be memorised and then executed five times while receiving performance feedback. **C.** Observation trial example. A sequence cue was followed by a video showing a hand executing the sequence five times, either correctly or incorrectly. Occasionally a question was asked whether there was an error in any of the five repetitions, and a response had to be made. **D.** The brain area coverage for fMRI analysis focused on premotor and parietal brain regions and did not include the cerebellum, occipital lobes, or inferior temporal lobes.

2.2.4 Scan acquisition

MRI data were acquired using a 3 Tesla Phillips Achieva MRI scanner (Philips Health Care, Eindhoven, Netherlands) fitted with a sensitivity-encoded (SENSE) 32-channel phased-array head coil.

Functional scans

Both scanning sessions consisted of 10 functional runs of the blood-oxygenation-level-dependent (BOLD) signal acquisitions (Ogawa et al., 1992), with two dummy scans and 136 whole-brain scans per run. Volumes were collected using a T2*-weighted single-shot gradient echo planar imaging sequence with the following parameters: TE = 30 ms, TR = 2.6 s, flip angle = 90°, 41 ascending slices with 2.3 mm thickness, 0.15 mm gap, and 2 x 2 mm^2 in-plane resolution (matrix size 96 x 96). The slice acquisition was focused on premotor and parietal brain regions; thus, the group average brain area coverage did not include the cerebellum, occipital lobes, or inferior temporal lobes (see Figure 2.1D).

Anatomical scan

The last scanning session (day 6) ended with a high-resolution whole-brain 3D anatomical scan acquired as a T1-weighted image (MP-RAGE, TE = 3.5 ms, TR = 12 ms, voxel resolution = 1 mm^3, slice thickness = 2 mm, flip angle=8°), which was used as an anatomical reference for each participant.

2.2.5 Data analysis

Observational training effect on sequence-specific learning

Participants were tested and scanned before and after the four days of observational training. In similarly designed physical training studies, both general skill learning (significant pre- to post-training performance improvement of both trained and untrained sequences) and sequence-specific learning (greater post-training performance for trained than untrained sequences) have been reported (Wiestler & Diedrichsen, 2013; Wiestler et al., 2014). In the present study, participants physically performed all eight sequences (four to-be-trained and four untrained) before the four days of observational training. Thus, the post-training performance improvement, at least partly, could be driven by the consolidation of the initial physical performance (Censor, Sagi, & Cohen, 2012). Here we were interested solely in the observational training effects. Therefore, the sequence-specific learning, driven by observational training, was assessed as the post-training difference between trained and untrained sequences. To correct for possible pre-training differences, we followed Wiestler and Diedrichsen's (2013) approach and calculated a linear regression between the pre-training difference (predictor) and the post-training difference (outcome). The intercept of the regression line was used as a measure of the post-training difference between Trained and Untrained conditions, correcting for possible pre-training differences. The linear regression approach was used in all subsequent analyses when comparing Trained and Untrained conditions post-training.

Behavioural performance

Participants' physical performance was assessed pre- and post-training, measuring the average sequence initiation time, ET, and error rate of the four trained (to-be-trained) and the four untrained sequences.

The sequence initiation time was measured as the duration between the "go" signal and the first keypress. The sequence ET was measured as the duration between the first and fifth keypresses. The error rate was measured as the percentage of incorrect sequence executions. Incorrectly executed trials were excluded from further analysis. Attention to the task during the observational training and scanning sessions was assessed as a percentage of accurate responses to the error question.

Imaging data

Imaging data were analysed using statistical parametric mapping (SPM) v12 (Wellcome Trust Centre for Neuroimaging, London), and custom-written MATLAB scripts. To correct for head motion, all images from a single scanning session (10 x 136 volumes) were spatially realigned to the first image of the session and slice-time corrected. The anatomical T1-weighted image was co-registered to the session-mean functional image and segmented to obtain parameters for spatial normalisation. The time series of each voxel were high-pass filtered with a cut-off frequency of 1/52 Hz, to remove low-frequency trends, and modelled for temporal autocorrelation across scans with the first-order autoregressive (AR(1)) process.

For the voxel-wise univariate and functional connectivity analysis, the normalisation parameters, obtained in the segmentation step, were used to normalise pre-processed functional images to the Montreal Neurological Institute (MNI) template brain with a resolution of 2 mm^3. Normalised images were then spatially smoothed with a 3D Gaussian kernel of 8 mm full width at half maximum (FWHM). MVPA was performed without normalisation and smoothing, to preserve high spatial resolution.

All statistical maps were thresholded at a single voxel level with a significance value of $p < 0.001$ and a minimum cluster size of 10 voxels. To control for false positive results, only brain regions reaching cluster familywise error (FWE) corrected significance at $p < 0.05$ are reported. For anatomical and cytoarchitectonic localisation, we used SPM Anatomy toolbox v2.0 (Eickhoff et al., 2005).

Univariate analysis

Normalised and smoothed data were analysed using a General Linear Model (GLM). A random-effects model was implemented at two levels. At the first level, single participant data were modelled by a single design matrix for all runs within each session. The design matrix contained 6 regressors of the following events: Trained videos, Untrained videos, an 'error' video, error questions/responses, Trained cues, and Untrained cues. Trained and Untrained video regressors (further named, 'Trained' and 'Untrained') represented the 13-second video duration (showing five repetitions of a single sequence execution). All regressors were modelled as boxcar functions, convolved with a haemodynamic response function (HRF).

The following contrasts of interest were created at the first level for both pre- and post-training scanning sessions: Trained > implicit baseline; Untrained > implicit baseline; Trained ⋃ Untrained > implicit baseline. In addition, the estimated beta weights for each condition within each run were used to calculate the intercept of the linear regression line between pre-training (predictor) and post-training (outcome) difference between Trained and Untrained beta weights for each session. The intercept was used as a measure of the post-training difference in brain activity between Trained and Untrained conditions, controlling for possible pre-training differences.

The second level group analyses were designed to achieve two main objectives:

1) *Identify brain regions engaged in action observation.* Here the pre-Trained ⋃ pre-Untrained > implicit baseline contrast images for each participant were entered into a one-sample t-test analysis to obtain group average results of brain areas engaged when watching keypress sequences in general, pre-training.
2) *Identify brain regions sensitive to observational training.* Here the pre- post-difference intercept images for each participant were entered into a one-sample t-test analysis to obtain group average results of brain areas showing the post-training difference in brain activity between Trained and Untrained conditions, accounting for pre-training differences.

Region of interest (ROI) definition

Practice-related brain activity changes have been linked to changes in interactions with functionally related brain regions (McIntosh, 1998) and to more specialised skill representations in the brain (Wiestler & Diedrichsen, 2013). Thus, following from the univariate analysis, the peak voxels of significant clusters showing the post-training difference between Trained and Untrained conditions (independent of the direction) were selected for further ROI based functional connectivity and MVPA analyses (see the next two sections for the analyses details). We note that our analysis approach is not circular (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009) because the univariate analysis of post-training difference is statistically independent to all subsequent analyses.

The ROIs were defined for each participant as follows (illustrated in Figure 2.2). First, 15 mm radius spheres centred on the group level voxels with the highest t-value of the post-training difference were created in the MNI space. Second, at a participant level, voxels with the highest post-training difference value within the 15 mm radius spheres were selected as the individual's peak voxels. This approach was taken to account for anatomical and functional variability in the areas responsive to the task across participants. Third, 10 mm radius spheres centred on the individuals' identified peak voxels were created for beta weight extraction (for visualisation purposes only) and functional connectivity analysis. Fourth, the 10 mm radius spheres were mapped from the MNI space onto individual subject anatomies for MVPA analysis.

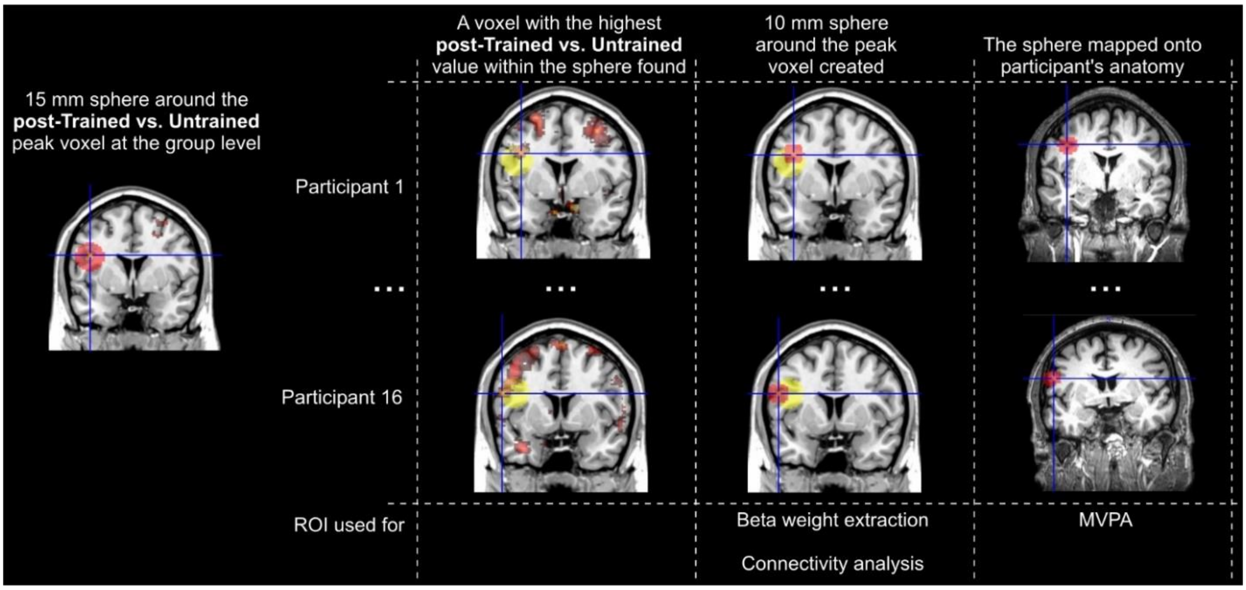


Figure 2.2. ROI definition procedure. The peak voxels of significant clusters showing the training-related brain activity changes were selected for ROI based functional connectivity and MVPA analyses. **First**, 15 mm radius spheres were created in the MNI space, centred on the group level voxels with the highest t-value of the post-training difference between Trained and Untrained conditions (independent of the direction). **Second**, at a participant level, each individual's peak voxels were identified within the group level 15 mm radius spheres. **Third**, 10 mm radius spheres centred on the identified individuals' peak voxels were created for beta weight extraction and functional connectivity analysis. **Fourth**, the 10 mm radius spheres were mapped from the MNI space onto individual subject anatomies for MVPA analysis.

Psycho-physiological interaction analysis

To identify how brain regions that are sensitive to observational training interact with other regions when watching Trained and Untrained sequences, we used a whole-brain Psycho-Physiological Interaction (PPI) analysis (Friston et al., 1997). The analysis was employed using the SPM toolbox gPPI (McLaren, Ries, Xu, & Johnson, 2012).

Subject-specific seed regions were areas that showed a significant post-training difference between Trained and Untrained conditions (see *Region of interest (ROI) definition* above). PPI models were specified at the subject-level using normalised and smoothed imaging data. First, the BOLD signal from the seed region was extracted and deconvolved to obtain an estimate of the neural activity time course in this region (Gitelman, Penny, Ashburner, & Friston, 2003). This step formed the physiological regressor. Second, each condition’s onset times were convolved with an HRF, creating psychological regressors. Third, each condition’s onset times were multiplied with the physiological regressor and then convolved with an HRF, which formed PPI regressors, representing the interaction between physiological activity and psychological context.

The regressors were then entered in a whole-brain GLM for each participant, to obtain the maps of connectivity estimates for each condition (PPI pre-Trained, PPI pre-Untrained, PPI post-Trained, and PPI post-Untrained). PPI estimates for each condition within each run were further used to obtain the post-training difference (intercept) between the Trained and Untrained conditions, correcting for possible pre-training differences.

In a second-level/group analysis, a random-effect one-sample t-test of the obtained intercept images was performed, to identify whether and where in the brain there was a stronger relationship with a seed region when watching post-Trained compared to post-Untrained (and vice versa) sequences.

Multi-voxel-pattern analysis

To test whether sequence observation is associated with sequence-specific representations, we used MVPA to analyse brain activity patterns that occur when watching the four sequences within each condition (Trained and Untrained). Note that our aim was not to discriminate between the Trained and Untrained sequences. Instead, as in the previous physical training study (Wiestler & Diedrichsen, 2013), we examined sequence-specific patterns within each condition separately and then compared the results across conditions, to determine whether the patterns are more distinct for the observationally trained sequences.

The dissimilarity between activity patterns was measured using cross-validated Mahalanobis distance (Diedrichsen, Provost, & Zareamoghaddam, 2016), which is closely related to linear discriminant analysis (LDA), and therefore termed linear discriminant contrast (LDC). In a recent study, LDC proved to be the most reliable MVPA measure, outperforming other more popular measures, such as pattern classification (LDA and support vector machine) and Pearson correlation (Walther et al., 2016).

LDC is a continuous dissimilarity measure, which includes multivariate noise normalisation (pre-whitening), cross-validation, and does not depend on activity baseline. Similar to LDA, LDC compares two conditions using a linear discriminant that has been estimated with independent data. However, instead of a binary decision, which is then converted into classification accuracy, LDC computes the mean difference between the two conditions measured along the linear discriminant. Cross-validation ensures that the measured dissimilarities are not due to the noisy data, but represent the true difference with a meaningful zero point (Diedrichsen et al., 2016; Walther et al., 2016). If the brain region differentiates between the two types of stimuli, the average cross-validated dissimilarity measure of the activity patterns should be above zero.

Here the LDC analysis was implemented using the RSA Toolbox (Nili et al., 2014) and custom-written MATLAB scripts. To obtain activity patterns for LDC analysis, a first-level GLM was estimated for each participant using the spatially realigned and slice-time corrected images, without normalisation and smoothing. A unique regressor for each of the eight sequences (four Trained, four Untrained) within each of the 10 runs was modelled as a boxcar function and convolved with an HRF. Each regressor averaged the brain activity across the two occurrences of the 13-second videos of each sequence within each run. The LDC analysis of the activity patterns was performed for each condition (Trained and Untrained) and each participant separately. The estimated beta weights of the voxels in each region (ROI or searchlight) were extracted and pre-whitened (Diedrichsen et al., 2016; Walther et al., 2016) to construct noise normalised activity patterns for each sequence within each run. As such, the input data for the LDC analysis consisted of 4 x 10 (four sequences, 10 runs) activation estimates for a set of 160 neighbouring voxels, selected by the ROI or searchlight approach (see below). Leave-one-run-out cross-validated LDC analysis was performed, and dissimilarity estimates averaged across the ten possible cross-validation folds.

Within each condition, we compared six pairs of activity patterns and averaged the resulting six measures to obtain the average dissimilarity estimate between the four sequences. An above zero dissimilarity estimate indicates that the examined region (ROI or searchlight) codes sequence-specific information.

ROI analysis

For ROI analysis, we used a random subspace approach (Diedrichsen, Wiestler, & Ejaz, 2013) to increase the reliability of LDC measures. From each ROI (see *Region of interest (ROI) definition* above), subsets of 160 voxels were randomly selected 1000 times. LDC analysis was performed on each subset, and dissimilarity estimates from all 1000 subsets were averaged to obtain the final LDC measure for each ROI and each condition: LDC pre-Trained, LDC pre-Untrained, LDC post-Trained, and LDC post-Untrained. Results were then subjected to statistical analyses. First, we estimated the average sequence-specific coding post-training. To do so, we averaged the results of LDC post-Trained and LDC post-Untrained and used a one-tailed t-test to test whether the average LDC value is above zero (indicating sequence-specific coding). Next, we assessed the post-training difference (intercept) between the conditions, correcting for the possible pre-training differences. All tests were Bonferroni-corrected for four comparisons.

Surface-based searchlight analysis

To identify brain regions coding sequence-specific information across the whole cortical surface (Kriegeskorte, Goebel, & Bandettini, 2006), we performed a surface-based searchlight analysis (Oosterhof, Wiestler, Downing, & Diedrichsen, 2011). Cortical surfaces were reconstructed from individual T1-weighted images using FreeSurfer (Dale, Fischl, & Sereno, 1999). Around each surface node, spheres of searchlights were defined and all voxels between pial and white-grey matter surface selected for analysis. The radius of each sphere was adjusted such that each searchlight contained exactly 160 voxels. The average searchlight radius was 10.37 mm.

For each searchlight, LDC analysis was performed for the four sequences within each condition as described in *ROI analysis* above. The dissimilarity estimate of each searchlight was assigned to the central voxel, constructing a surface map of dissimilarity estimates. The acquired individual subject maps (LDC pre-Trained, LDC pre-Untrained, LDC post-Trained, and LDC post-Untrained) were then normalised to the MNI template, with a resolution of 2 mm^3, and spatially smoothed, with a 3D Gaussian kernel of 4 mm FWHM.

The normalised and smoothed maps were then entered into a second-level random-effect analysis to obtain group average results of brain areas that code sequence-specific information when watching sequences pre-training and post-training (one-sample t-test of

LDC pre-Trained ∪ LDC pre-Untrained and of LDC post-Trained ∪ LDC post-Untrained), and post-training difference (intercept) between the Trained and Untrained conditions, correcting for possible pre-training differences.

2.2.6 Data sharing

Stimuli, behavioural and ROI analysis data, and code written by authors for this study are freely available at https://github.com/dcdace/E2fMRI_MVPA_PPI/. Unthresholded fMRI maps, LDC maps and group ROIs are uploaded at http://neurovault.org/collections/1892/.

2.3 Results

2.3.1 Performance improvement

After the four days of observational practice, the trained sequences were initiated and performed faster than the untrained sequences. Hence, it is plausible to assume that the acquired skill was sequence-specific and acquired through the observational practice, not just an effect of the sequence execution at pre-test when both trained and untrained sequences were physically performed.

Post-training, sequence initiation time for the trained sequences (M = 600 ms, within-subject (Cousineau, 2005) 95% CI (2.13 x SE for df = 15) [526 ms, 674 ms]) was significantly faster than for the untrained sequences (M = 684 ms, within-subject 95% CI [612, 756]), $t_{14} = 2.238$, $p = 0.042$, $d_z = 0.56$, $B_0 = -84$ ms, 95% CI [-165, -4] (Figure 2.3A). ET for the trained sequences (M = 1338 ms, within-subject 95% CI [1215 ms, 1461 ms]) was significantly faster than for the untrained sequences (M = 1464 ms, within-subject 95% CI [1365, 1562]), $t_{14} = 3.495$, $p = 0.004$, $d_z = 0.87$, $B_0 = -115$ ms, 95% CI [-185, -45] (Figure 2.3B). Error rate did not differ between the two conditions (post-Trained M = 12%, within-subject 95% CI [7, 18]; post-Untrained M = 13%, within-subject 95% CI [9, 18]), $t_{14} = 0.319$, $p = 0.754$, $d_z = 0.08$, $B_0 = -0.6\%$, 95% CI [-5, 4] (Figure 2.3C).

During the observational practice and scanning sessions, attention to the task was assessed by accurate responses to the error question. The mean accuracy across the four training days was 87%, 95% CI [81%, 93%]. On average, accuracy improved across the four training days (Figure 2.3D), but the difference was not significant, as measured by a 4-way repeated-measures analysis of variance, $F_{3,42} = 1.076$, $p = 0.370$. The average accuracy during the scanning sessions was 69%, 95% CI [58%, 80%], with no significant difference between the two sessions, $t_{15} = 0.786$, $p = 0.444$, $d_z = 0.20$. The difference between the accuracy of trained and untrained conditions in the scanning sessions was not measured.

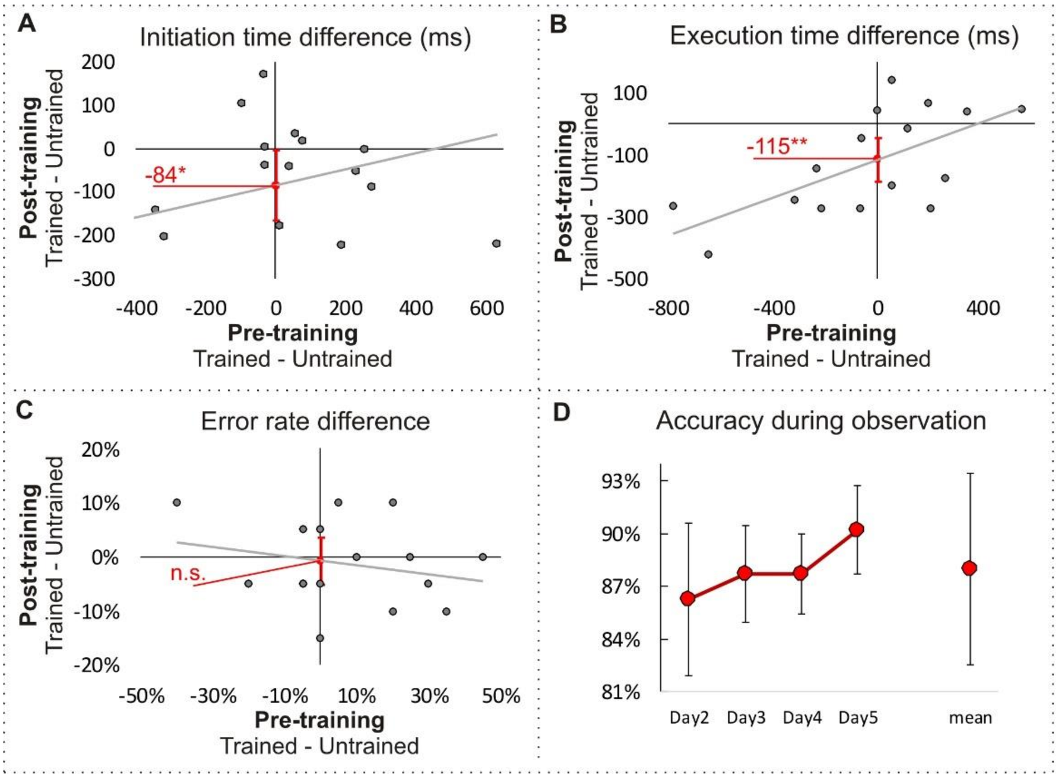


Figure 2.3. Behavioural results. A., **B.** and **C.** Pre- and post-training difference in initiation time, ET and error rate between trained and untrained sequences. The training effect was measured as the intercept of the regression line between the pre-training difference (predictor) and the post-training difference (outcome). The intercept represents the predicted post-training difference if the pre-training difference is zero. This method reduces the noise of unwanted differences in the difficulty of trained and untrained sequences and thus allows a more accurate measurement of the training effect. Error bars represent 95% CI (2.13 x SE for df = 15) of the intercept. * $p < 0.05$, ** $p < 0.01$, n.s.: non-significant at $p < 0.05$. **D.** Group-averaged accuracy in response to the error question during observational training. Error bars represent within-subject (Cousineau, 2005) 95% CI (2.13 x SE for df = 15).

2.3.2 Frontoparietal activation during action observation

To identify brain regions engaged when watching sequences in general, we assessed a group average of pre-Trained ∪ pre-Untrained > implicit baseline contrast. Brain regions emerging from this contrast included bilateral superior and inferior parietal lobules, intraparietal sulci, dorsal premotor cortices (including supplementary motor area), hippocampi, and left ventral premotor cortex. A list of the major peaks of activated clusters is given in Table 2.1 and all activated areas visualised in Figure 2.4A. Brain activity maps of Trained and Untrained conditions pre- and post-training are visualised in Figure 2.4B.

Apart from no activation in the primary motor areas, the activated areas were closely similar to those reported in the physical practice study by Wiestler and Diedrichsen (2013) on which our study was based. Overall, the activated frontoparietal regions correspond to the largely bilateral action observation network (Caspers, Zilles, Laird, & Eickhoff, 2010; Cross et al., 2009).

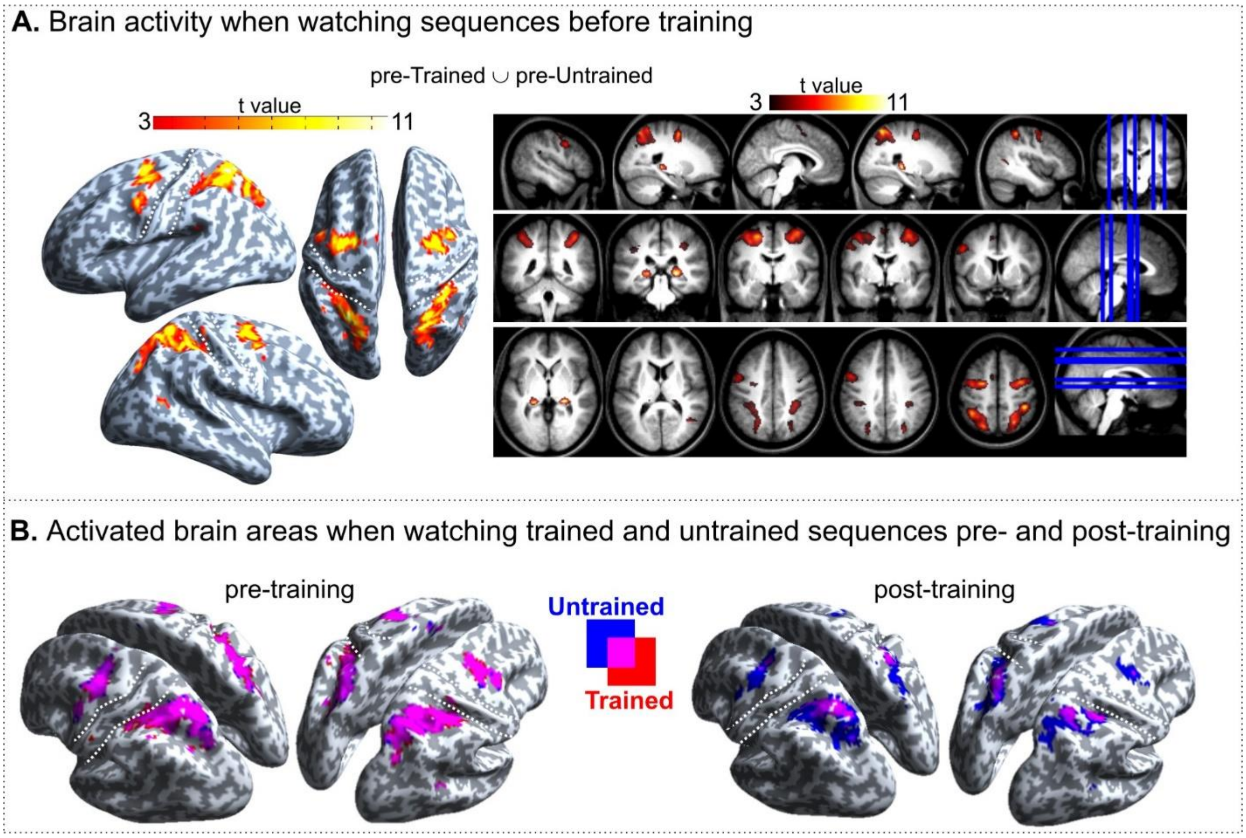


Figure 2.4. Univariate results, reported at $p < 0.001$(uncorrected), $k = 10$. White dotted lines mark central and postcentral sulci. **A.** Activated brain regions when watching sequences before the training (pre-Trained ∪ pre-Untrained > implicit baseline). Statistical map overlaid on inflated standard MNI cortical surface (SPM12) and a group-average T1-weighted image in MNI template space. Clusters with cluster FWE-corrected significance at $p < 0.05$ reported in Table 2.1. **B.** Brain activity maps of Trained (red) and Untrained (blue) conditions pre- and post-training. Statistical maps overlaid on inflated standard MNI cortical surface (SPM12).

Table 2.1. Activated brain regions when watching sequences before the training (pre-Trained ∪ pre-Untrained > implicit baseline), as shown in Figure 2.4A.

Anatomical location	**Cytoarchitectonic location**	**Peak MNI coordinates x y z**	**Cluster level voxels**	**$P_{FWE\text{-}corr}$**	**Voxel-level $P_{FWE\text{-}corr}$**	**t_{15}**
L Superior parietal lobule	7PC	-30 -56 60	1845	< 0.001	0.001	11.48
L Superior parietal lobule	7A	-20 -70 56			0.010	9.21
L Intraparietal sulcus	hIP3	-36 -50 54			0.014	8.98
R Inferior parietal lobule	Area 2	40 -40 54	1702	< 0.001	0.002	10.61
R Superior parietal lobule	7A	24 -64 58			0.003	10.19
R Intraparietal sulcus	hIP3	26 -56 58			0.010	9.17
L dPM, Superior frontal gyrus		-20 -6 54	1261	< 0.010	0.008	9.38
L vPM, Precentral gyrus		-32 -8 48			0.051	7.90
L vPM, Precentral gyrus	Area 44	-48 4 38			0.117	7.19
R dPM, Middle frontal gyrus		34 -4 54	759	< 0.001	0.013	9.00
R Hippocampus		22 -32 0	179	0.010	0.000	12.50
L Hippocampus		-22 -34 0	123	0.046	0.002	10.58

Results thresholded at a single voxel level, $p < 0.001$, $k = 10$ voxels. Only clusters with cluster FWE-corrected significance at $p < 0.05$ are shown, and up to three local maxima when a cluster has multiple peaks more than 8 mm apart.
L, left; R, right; IPS, intraparietal sulcus; dPM, dorsal premotor cortex; vPM, ventral premotor cortex.

2.3.3 Frontoparietal activity decrease

After the four days of observational practice, multiple brain regions showed reduced brain activity when watching trained compared to untrained sequences. No regions with higher activity for trained compared to untrained were found (as in Wiestler & Diedrichsen, 2013). Reduced activity when watching trained sequences included clusters in the right superior parietal lobule (extending across right precuneus and left superior and inferior parietal lobules), bilateral dorsal premotor cortices, and left ventral premotor cortex (see Table 2.2 and Figure 2.6A).

Decreased activity may indicate more efficient neural recruitment resulting from a strengthened functional coupling with other involved brain areas and/or more specialised representations of the trained sequences. To investigate this further, we selected the four peak regions (see Table 2.2) for PPI and MVPA analyses.

Table 2.2. Brain regions showing lower activity for trained compared to untrained sequences post-training, as shown in Figure 2.6A. The opposite (post-Trained > post-Untrained) did not result in any significant areas.

		Peak MNI coordinates	**Cluster level**		**Voxel-level**	
Anatomical location	**Cytoarchitectonic location**	**x y z**	**voxels**	$\mathbf{P_{FWE\text{-}corr}}$	$\mathbf{P_{FWE\text{-}corr}}$	$\mathbf{t_{14}}$
R Superior parietal lobule	7A	22 -68 56	1710	< 0.001	0.007	9.43
R Precuneus		10 -58 48			0.068	7.86
L Intraparietal sulcus	hIP3	-28 -50 40			0.210	7.16
R dPM, Superior frontal gyrus		30 -4 58	610	< 0.001	0.049	8.07
R dPM, Precentral gyrus		28 -6 50			0.066	7.88
R dPM, Posterior-medial frontal cortex		16 -4 62			0.979	5.09
L vPM, Inferior frontal gyrus (opercularis)	Area 44	-44 2 24	372	< 0.001	0.708	5.94
L vPM, Inferior frontal gyrus (opercularis)	Area 44	-56 8 10			0.891	5.50
L vPM, Precentral gyrus	Area 44	-50 6 20			0.958	5.24
L dPM, Superior frontal gyrus		-24 -4 60	321	< 0.001	0.044	8.14
L dPM, Middle frontal gyrus		-24 -6 50			0.814	5.71
L dPM, Middle frontal gyrus		-12 -4 58			0.994	4.88

Results thresholded at a single voxel level, p < 0.001, k = 10 voxels. Only clusters with cluster FWE-corrected significance at p < 0.05 are shown, and up to three local maxima when a cluster has multiple peaks more than 8 mm apart.
L, left; R, right; IPS, intraparietal sulcus; dPM, dorsal premotor cortex; vPM, ventral premotor cortex.

2.3.4 PPI results: Strengthened coupling with a contralateral parietal operculum

We used PPI analysis to investigate how the four ROIs that showed lower brain activity for trained compared to untrained sequences (see Table 2.2, Figure 2.6A and *2.2.5 Data analysis-Region of interest (ROI) definition*) interact with other brain regions when watching trained versus untrained (and vice versa) sequences post-training.

No regions showed higher functional connectivity with any of the four ROIs when watching post-Untrained compared to post-Trained sequences. When watching post-Trained compared to post-Untrained sequences, right superior parietal lobule, right dorsal premotor cortex, and left ventral premotor cortex showed increased functional connectivity with a contralateral parietal operculum (OP4; see Table 2.3 and Figure 2.6C).

Table 2.3. Brain regions showing increased functional connectivity with right SPL, right dPM, left vPM, and left dPM when watching post-Trained vs post-Untrained sequences (visualised in Figure 2.6C).

		Peak MNI coordinates	**Cluster level**		**Voxel-level**	
Anatomical location	**Cytoarchitectonic location**	**x y z**	**voxels**	**$p_{FWE\text{-}corr}$**	**$p_{FWE\text{-}corr}$**	**t_{14}**
Seed region: R SPL						
L Parietal operculum	OP4	-48 -16 12	83	0.002	0.994	5.20
L Parietal operculum	OP4	-58 -14 10			1	4.61
Seed region: R dPM						
L Parietal operculum	OP4	-48 -16 10	105	0.001	0.849	5.93
L Parietal operculum	OP1	-46 -24 10			1	4.63
L Parietal operculum	OP1	-54 -24 6			1	4.33
Seed region: L vPM						
R Parietal operculum	OP4	48 -6 16	68	0.004	0.468	6.68
R Parietal operculum	3a	44 -12 26			1	4.45
R Parietal operculum		52 -14 20			1	3.97
Seed region: L dPM						
-	-	-	-	-	-	-

Results thresholded at a single voxel level, $p < 0.001$, $k = 10$ voxels. Only clusters with cluster FWE-corrected significance at $p < 0.05$ are shown, and up to three local maxima when a cluster has multiple peaks more than 8 mm apart.
L, left; R, right; SPL, Superior parietal lobule; dPM, dorsal premotor cortex; vPM, ventral premotor cortex.

2.3.5 MVPA results: Sequence-specific representations of observed actions

LDC analysis was used to test whether a particular brain region (ROI or searchlight) codes sequence-specific information and whether the coding is more specialised for trained compared to untrained conditions. The average dissimilarity (LDC value) of activity patterns between the four sequences within each condition was used as a measure of sequence-specific representations.

ROI results

To test whether changes in brain activity could indicate more efficient neural recruitment resulting from more specialised sequence-specific representations of the trained sequences, we evaluated the four ROIs, that showed lower brain activity for trained compared to untrained sequence (see Table 2.2, Figure 2.6A and *2.2.5 Data analysis-Region of interest (ROI) definition*). Each ROI contained approximately 325 (SD = 48.83) voxels.

On average across Trained and Untrained conditions post-training, sequence-specific coding was found in the right superior parietal lobule, left ventral premotor cortex, and left dorsal premotor cortex, but not in the right dorsal premotor cortex. None of the ROIs showed a difference between the Trained and Untrained conditions. Detailed results are presented in Table 2.4 and plotted in Figure 2.6B.

Table 2.4. Sequence-specific coding in ROIs (visualised in Figure 2.6B).

ROI	Mean LDC [95% CI], One-sample, one-tailed t-test	Post-Trained > Post-Untrained
R SPL	Pre: 0.68 [0.15, 1.21], $t_{(15)} = 2.7$, $p = 0.033$, $d_z = 0.68$ Post: 0.42 [0.17, 0.66], $t_{(15)} = 3.08$, $p = 0.015$, $d_z = 0.77$	$B_0 = 0.41$, 95% CI [-0.22, 1.05], n.s.
R dPM	Pre: 0.35 [0.1, 0.6], $t_{(15)} = 2.91$, $p = 0.021$, $d_z = 0.73$ Post: 0.04 [-0.16, 0.25], n.s.	$B_0 = -0.04$, 95% CI [-0.64, 0.57], n.s.
L vPM	Pre: -0.05 [-0.3, 0.2], n.s. Post: 0.29 [0.11, 0.48], $t_{(15)} = 2.59$, $p = 0.041$, $d_z = 0.65$	$B_0 = 0.22$, 95% CI [-0.26, 0.70], n.s.
L dPM	Pre: 0.24 [-0.1, 0.58], n.s. Post: 0.35 [0.10, 0.63], $t_{(15)} = 2.69$, $p = 0.034$, $d_z = 0.67$	$B_0 = -0.14$, 95% CI [-0.66, 0.39], n.s.

LDC, Linear discriminant contrast; L, left; R, right; SPL, Superior parietal lobule; dPM, dorsal premotor cortex; vPM, ventral premotor cortex; n.s., non-significant.

Surface-based searchlight results

To further explore sequence-specific coding across the whole cortical surface, we ran surface-based searchlight analysis for each condition (the resulting t-maps, are shown in Figure 2.5A&B, right panel).

First, we were interested where in the brain keypress sequence observation is associated with sequence-specific representations. Pre-training (averaged across pre-Trained and pre-Untrained conditions), sequence-specific representations were found in the right anterior intraparietal sulcus and posterior superior parietal lobule (see Table 2.5 and Figure 2.5A). Post-training (averaged across post-Trained and post-Untrained conditions), sequence-specific representations were found in bilateral supramarginal gyri, anterior intraparietal sulci (homologous to macaque AIP; Culham, Cavina-Pratesi, & Singhal, 2006), left anterior superior parietal lobule, left primary motor and somatosensory cortices, and right parietal operculum (see Table 2.5 and Figure 2.5B).

Next, we investigated observational practice effects on sequence-specific representations by a map-wise analysis of a post-training difference (intercept) between the Trained and Untrained conditions, correcting for possible pre-training differences. No regions showed difference between the two conditions at a cluster FWE-corrected threshold of $p < 0.05$.

Finally, we inspected the sequence-specific representations globally averaging over all involved cortical regions. The average LDC measure of the post-Trained sequences was higher than of the post-Untrained sequences, however the difference was not significant, $t_{14} = 1.128$, $p = 0.278$, $d_z = 0.28$, $B_0 = 0.155$, 95% CI [-0.139, 0.449] (Figure 2.5C). Similarly, the average cortical surface area coding sequence-specific representations of the post-Trained sequences was larger than of the post-Untrained, but the difference was not significant, $t_{14} = 1.935$, $p = 0.073$, $d_z = 0.48$, $B_0 = 0.34\ cm^2$, 95% CI [-0.035, 0.715] (Figure 2.5D).

Although the present study focused on observational practice effects on sequence-specific, not general skill, learning, here we thought to explore how the sequence-specific representations change from pre- to post-training, by assessing a Day (pre-training, post-training) * Type (Trained, Untrained) interaction of the average LDC and cortical surface area coding sequence-specific representations (Figure 2.5C&D). There was no significant Day*Type interaction for the LDC ($F_{1,15} = 1.435$, $p = 0.250$), but there was a significant Day*Type interaction for the average cortical surface area coding sequence-specific representations ($F_{1,15} = 4.874$, $p = 0.043$). A post hoc paired sample t-test revealed a significant increase in the cortical area coding sequence-specific representations from pre- to post-training for the Trained sequences ($M = 0.54$ cm^2 95% CI [0.05, 1.03], $t_{15} = 2.36$, $p = 0.032$, $d_z = 0.59$).

Table 2.5. Brain regions showing sequence-specific coding for post-Trained + post-Untrained conditions, shown in Figure 2.5A.

Anatomical location	Cytoarchitectonic location	Peak MNI coordinates x y z	Cluster level voxels	 $P_{FWE-corr}$	Voxel-level $P_{FWE-corr}$	 t_{15}	Average LDC
Pre-training							
R Intraparietal sulcus	hIP3	22 -62 58	453	< 0.001	0.543	5.88	0.95
R Superior parietal lobule	7A	20 -68 50			0.590	5.79	1.02
R Superior parietal lobule		20 -56 48			0.914	5.04	0.52
Post-training							
L Supramarginal gyrus	PFop	-56 -26 22	269	0.001	0.377	6.32	0.82
L Supramarginal gyrus	PFt	-56 -24 32			0.949	4.96	0.74
L Supramarginal gyrus	PFt	-66 -26 38			0.995	4.53	0.30
L M1, Precentral gyrus	4a	-50 -10 42	157	0.020	0.170	7.04	0.77
L M1, Postcentral gyrus	4p	-42 -8 34			0.849	5.29	0.32
L S1, Postcentral gyrus	3b	-46 -16 48			0.994	4.57	0.88
R Intraparietal sulcus	hIP2	48 -38 42	145	0.029	0.971	4.83	0.96
R Supramarginal gyrus	PF	58 -40 30			0.997	4.46	0.74
R Inferior parietal lobule	Area 2	48 -36 52			1.000	4.24	0.71
L Intraparietal sulcus	hIP2	-46 -48 54	143	0.030	0.907	5.12	0.92
L Superior parietal lobule	5L	-32 -42 46			0.970	4.48	0.55
R Parietal operculum	OP4	58 -8 12	134	0.039	0.874	5.22	0.70

Results thresholded at a single voxel level, $p < 0.001$, $k = 10$ voxels. Only clusters with cluster FWE-corrected significance at $p < 0.05$ are shown, and up to three local maxima when a cluster has multiple peaks more than 8 mm apart.
L, left; R, right; M1, Primary motor cortex; S1, Primary somatosensory cortex; S2, Secondary somatosensory cortex; IPL, Inferior parietal lobule; IPS, Intraparietal sulcus; SPL, Superior parietal lobule.

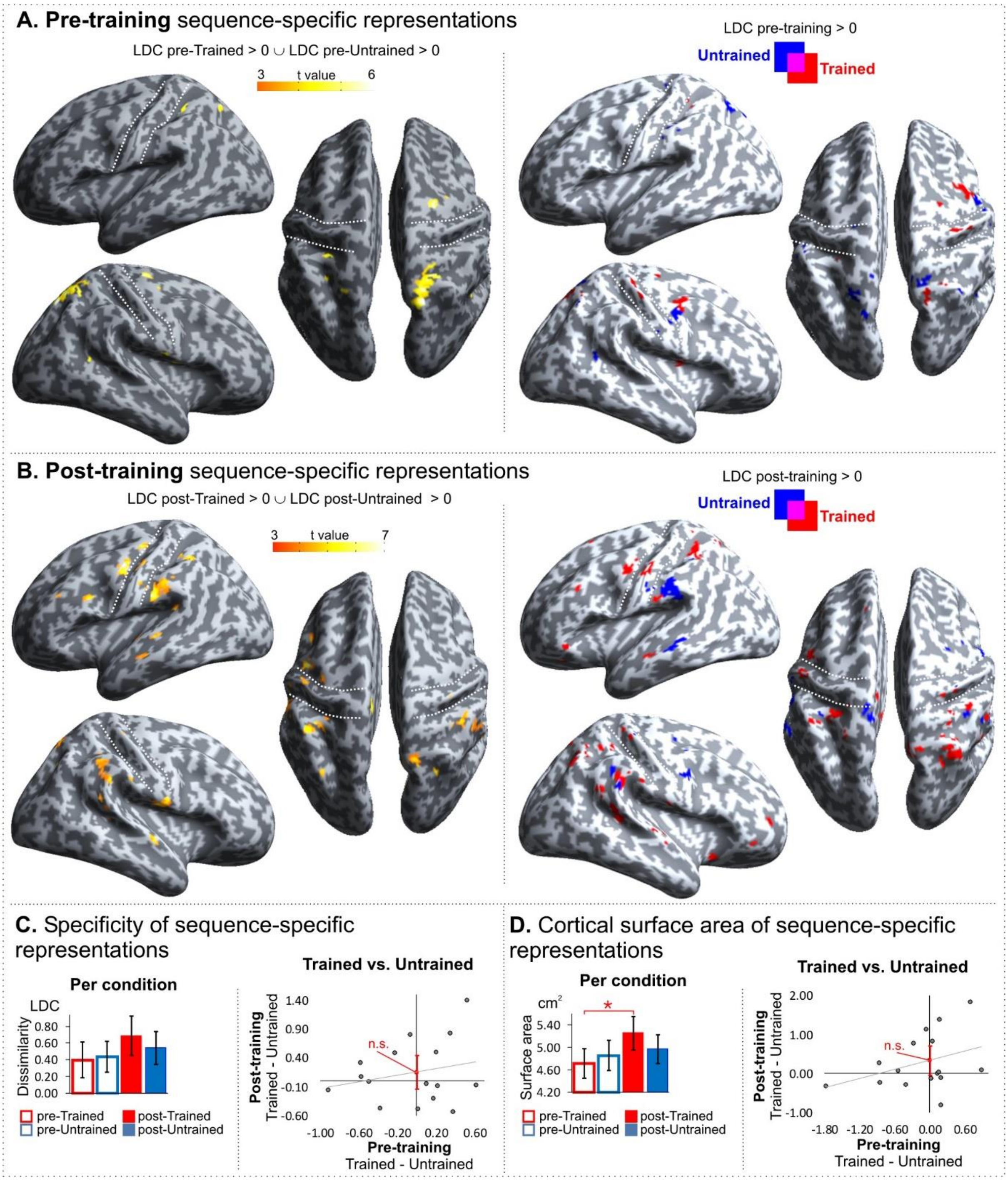


Figure 2.5. Surface-based searchlight results, reported at $p < 0.001$ (uncorrected), k = 10. Clusters with cluster FWE-corrected significance at $p < 0.05$ reported in Table 2.5. Statistical maps overlaid on inflated standard MNI cortical surface (SPM12). White dotted lines mark central and postcentral sulci. **A.** Pre-training sequence-specific representations. **B.** Post-training sequence-specific representations. **C.** and **D.** Specificity (the average LDC measure) of sequence-specific representations and the cortical surface area coding sequence-specific representations averaged over all involved cortical regions per condition (left; Error bars represent within-subject 95% confidence intervals (Cousineau, 2005); * $p < 0.05$) and pre- and post-training difference (right; Error bars represent 95% CI of the intercept n.s.: non-significant at $p < 0.05$).

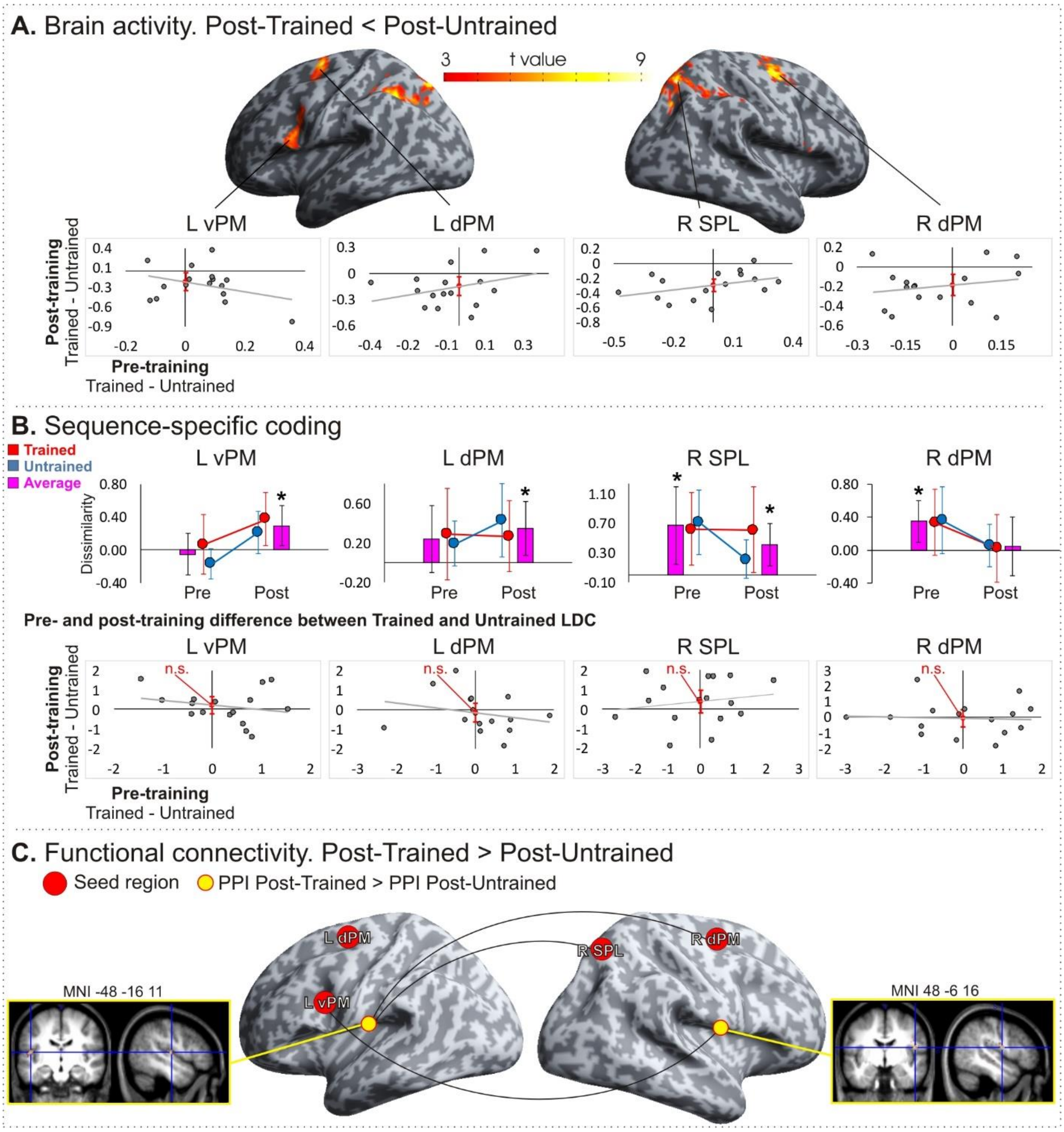


Figure 2.6. ROI analysis results. L, left; R, right; vPM, ventral premotor cortex; dPM, dorsal premotor cortex; SPL; superior parietal lobule. **A.** Univariate results of post-training difference (intercept) between Trained and Untrained conditions. Statistical map overlaid on inflated standard MNI cortical surface (SPM12) and reported at $p < 0.001$ (uncorrected), k = 10; clusters with cluster FWE-corrected significance at $p < 0.05$ reported in Table 2.2. Plots illustrate pre- and post-training difference in beta weights between Trained and Untrained conditions in the four significant regions selected for further ROI analyses (see *2.2.5 Data analysis-Region of interest (ROI) definition*). Error bars represent 95% CI of the intercept. **B.** Top panel: MVPA results of sequence-specific coding pre- and post-training in the four ROIs, showing dissimilarity estimate (average LDC value) between the sequences within the Trained and Untrained conditions and across both conditions on average (reported in Table 2.4). Error bars represent within-subject 95% confidence intervals (Cousineau, 2005); * $p < 0.05$. Bottom panel: Pre- and post-training difference between Trained and Untrained LDC. Error bars represent 95% CI of the intercept; n.s. – non-significant. **C.** PPI results, showing the four seed regions and regions with increased functional connectivity with the particular seed region when watching Trained compared to Untrained sequences post-training (reported in Table 2.3).

2.4 Discussion

The results of this study show practice-related behavioural performance improvement (Aim 1, see *2.1 Introduction*), brain activity decrease (Aim 2), and functional connectivity increase (Aim 3). Furthermore, for the first time, our results demonstrate that neural representations of observed actions are highly specialised (Aim 4). A mere observation of kinematically matched keypresses evokes distinguishable keypress-sequence-specific activity patterns in frontoparietal brain regions. While it would be plausible to explain practice-related results by more specialised representations of the observationally trained actions (Aim 5), our study does not support this reasoning. We discuss our results in the light of previous literature and present possible explanations of why we did not find more distinct representations of the trained actions.

2.4.1 Observational practice facilitates motor skill learning

Our results showed that after the four days of observational practice, the trained sequences were initiated and performed faster than the untrained sequences. This finding contributes to the evidence that motor skills, including keypress sequences, can be learned by observation without overt physical practice (Bird & Heyes, 2005; Heyes & Foster, 2002; Lago-Rodríguez & Cheeran, 2014; Vogt & Thomaschke, 2007). Although not controlled for in the present study, previous reports show that motor sequence performance improvement cannot be explained solely by memorising the digit sequence or by the familiarity with the spatiotemporal pattern of the sequence obtained by stimulus observation. Instead, observing the actual action contributes to performance improvement (Boutin et al., 2010; Van Der Werf, Van Der Helm, Schoonheim, Ridderikhoff, & Van Someren, 2009). Substantial evidence suggests that the shared neural mechanisms between action perception and execution (Gentsch et al., 2016; Rizzolatti et al., 2014) make the motor skill learning by observation possible (Brass & Heyes, 2005; Jeannerod, 1994; Mattar & Gribble, 2005; Vogt, 1996).

2.4.2 Practice-related brain activity decrease and functional connectivity increase imply more efficient neural processing

We found that keypress sequence observation engaged premotor and parietal brain regions (occipital cortex was not included in the analysis). Furthermore, brain activity (BOLD response) in these regions reduced when watching trained compared to untrained sequences.

Reduced activity was specifically found in the right superior parietal lobule, left ventral premotor cortex, and bilateral dorsal premotor cortices. These regions are part of a frontoparietal network involved in a wide range of processes, including working memory, attention, and mental imagery (Ikkai & Curtis, 2011; Lückmann, Jacobs, & Sack, 2014; Rottschy et al., 2012), as well as action observation and execution (Caspers et al., 2010; Gazzola & Keysers, 2009; Molenberghs et al., 2012; Oosterhof, Tipper, & Downing, 2013; Rizzolatti & Sinigaglia, 2010).

Reduced activity in frontoparietal brain regions may reflect lower cognitive demand (Culham, Cavanagh, & Kanwisher, 2001; Lu et al., 2016; Maximo, Neupane, Saxena, Joseph, & Kana, 2016) when watching the trained sequences. Reduced cognitive demand is a typical consequence of skill learning when initial effortful performance shifts towards automaticity (Fitts & Postner, 1967; Kelly & Garavan, 2005). The transition to automaticity coincides with decreased brain activity in attention-related regions and more efficient neural processing in task-specific regions (Floyer-Lea & Matthews, 2004; Kelly & Garavan, 2005; Poldrack et al., 2005). Such changes are reported for both cognitive and motor skill learning and have been suggested as a marker of training-related gains (Patel, Spreng, & Turner, 2013).

In our study, the task during the scanning sessions involved holding in working memory the five-digit sequence, visual discrimination (was the correct sequence executed?), and motor learning of the observed sequence. Consequently, lower cognitive demand, due to practice, should lead to increased neural efficiency in the task-specific (visual discrimination and motor processing) regions and thus improve task performance. We did not compare the accuracy of responses to the error question between trained and untrained conditions during the scanning sessions. However, improved action discrimination, following observational practice, has been reported before (Black & Wright, 2000; Lago-Rodriguez, Lopez-Alonso, & Fernández-del-Olmo, 2013; Maslovat et al., 2010b). It is acknowledged that observational practice facilitates both action discrimination and motor learning (for a review, see Lago-Rodríguez & Cheeran, 2014). Our behavioural results confirmed the motor performance improvement.

Moreover, three of the four brain regions that showed practice-related activity decrease also showed stronger coupling with a contralateral parietal operculum when watching trained compared to untrained sequences. Decreased activity and strengthened connectivity with the parietal operculum may indicate enhanced higher-order sensory-motor processing during sequence observation and possibly contribute to the motor learning.

Several studies have reported an association between decreased activity and increased connectivity within task-specific brain regions following practice (Büchel, Coull, & Friston, 1999; Keller & Just, 2016; McIntosh, Rajah, & Lobaugh, 1999; Wu, Chan, & Hallett, 2008). It is interpreted as a more efficient neural processing to achieve the task (Kelly & Garavan, 2005). Parietal operculum, the location of the secondary somatosensory area, is a highly heterogeneous brain region that plays an important role in sensory-motor integration and motor control (Cattaneo, Maule, Tabarelli, Brochier, & Barchiesi, 2015; Eickhoff et al., 2010; Maule, Barchiesi, Brochier, & Cattaneo, 2015). It stores high-level (often, goal-related and modality independent) action information that is transferred to lower-level motor areas once the action is implemented (Cattaneo et al., 2015; Dijkerman & de Haan, 2007; Fiehler, Engel, & Rösler, 2007; Maule et al., 2015; Taoka, Tanaka, Hihara, Ojima, & Iriki, 2013). Furthermore, it contains neurons with bilateral receptive fields and connections (Ruben et al., 2001; Taoka et al., 2013), which might explain why we see strengthened coupling with the contralateral area.

Overall, the performance improvement, frontoparietal activity decrease, and strengthened coupling with the secondary somatosensory area indicate greater neural efficiency for the trained sequences. Increased neural efficiency could be related to more established internal representations of the trained sequences, as reported in the previous physical practice study by Wiestler and Diedrichsen (2013). The specialised representations would reduce the planning and preparation time required to initiate and execute the action (Diedrichsen & Kornysheva, 2015), as was demonstrated by our post-training performance results.

2.4.3 Movement-sequence-specific representations of observed actions

Here, for the first time, we investigated whether neural representations of observed actions discriminate between the sequential order of movements and whether the representations become more specialised with observational practice. Our results revealed multiple, predominantly parietal, brain regions that were sensitive to the sequential order of observed keypresses. Before the training, sequence-specific representations were found in the right superior parietal area, the region involved in spatial encoding (Fogassi & Luppino, 2005; Gallivan & Culham, 2015). After the four days of practice, sequence-specific representations (averaged across trained and untrained sequences) were found in the anterior inferior parietal lobule (aIPL), including bilateral supramarginal gyri and anterior intraparietal sulci, as well as right parietal operculum, and left primary motor and sensorimotor cortices. To a lesser extent (revealed by ROI, but not searchlight analysis) sequence-specific representations were also found in the left ventral and dorsal premotor cortices and right superior parietal lobule. The brain areas with sequence-specific representations in the present observational practice study largely overlap with the areas reported in the physical practice study by Wiestler and Diedrichsen (20013). However, in addition to the premotor and parietal areas, Wiestler and Diedrichsen also reported sequence-specific representations in the right primary motor cortex and supplementary and pre-supplementary motor areas.

In terms of sequential processing in general, it is recognised that behavioural sequences are controlled by central plans that combine multiple discrete movements into single action units or chunks (Dehaene, Meyniel, Wacongne, Wang, & Pallier, 2015; Lashley, 1951; Rhodes et al., 2004; Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007). The unified structure of a movement sequence is pre-programmed before the execution to ensure that movements are carried out without interruptions as coherent, fluent behaviour (Abrahamse et al., 2013; Averbeck, Chafee, Crowe, & Georgopoulos, 2002; Baldauf, 2011; Baldauf, Wolf, & Deubel, 2006; Baldauf, Cui, & Andersen, 2008; Halford, Wilson, & Phillips, 1998; Keele et al., 1995; Sakai et al., 2004). The aIPL plays a crucial role in chunking and encoding the abstract unified spatiotemporal structures of performed movement sequences (Grafton et al., 1998; Jubault, Ody, & Koechlin, 2007; Wymbs, Bassett, Mucha, Porter, & Grafton, 2012). Furthermore, the aIPL encodes overarching action plans or goals of planned and performed (Fogassi et al., 2005; Gallivan, McLean, Valyear, & Culham, 2013; Króliczak, Piper, & Frey, 2016; Valyear & Frey, 2015), as well as observed (Dinstein et al., 2008; Grafton & Hamilton, 2007; Jastorff et al., 2010; Oosterhof et al., 2010; Peeters et al., 2009; Ramsey & Hamilton, 2010) actions. Such an overarching representation of an abstract unified action structure is kept active throughout the action duration to monitor its correct implementation (Bonini et al., 2011; Hamilton & Grafton, 2006; Jubault et al., 2007; Rizzolatti et al., 2014). Damage in the aIPL impairs the ability to produce coherent, purposeful actions (apraxia; Bieńkiewicz, Brandi, Goldenberg, Hughes, & Hermsdörfer, 2014), as well as recognising actions produced by others (Buxbaum, Kyle, & Menon, 2005; Rothi, Heilman, & Watson, 1985), and action imagination (Sirigu et al., 1996).

The ventral premotor cortex has strong connections with the aIPL (Rizzolatti et al., 2014) and is also involved in sequence chunking and encoding (Alamia et al., 2016; Koechlin & Jubault, 2006; Wymbs et al., 2012). However, it may encode more concrete, lower-level action features (Cook & Bird, 2013; Wurm & Lingnau, 2015), and the hierarchical rather than temporal structure of sequences (Koechlin & Jubault, 2006; but see Kornysheva & Diedrichsen, 2014). Likewise, dorsal premotor regions encode goal-related abstract action representations (Cisek, Crammond, & Kalaska, 2003; Gallivan et al., 2013; Shen & Alexander, 1997; Wiestler et al., 2014).

In line with the above reports, sequence-specific activity patterns in the aIPL and premotor regions suggest that the observed keypress sequences were encoded as abstract spatiotemporal structures of unified actions. Noteworthy, the sequence-specific representations in the aIPL were not found before the training. There are at least three complementary explanations for this finding.

First, it is possible that before the training, when participants had the first visual experience with the presented keypress videos, sequence-specific representations mainly reflected spatial processing of movement features. Perhaps general familiarity with the task was necessary to perceive the movements as more meaningful, unified actions. This reasoning is in agreement with the view that motor representations of the perceived actions are evoked only if the particular action is in the observer’s own motor repertoire (Giese & Rizzolatti, 2015), otherwise action perception is based on visual analysis of the action elements (Buccino et al., 2004). Second, it is possible that the average of trained and untrained post-training sequence-specific representations reported here was mainly driven by the trained sequences and reflect practice-related effect. Third, a generalisation of learning to the untrained sequences is probable, particularly as many movement pairs were shared between trained and untrained sequences. These explanations also apply to the post-training, but not pre-training, sequence-specific representations found in the right parietal operculum. The right parietal operculum has been implicated in the memory storage and retrieval of movement sequence representations and planned actions (Jubault et al., 2007; Valyear & Frey, 2015). This corresponds to our results that some experience with the sequences was needed to form the sequence-specific and likely memory-related representations in this area.

Post-training, but not pre-training, sequence-specific representations were also found in the left (ipsilateral to the model’s hand) primary motor and sensorimotor cortices, lateral from the traditional hand area (Yousry et al., 1997). The sequential representations in this area may reflect subvocal rehearsal of number strings. This possibility was also recognised in the previous studies on sequence-specific representations of performed actions (Kornysheva & Diedrichsen, 2014; Wiestler & Diedrichsen, 2013; Wiestler et al., 2014). However, it is not clear why such representations would not also be encoded during the first scanning session.

Overall, post-training the average cortical area that showed sequence-specific activity patterns was larger than pre-training, and the difference was significant for the trained sequences. Likewise, the average dissimilarity between sequence activity patterns increased from pre- to post-training; however, the increase was not significant. As said before, pre- to post-training differences may reflect general familiarity with the task or training effects that generalise to untrained sequences. Future studies should investigate these possibilities more thoroughly. Though, the focus of the present study was not the general skill learning (pre- to post-training difference), but the sequence-specific learning. Specifically, we were interested whether at post-training the representations of the trained sequences are more specialised than for the untrained sequences. Previous action execution studies have associated more specialised movement sequence representations with better performance (Averbeck et al., 2002; Wiestler & Diedrichsen, 2013).

However, our results did not show any significant differences between the specificity of trained and untrained sequence representations at post-training. Several complementary explanations are possible. First, possibly there was not enough statistical power to detect subtle differences in the specificity of trained compared to untrained sequence representations. Perhaps, the internal representations of observed, compared to executed sequences, are less distinct in general and differences between trained and untrained sequence representations are subtler and more difficult to detect. Second, the more specialised representations of the trained sequences might emerge when performing the action. Thus, future studies should investigate the observational practice effects on sequence-specific representations of performed actions. Third, it is possible that brain areas with more specialised representations of observed sequences were not covered with our analysis. For example, cerebellum and basal ganglia play an important role in motor learning both by physical (Doyon et al., 2009) and observational (Frey & Gerry, 2006; Torriero et al., 2011) practice.

2.4.4 Conclusions

To our knowledge, the present study is the first to report highly specialised, movement-sequence-specific neural representations of observed actions. Such representations are particularly encoded at an abstract level of motor hierarchy which is likely shared with planning one’s own actions (Prinz, 1997). The highly specialised neural representations of observed actions highlight the effectiveness of observers’ own motor program engagement during action observation. The present study confirms that observational practice facilitates motor skill learning. As with physical practice, observational practice leads to decreased activity and increased connectivity within task-specific brain regions, implying more efficient neural processing to accomplish the task. It would be plausible to explain the practice-related performance and neural processing improvement by more specialised neural representations of the observationally practised actions; however, the present study did not confirm this reasoning.

CHAPTER 3

Anodal tDCS over the primary motor cortex provides no advantage to learning motor sequences through observation

3.1 Introduction

Learning a new motor skill is a time-consuming and effortful process. A number of previous studies show that motor skill learning can be facilitated by anodal transcranial direct current stimulation (tDCS) of the primary motor cortex (M1) during skill acquisition (for reviews, see Ammann et al., 2016; Buch et al., 2016; Hashemirad et al., 2016; Reis & Fritsch, 2011). It is well established that motor learning increases excitability of M1 and strengthens synaptic connections within M1 through long-term potentiation (LTP)-like mechanisms (Rioult-Pedotti et al., 2000; Sanes & Donoghue, 2000; Spampinato & Celnik, 2017). Similarly, applying an anodal current through the scalp over M1 via tDCS increases excitability of cortical neurons under the surface area of the electrode (Nitsche & Paulus, 2000; Nitsche et al., 2008). The stimulation aftereffects last for more than an hour after a single stimulation session (Nitsche & Paulus, 2001) and are related to LTP-like changes in synaptic plasticity (Stagg & Nitsche, 2011). Thus, anodal tDCS modulates cortical excitability and synaptic plasticity in a similar manner as motor learning. Simultaneous motor task performance and anodal tDCS application (so-called “online” stimulation) likely induces additive effects of the synaptic modification and facilitates motor learning (Stagg & Nitsche, 2011). In addition, compared to single stimulation sessions, consecutive multiple day sessions generally produce higher tDCS effects (Hashemirad et al., 2016), showing a cumulative increase in cortical excitability (Alonzo, Brassil, Taylor, Martin, & Loo, 2012) and a positive effect on motor skill consolidation and retention (Reis et al., 2009; Saucedo Marquez, Zhang, Swinnen, Meesen, & Wenderoth, 2013).

To some extent, motor skills can also be learned by watching others, without overt physical practice. Several theories suggest that action observation engages an observer's own motor system by establishing internal representations of the motor programs required to perform the action (for a review, see Gentsch et al., 2016). Premotor and parietal brain regions are consistently reported as engaged during both action execution and observation and are the core regions of a so-called human mirror system (Iacoboni, Molnar-Szakacs, Gallese, Buccino, & Mazziotta, 2005; Rizzolatti & Sinigaglia, 2010). Although M1 is not typically considered as part of the mirror system, there is growing evidence that it plays an important role in learning by observation. Electrophysiological recordings in monkeys show M1 cells with mirror-like properties and cells engaged in a mental rehearsal of observed actions **(**Dushanova & Donoghue, 2010; Tkach, Reimer, & Hatsopoulos, 2007; Wahnoun, He, & Tillery, 2006**).** A number of human transcranial magnetic stimulation (TMS) studies have reported M1 involvement during action observation (Alaerts, Swinnen, & Wenderoth, 2009; Alaerts, de Beukelaar, Swinnen, & Wenderoth, 2012; de Beukelaar, Alaerts, Swinnen, & Wenderoth, 2016; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Koch et al., 2010; Naish, Barnes, & Obhi, 2016) and motor memory formation in M1 during observational learning (Celnik et al., 2006; Stefan, 2005). Moreover, repetitive TMS (inducing a temporary "virtual lesion") of M1 reduces the benefits of motor learning by observation (Brown, Wilson, & Gribble, 2009) and disrupts action perception (Palmer, Bunday, Davare, & Kilner, 2016). Beneficial effects of anodal tDCS over M1 are reported for learning through motor imagery (Foerster et al., 2013; Saimpont et al., 2016), which shares common mechanisms of observational learning (Jeannerod, 2001; Vogt, Rienzo, Collet, Collins, & Guillot, 2013). Crucially, M1 activity during observation might be a critical factor for the success of motor skill learning via observation (Aridan & Mukamel, 2016). If this is indeed the case, then it is possible that increasing M1 excitability during observational learning would facilitate learning success in a similar manner as that reported for learning by physical practice.

Here, for the first time, we investigate whether applying anodal tDCS over M1 during multiple-day observational practice of keypress sequences facilitates practice effects on sequence-specific skill acquisition and retention. We hypothesise that observational practice coupled with the anodal tDCS should have beneficial effects compared to observational practice alone, as reported for learning by physical practice.

3.2 Method

3.2.1 Participants

Fifty-five participants consented to participate in the study. Five participants did not finish all sessions and were excluded from the analysis. The final sample comprised 50 participants: 14 males and 36 females, 18 to 30 years old (M = 20.60 years, SD = 2.40). All participants were right-handed (based on self-report) Bangor University student volunteers with normal or corrected-to-normal vision, no history of neurological or psychiatric disorders, no contraindications to TMS or tDCS (personal/family history of epilepsy or seizures, metal or implants in the body, frequent headaches, history of serious head injury, heart disease, possibility of being pregnant), and not taking any medication that affects brain function (e.g., anti-epileptic medication, tranquilizers, anti-depressants). Prior to the first stimulation session, participants were assigned to the sham (N = 24) or active stimulation (N = 26) group (see section 3.2.3 for assignment procedure). There were no significant differences between the groups regarding demographics and baseline performance (summarised in Table 3.1). Participants provided their written informed consent prior to beginning all experimental procedures and either received eight course credits or were paid £30 for their participation following completion. The study was conducted in accordance with the Declaration of Helsinki and all procedures were approved by the Ethics Committee of the School of Psychology at Bangor University (approval number: 2016-15675) and the UK Ministry of Defence Research Ethics Committee.

3.2.2 Stimuli and procedure

The same keypress sequence learning paradigm was used as in the previous chapter with the same set of stimuli and the same sequence execution and observation trials (see *2.2.2 Stimuli*). The motor task required learning four keypress sequences with the left (non-dominant) hand by watching videos of an actor executing the sequences. Experimental procedure and all scripts are available at https://github.com/dcdace/E3tDCS.

Participants underwent six testing sessions (Figure 3.1; Appendix 3.1). On the first day of testing (day 1), participants' left-hand motor area was localised with TMS (see *3.2.3 Motor cortex stimulation-Right M1 localisation* for details). After the localisation procedure, participants received task instructions and completed three single sequence execution trials to ensure they understand the task. The familiarisation procedure was followed by a pre-test, which was immediately followed by the first observational practice session. The observational practice sessions continued the next three consecutive days (day 2 to day 4). For most participants, sessions were arranged at the same time of the day as the first practice session (with a 1.5 to 2.5-hour difference for three participants in the sham group, and a 0.5 to 1.5-hour difference for four participants in the active stimulation group). The day after completing the last observational practice session, participants performed a post-test (day 5), and a week later they returned to the lab one final time to perform a retention-test (day 12).

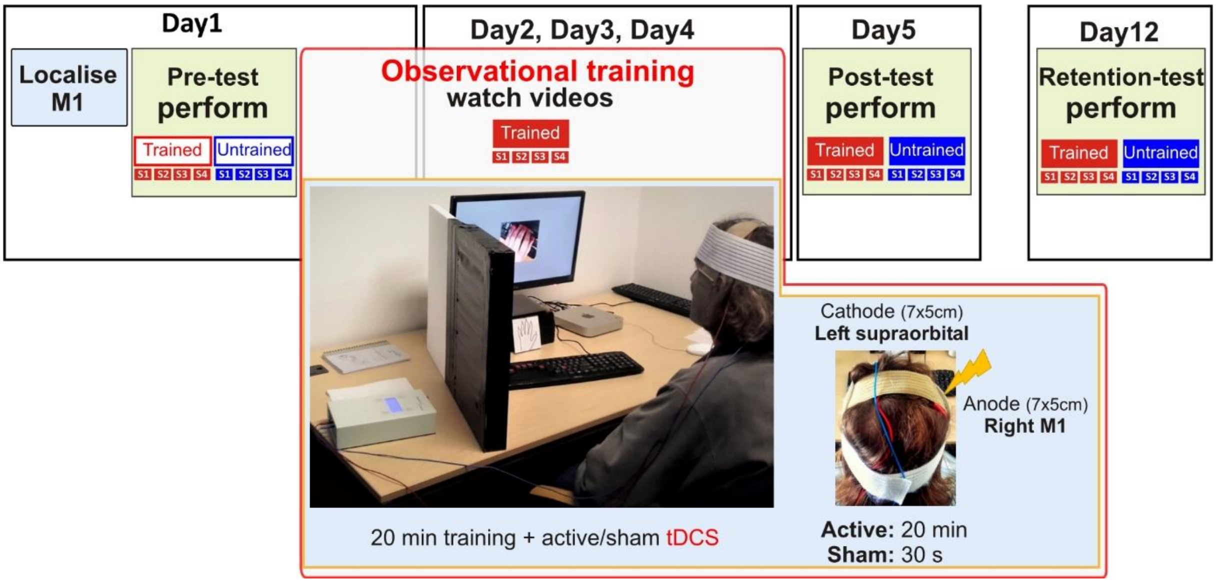


Figure 3.1 Experimental procedure. The experiment involved pre-test, four 20-minute-long training sessions coupled with tDCS, post-test, and retention-test. In the pre-, post- and retention-tests, participants executed eight keypress sequences (four of them to be trained, the other four untrained) with the left (non-dominant) hand. In the training sessions, participants watched videos of a model’s left hand executing four of the eight sequences. During the training, participants received either sham or active (1 mA) 20-minute stimulation of the right motor cortex (35cm^2 large area centred on the left-hand motor area M1).

Testing sessions

The pre-, post-, and retention-test sessions were identical to the pre- and post-training sessions described in the previous chapter (see *2.2.3 Procedure*). Briefly, participants executed four trained (or to-be-trained) and four untrained sequences in a random order with their left (non-dominant) hand. Each sequence execution trial started with a 5-digit cue (for 2.7 s), indicating the sequence of keypresses. The cue was then replaced with a cross, serving as a “go” signal to execute the given sequence five times as quickly and accurately as possible. After five executions of the same sequence, the trial ended, and the next sequence was cued.

Participants’ performance was assessed as the average sequence initiation time, execution time and error rate for the four trained (to-be-trained) and the four untrained sequences. The error rate was measured as the percentage of incorrect sequence executions. Incorrectly executed trials were excluded from initiation time and execution time measurements. The initiation time was measured as the duration between the “go” signal and the first keypress. The execution time was measured as the duration between the first and fifth keypresses.

Observational training sessions

During the observational training sessions, participants received either sham or active brain stimulation while watching videos of the model’s left hand executing four sequences. Each video showed five repetitions of the same sequence. A trial started with a 5-digit cue (for 2.6 s), indicating the sequence to be executed, followed by a video (13 s) showing five executions of the cued sequence. Participants were instructed to watch whether the hand executed the correct sequence all five times. Occasionally participants were asked whether there was an error in any of the five executions – the error question.

Each practice session was divided into three blocks, separated by a one-minute rest period. Within each block, 20 videos were presented in a random order: each sequence video four times, and one ‘error video’ (with at least one incorrect sequence execution) for each sequence. The error question was asked randomly 5-7 times per block. At the end of each block, participants received feedback on how accurately they spotted the incorrect sequence executions. During each session, participants saw a correct execution of each sequence at least 60 times (3 blocks, 4 videos per block, 5 repetitions per video, plus some correct repetitions in the ‘error video’). The whole training session lasted approximately 20 minutes and was coupled with 20-minutes of sham/active tDCS.

3.2.3 Motor cortex stimulation

Right M1 localisation

Single-pulse TMS was used to localise the left-hand motor area. The TMS coil was positioned on the right hemisphere, slightly anterior and ventral to the vertex of the skull to induce a muscle twitch in the relaxed fingers of the left-hand. The stimulator output was started at 45% and increased in steps of 2-5% until a visible twitch was observed. The stimulator output never exceeded 80%, and participants received no more than 20 pulses in total, with an inter-pulse interval kept to at least 5 seconds. The optimal location at which TMS evoked a just-noticeable finger twitch was marked on the participant’s scalp with a surgical marker. For nine participants, a visible twitch was not observed following this procedure, and the motor hand area was instead marked per position C4 of the EEG 10-20 system (Jasper, 1958). The localisation procedure was performed only on the first testing session, and the marked M1 location was renewed with the surgical marker before each stimulation session.

The nine participants whose M1 area could not be localised using TMS were assigned to the sham group as the precise location of the stimulated area was not critical for sham stimulation. We acknowledge that random assignment, independent of localisation procedure, would have been a better approach. The reasons why we could not evoke a visible twitch in some participants may include the extent of representation of the hand area and/or its accessibility via the cortical surface. To our knowledge, no evidence suggests that these factors could affect participants' ability to learn the motor task, and thus should not disadvantage the performance results of the sham group. However, to ensure that the observed group differences are not driven by the non-random assignment to groups, we repeated the analysis of observational training and stimulation effects with the nine non-TMS localised participants excluded. The results of this analysis (see Appendix 3.2) showed no meaningful differences from the results with all participants included. This suggests that the non-random group assignment did not systematically bias our findings. Nevertheless, in the present study, any conclusions about the tDCS effects can only be generalised to a population with relatively easily excitable motor cortex as TMS threshold is an important consideration for the tDCS stimulation (Labruna et al., 2016).

Stimulation parameters

We performed a single-blinded protocol. Participants were semi-randomly assigned to the sham or active stimulation group, keeping gender balanced between the groups and ensuring that the motor hand area of the active group was localised using the TMS procedure described above. Participants were told that they would receive stimulation for up to 20 minutes, not specifying the exact length of the stimulation and not revealing the existence of two stimulation groups. During each practice session, the sham group received 30 seconds, and the active group received 20 minutes of tDCS.

A 1 mA constant current was delivered using a battery-driven DC-stimulator Plus (NeuroConn GmbH, Ilmenau, Germany) via a pair of conductive-rubber electrodes placed into saline-soaked sponges (7 x 5 cm; 0.029 mA/cm^2 current density). The electrodes were secured with elastic bands. The contact impedance was monitored throughout the session to ensure it stayed below 15 kΩ.

The anode was centred over the previously marked right M1. Due to the electrode size, the stimulation likely extended into premotor and anterior parietal cortices as well. The cathode was placed on the left supraorbital ridge (see Figure 3.1). The current was ramped up to 1 mA over 10 seconds, held constant for either 30 seconds (sham) or 20 minutes (active), and then ramped down over 10 seconds. This method is recommended to reliably blind participants to stimulation condition and ensure similar sensations for sham and active stimulation groups (Woods et al., 2015).

The observational training task started one minute after stimulation onset, to allow time for participants to adapt to the stimulation sensations and to ensure they felt comfortable with carrying on with the task. The stimulation ended about one minute before the end of the task.

Sensations questionnaire

After each training session, participants provided information on the intensity of experienced sensations (itching, pain, burning, heat, pinching, metallic taste, fatigue), the timing of any discomfort (when did the discomfort begin and how long did it last?), and the perceived impact of the stimulation on their performance (adapted from Fertonani, Ferrari, & Miniussi, 2015; see Appendix 3.3). At the end of the experiment (day 12) participants were debriefed and asked whether they think they received sham or active stimulation.

3.2.4 Data analysis

All statistical analysis was performed using R (v3.3.2, 2016-10-31) in RStudio (v1.0.136, 2016-12-21, RStudio, Inc, Boston, MA). Graphs were produced in MS Excel 2016 (Microsoft, Redmond, WA, USA). The Excel files, raw data and scripts with all analysis procedures and for reproducing results are available at https://github.com/dcdace/E3tDCS.

Although we had a directional a priori hypothesis, all p-values are reported two-tailed following recommended criteria for appropriate use of one-tailed tests (Kimmel, 1957; Lombardi & Hurlbert, 2009; Ruxton & Neuhäuser, 2010). Specifically, unpredicted results in the opposite direction (M1 stimulation having a negative effect on learning by observation) would not be meaningless and would motivate further investigation.

Given the total sample size of 50, the study had 80% power to detect effects of tDCS that are conventionally considered large (Cohen’s d = 0.81; the effect size was estimated with a *power.t.test* function in R for a two-sample, two-sided t-test with 25 observations per group). Three previous multiple stimulation session (3-5 consecutive days, 20-25 min per day, 1-2 mA, ~12.5 participants per group) M1 anodal-tDCS physical training studies reported large tDCS effects ranging from 0.95 to 1.33 Cohen's d (Reis et al., 2009; Saucedo Marquez et al., 2013; Waters-Metenier, Husain, Wiestler, & Diedrichsen, 2014).

For the assessment of tDCS effects, we complemented null hypothesis testing with a Bayesian analysis to provide evidence for or against a null result. We used the *generalTestBF* function of the R package BayesFactor v0.9.12-2 (Morey, Rouder, Love, & Marwick, 2015) with its default parameters. The Bayesian test produced a Bayes factor to allow quantification of evidence in favour of either the alternative (BF_{10}) or null (BF_{01}) hypothesis based on prior beliefs and the present data. To describe the Bayes factor results we used Jeffreys (1961) classification scheme and reported both BF_{10} and BF_{01}. Jeffreys proposed benchmarks for evaluating the strength of evidence as anecdotal (BF_{10} 0-3), substantial (BF_{10} 3-10), strong (BF_{10} 10-30), very strong (BF_{10} 30-100), and decisive (BF_{10} 100-∞). These Bayes Factors can be readily interpreted as a ratio of evidence in favour of the experimental effect compared to the null effect. For example, a BF_{10} of 3 would represent that the experimental effect is three times more likely than the null (substantial evidence for the effect), given the data.

The significance threshold for all statistical comparisons was $p < 0.05$. If not specified otherwise, all sample means are reported with their 95% confidence intervals in squared brackets. Confidence intervals were calculated as SE*2.10, for simplicity rounding the critical t-values 2.07 (for df 23 in the sham group) and 2.06 (for df 25 in the active group) up to one decimal point.

3.3 Results

3.3.1 Group characteristics and sensations during training sessions

Gender proportion between sham and active stimulation groups was compared using a Chi-square test. Mann-Whitney U tests were used to compare group age and experienced sensations during the training sessions. Participants' baseline performance (pre-training average of trained and untrained sequences) was compared using an independent measures t-test. Results are summarised in Table 3.1. The reported sensations for each training day are summarised in Table 3.2 and averages of all training days plotted in Figure 3.2.

Table 3.1 Group characteristics and self-reported sensations during training sessions.

	Sham (N = 24)	Active (N = 26)	Group difference (p-value)
Demographics			
Gender (male:female)	8:16	6:20	0.623
Age (years; M ±SD)	20.96 ±2.97	20.27 ±1.71	0.446
Baseline performance			
Pre-test initiation time (s; M ±SD)	0.77 ±0.25	0.89 ±.30	0.117
Pre-test execution time (s; M ±SD)	1.92 ±0.57	2.02 ±0.68	0.590
Pre-test error rate (%; M ±SD)	25 ±13	30 ±15	0.203
Sensations			
Strongest (M ±SD)	1.23 ±0.49	1.46 ±0.79	0.478
Affected (M ±SD)	**0.16 ±0.32**	**0.30 ±0.36**	**0.037**
Lasted (M ±SD)	**1.14 ±0.48**	**1.79 ±0.71**	**0.001**

Shaded fields highlight variables that significantly differed between the sham and active stimulation groups. Strongest: the strongest reported sensation intensity level (0-4); Affected: how much did sensations affect performance (0-4); Lasted: when did the discomfort stop (0-3)

Table 3.2 Frequencies of self-reported sensations during the training sessions.

The strongest intensity of discomforting sensations

	Day 1					**Day 2**					**Day 3**					**Day 4**				
	0: none, 1: mild, 2: moderate, 3: considerable, 4: strong																			
	0	**1**	**2**	**3**	**4**	**0**	**1**	**2**	**3**	**4**	**0**	**1**	**2**	**3**	**4**	**0**	**1**	**2**	**3**	**4**
Sham	1	12	10	1	-	4	11	8	1	-	2	15	7	-	-	5	14	5	-	-
Active	2	11	8	3	2	2	18	2	3	1	2	15	4	2	3	3	16	5	2	-

How much did the sensations affect performance?

	Day 1					**Day 2**					**Day 3**					**Day 4**				
	0: not at all, 1: slightly, 2: considerably, 3: much, 4: very much																			
	0	**1**	**2**	**3**	**4**	**0**	**1**	**2**	**3**	**4**	**0**	**1**	**2**	**3**	**4**	**0**	**1**	**2**	**3**	**4**
Sham	19	5	-	-	-	20	4	-	-	-	22	2	-	-	-	21	2	1	-	-
Active	18	7	-	1	-	20	6	-	-	-	18	7	1	-	-	20	6	-	-	-

When did the discomfort stop?

	Day 1				**Day 2**				**Day 3**				**Day 4**			
	ns: no sensations, 1: quickly, 2: middle of the block, 3: end of the block															
	ns	**1**	**2**	**3**	**ns**	**1**	**2**	**3**	**ns**	**1**	**2**	**3**	**ns**	**1**	**2**	**3**
Sham	1	15	4	4	4	14	4	2	2	19	3	-	5	18	-	1
Active	2	6	9	9	2	11	7	6	2	8	7	9	3	9	8	6

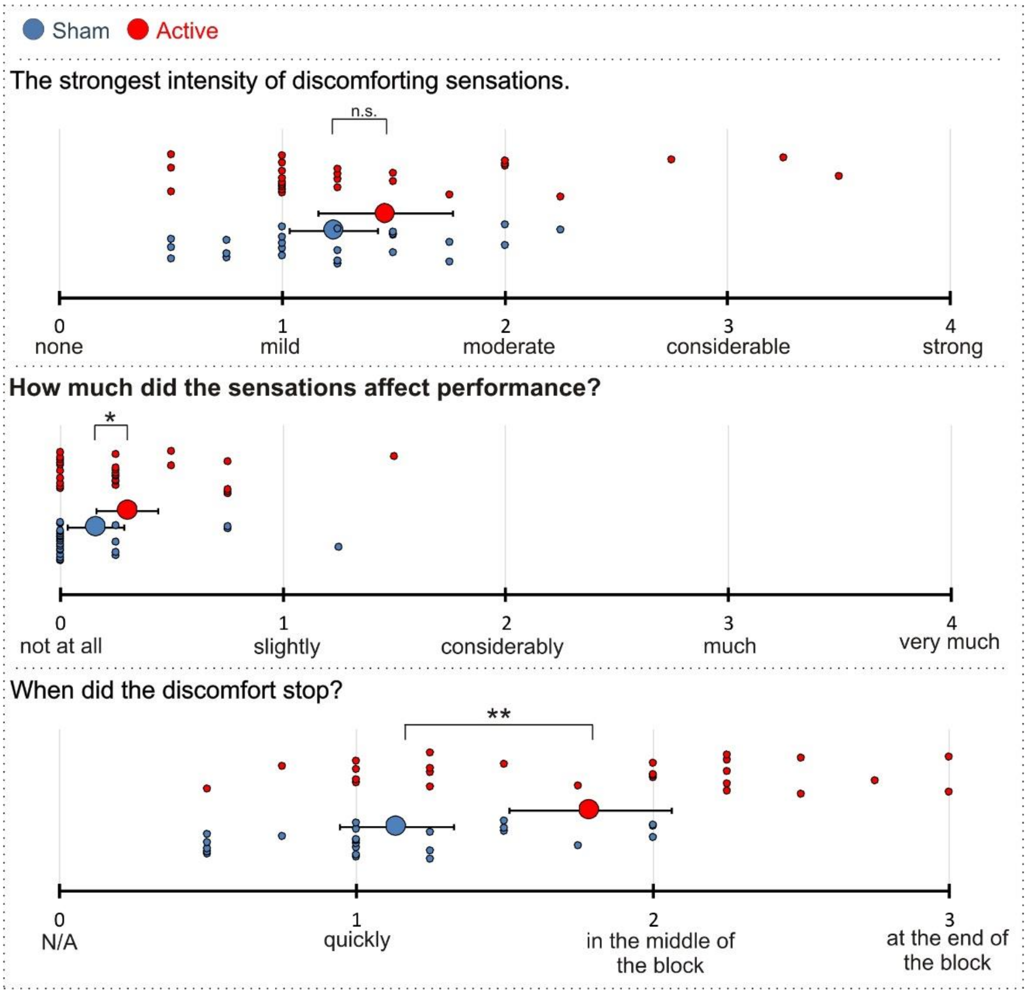


Figure 3.2. The 4-day average values of self-reported sensations during the training sessions. Large dots: group averages; small dots: individual participant values; red: active; blue: sham; error bars: 95% CI; * $p < 0.05$, ** $p < 0.01$.

There were no significant differences in gender, age, and baseline performance between the groups. All participants experienced some discomforting sensations (itching, pain, burning, heat, taste, or fatigue) during at least one of the four stimulation sessions. On average, participants reported mild to moderate sensations, with some participants from the active group reporting strong sensations. There was also no significant difference between the groups in the reported sensation intensity levels. For the active stimulation group, the sensations lasted significantly longer compared to the sham group. Seven (29%) sham and 16 (62%) active group participants reported that their performance was affected by the discomforting sensations during at least one of the sessions. A majority (91%) of them reported that their performance was only ‘slightly’ affected. One participant from the sham group was ‘considerably’ affected in one of the sessions, and one participant from the active group was ‘considerably’ affected in one session and ‘much’ affected in another session. On average, the active stimulation group reported being significantly more affected than the sham group.

There were small but significant sensation differences between the sham and active stimulation groups. The sham protocol should provide comparable sensations to the active stimulation protocol (Woods et al., 2015). However, small but significant sensation differences between the stimulation groups, using comparable protocols to ours, have been reported before (Fertonani et al., 2015), raising an issue that the widely accepted sham stimulation procedure may not be sufficiently effective.

Following the recommendation of Fertonani et al. (2015), at the end of the experiment, we asked participants whether they think they received sham or active stimulation. In total, 54% thought they received active stimulation, 32% thought they received sham stimulation, and 14% did not know. There was no significant difference between the two groups regarding which kind of stimulation they thought they received ($\chi^2 = 1.24$, $p = 0.538$), thus confirming the success of the blinding procedure.

3.3.2 Accuracy during training sessions

During the observational practice sessions, attention to the task was assessed by accurate responses to the error question (spotting incorrectly executed sequences). The overall accuracy was 83%, significantly ($p < 0.001$) higher than a 50% chance level (yes/no answers), confirming that participants paid attention to the task. The average accuracies for each group and day are plotted in Figure 3.3D. On average, across the four training days, the sham group performed better (M = 86% [82%, 90%]) than the active group (M = 81% [77%, 85%]), with a marginally significant difference between the two groups ($t_{47.27} = 1.99$, $p = 0.052$, $d = 0.56$).

The difference in the error detection accuracy between the groups was an unexpected finding. We cannot rule out that anodal tDCS of M1 had some negative effects on the error detection accuracy. However, we do not have any a priori or theoretical grounds to support this suggestion. Another possibility is that the discomforting sensations influenced the error detection accuracy during the training sessions that, as reported above, affected the stimulation group more than the sham group. This possibility is supported by a significant negative correlation between the average accuracy and the average self-report on how much performance was affected by the discomforting sensations (Kendall’s tau-b = -0.296, $p = 0.008$; across both groups).

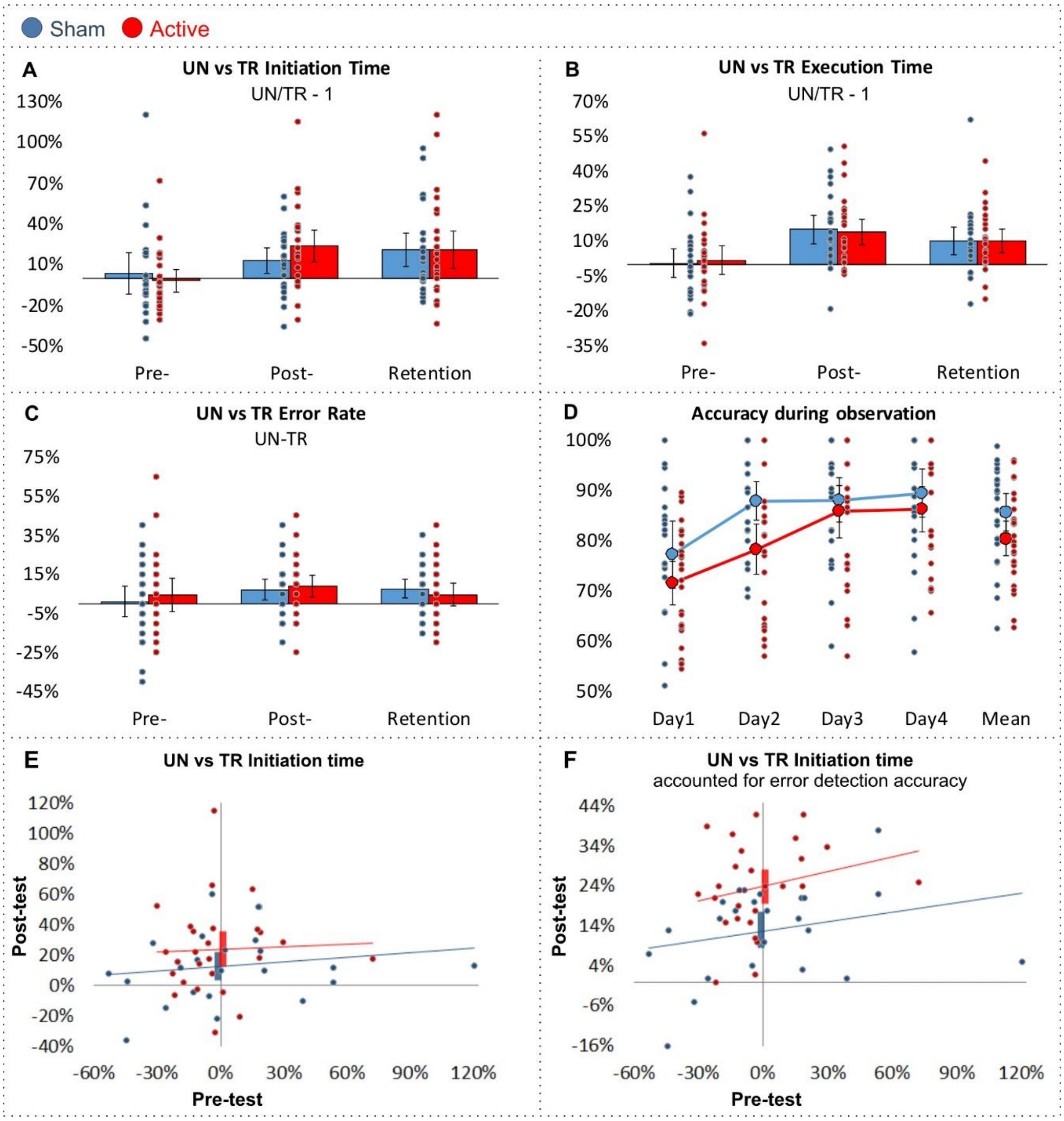


Figure 3.3. Performance results. Pre-, post-, and retention-test difference in initiation time (**A**), execution time (**B**), and error rate (**C**) between trained (TR) and untrained (UN) sequences for sham (blue) and active (red) stimulation groups. **D.** Error detection accuracy during observational practice sessions. **A-D.** Bars and large dots: group averages; small dots: individual participant values; error bars: 95% CI. **E.** Regression lines of pre-test (predictor) and the post-test difference between trained and untrained sequence initiation times for sham (blue) and active (red) stimulation groups. Intercepts of the regression lines represent the predicted post-test difference if the pre-test difference is zero. Vertical bars represent 95% CIs of intercepts **F.** Same as E, but post-test difference corrected for error detection accuracy during training sessions.

Observational training effects depend on the attention paid to the videos and on the general ability to perceive the videos. The error detection accuracy was an indirect measure of these factors. The lower error detection accuracy for the active stimulation group raises a concern that the stimulation effect might have been confounded by the active group not being able to learn from the videos as well as the sham group (e.g., due to stimulation-related discomfort affecting attention). To account for this possibility, we complement the planned analysis with a secondary analysis including the mean error detection accuracy as a covariate when assessing the stimulation effect.

3.3.3 Observational training effects on sequence-specific learning

The effect of observational training on sequence-specific learning was assessed as a post-training (separately for the post-test and retention-test) difference between the trained and untrained sequence initiation time, execution time, and error rate. For the sequence initiation time and execution time, we measured a percentage difference (untrained/trained-1), but for the error rate (to avoid dividing by zero), we calculated an absolute difference (untrained-trained) between the trained and untrained sequences (results of these measures are plotted in Figure 3.3A-C). To correct for possible pre-training differences, we performed a linear regression between the pre-training difference (predictor) and the post-training difference (outcome; see Figure 3.3E for an example plot). The intercept of the regression line was used as a measure of the post-training difference between trained and untrained sequences, controlling for possible pre-training differences. This method reduces the noise of unwanted differences in the difficulty of trained and untrained sequences and thus allows a more accurate measurement of the training effect.

Both groups showed significant observational training effects at both post-test and retention-test on all three performance measures, with medium to large effect sizes ($d_z = 0.52 – 1.02$). Except, the active stimulation group demonstrated no effect on error rates at retention-test. Detailed results are provided in Table 3.3.

3.3.4 tDCS effects on sequence-specific learning by observation

Primary analysis

The effect of stimulation on sequence-specific learning was assessed by comparing observational training effects (the post-training ~ pre-training regression line intercepts) between the sham and active stimulation groups. The performed analysis of covariance (ANCOVA) did not reveal any significant difference between the two groups on any of the three measures either at post-test or retention-test (Figure 3.3E plots post-test initiation time results). The Bayes factor analysis returned anecdotal to substantial evidence against the stimulation effect. Detailed results are provided in Table 3.3.

Secondary analysis: accounting for error detection accuracy

Due to concern that the stimulation effect could be confounded by sensation and error detection differences (both of which were negatively correlated) between the sham and active stimulation groups, we added the mean error detection accuracy as a covariate to the previous ANCOVA model and repeated the group comparison analysis.

The corrected analysis revealed evidence for the stimulation effect on the percentage difference between trained and untrained sequence initiation times at post-test. Compared to the sham group, the active stimulation group showed a greater difference on this measure (see Figure 3.3F). The error detection accuracy significantly predicted the outcome ($\beta = 0.431$, $p = 0.003$; the better the accuracy during training, the faster initiation time of trained relative to untrained sequences at post-test). All other measures showed anecdotal to substantial evidence against the stimulation effect when accounting for the error detection accuracy. Detailed results are provided in Table 3.3.

Table 3.3. Observational practice effects and tDCS effects on sequence-specific learning.

		Observational training effect (trained vs. untrained performance)		**tDCS effect (group difference)**	**tDCS effect, accounted for the accuracy during training sessions**
		Sham	**Active**		
Initiation time	**Post**	$t_{22} = 2.65$, $p = 0.015$, $B_0 = 13\%$, $d_z = 0.54$.	$t_{24} = 4.02$, $p < 0.001$, $B_0 = 24\%$, $d_z = 0.79$.	$t_{47} = 1.50$, $p = 0.141$, $d = 0.44$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.70/1.43$).	$t_{46} = 2.48$, $p = 0.017$, $d = 0.73$, anecdotal evidence for the effect ($BF_{10}/BF_{01} = 2.41/0.41$).
	Ret.	$t_{22} = 3.21$, $p = 0.004$, $B_0 = 21\%$, $d_z = 0.66$.	$t_{24} = 2.87$, $p = 0.008$, $B_0 = 21\%$, $d_z = 0.56$.	$t_{47} = 0.05$, $p = 0.961$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.29/3.49$).	$t_{46} = 0.01$, $p = 0.992$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.29/3.45$).
Execution time	**Post**	$t_{22} = 5.02$, $p < 0.001$, $B_0 = 15\%$, $d_z = 1.02$.	$t_{24} = 4.75$, $p < 0.001$, $B_0 = 14\%$, $d_z = 0.93$.	$t_{47} = -0.37$, $p = 0.710$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.30/3.31$).	$t_{46} = -0.49$, $p = 0.624$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.31/3.20$).
	Ret.	$t_{22} = 4.02$, $p = 0.001$, $B_0 = 10\%$, $d_z = 0.82$.	$t_{24} = 3.99$, $p = 0.001$, $B_0 = 10\%$, $d_z = 0.78$.	$t_{47} = -0.06$, $p = 0.950$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.28/3.55$).	$t_{46} = -0.02$, $p = 0.984$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.29/3.43$).
Error rate	**Post**	$t_{22} = 2.56$, $p = 0.018$, $B_0 = 7\%$, $d_z = 0.52$.	$t_{24} = 2.89$, $p = 0.008$, $B_0 = 9\%$, $d_z = 0.57$.	$t_{47} = 0.47$, $p = 0.644$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.31/3.20$).	$t_{46} = 0.20$, $p = 0.845$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.31/3.28$).
	Ret.	$t_{22} = 2.99$, $p = 0.007$, $B_0 = 7\%$, $d_z = 0.61$.	$t_{24} = 1.45$, $p = 0.161$, $B_0 = 4\%$, $d_z = 0.28$.	$t_{47} = -0.81$, $p = 0.420$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.37/2.71$).	$t_{46} = -1.05$, $p = 0.298$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.44/2.27$).

Shaded fields highlight non-significant effects.

Importantly, although the active group outperformed the sham group on the initiation time of trained relative to untrained sequences at post-test, this does not mean that the active group initiated sequences faster. Here we measured the relative difference between trained and untrained sequences to assess stimulation effects on sequence-specific learning. However, it is known that general skill learning (post-training improvement of untrained sequences) occurs too (Janacsek & Nemeth, 2013; Meier & Cock, 2014). Thus, the observed group difference of the sequence-specific learning-related initiation times at post-test could be due to differences in the performance generalisation to the untrained sequences.

Indeed, the pre/post percentage difference of the untrained sequence initiation times was greater for the sham group (M = 36% [18%, 54%]) compared to the active group (M = 19% [6%, 32%]). The difference was significant when accounting for error detection accuracy during training sessions ($p = 0.045$). The trained sequence pre/post initiation times were not significantly different between the two groups ($p = 0.749$). Neither pre/retention untrained sequence initiation times, nor any other measure (pre/post or pre/retention execution times and error rates, corrected for error detection accuracy) showed group differences in performance generalisation to the untrained sequences.

3.4 Discussion

The results of this study showed no evidence that anodal tDCS over M1 facilitates motor sequence learning by observation, unlike previously reported for learning by physical practice (Ammann et al., 2016; Buch et al., 2016; Hashemirad et al., 2016; Reis & Fritsch, 2011). Learning by observation and by physical practice share common neural mechanisms, including M1 engagement during skill practice (Celnik et al., 2006; Stefan, 2005). Crucially, M1 activity during observational practice might be a critical factor for learning success (Aridan & Mukamel, 2016). Based on this evidence, we hypothesised that observational practice coupled with the anodal tDCS over M1 will have beneficial effects compared to observational practice alone. However, our results did not confirm this hypothesis.

Both active and sham stimulation groups benefited from observational practice, replicating previous findings that motor skills can be learned by observation without overt physical practice (Heyes & Foster, 2002; Lago-Rodríguez & Cheeran, 2014; Osman et al., 2005; Vogt & Thomaschke, 2007). Moreover, the learned skill in our task was retained for at least a week. However, M1 stimulation did not provide an advantage to learning the motor sequences by observation. The Bayesian analyses results revealed anecdotal to substantial evidence in favour of the null hypothesis. For example, for the tDCS effect on sequence-specific execution time at post-test, the null hypothesis was 3.39 times more likely than the alternative hypothesis. Below we discuss some of the possible explanations for this null effect.

3.4.1 M1 may not be critically involved in motor sequence learning by observation

It is possible that M1 is not critically involved in learning keypress sequences by observation. Although there is a consensus of shared mechanisms between action observation and execution, a debate continues over their exact nature, as well as which aspects of the motor hierarchy action observation involves (Giese & Rizzolatti, 2015; Grafton & Hamilton, 2007; Rizzolatti et al., 2014). Functional magnetic resonance imaging studies consistently report premotor and parietal activation during action observation (Caspers et al., 2010; Molenberghs et al., 2012; Rizzolatti & Sinigaglia, 2010). These are the core regions of the so-called human mirror system (Iacoboni et al., 2005; Rizzolatti & Sinigaglia, 2010), and their engagement is also implicated at abstract levels of motor hierarchy, such as action understanding and planning (Grafton & Hamilton, 2007).

Although M1 is not typically considered as part of the human mirror system, there is substantial evidence of M1 involvement during action observation (Alaerts et al., 2009, 2012; de Beukelaar et al., 2016; Brown et al., 2009; Celnik et al., 2006; Fadiga et al., 1995; Koch et al., 2010; Naish et al., 2016; Palmer et al., 2016; Stefan, 2005). Nevertheless, the functional role of M1 engagement during action observation remains unclear. Several studies have questioned the notion of motor-driven learning by observation, arguing instead that perceptual and cognitive processes drive it (Lim, Larssen, & Hodges, 2014; Maslovat et al., 2010b; Vannuscorps & Caramazza, 2016). While primary motor areas might be engaged during action observation, their involvement might not be critical to influence the process of observational learning significantly.

In addition, M1 engagement during observational learning might be task dependent. For example, Aridan and Mukamel (2016) reported a positive relationship between M1 activity during action observation and the success of motor skill learning via observation only if the observed model's performance was faster than the observer's performance at baseline. In our study, the model executed sequences at an intermediate performance level (M = 2.29 s per sequence execution; see *2.2.2 Stimuli-Videos*), which on average was slower than the baseline performance of active (M = 2.02 s) and sham (M = 1.92 s) stimulation groups. Perhaps the observers in our study were not sufficiently challenged by the comparatively slow model performer and consequently did not engage M1 as they might if the model performed at an expert level. Future studies could further explore whether anodal tDCS over M1 facilitates learning by observation when the observed model is performing at an expert level that consistently exceeds the observer's baseline performance.

Importantly, tDCS is not an appropriate tool for assessing M1 involvement in learning by observation. The focality of tDCS is very limited. Due to the electrode size (7 x 5 cm), the stimulation in our study may have extended beyond M1 into nearby premotor and anterior parietal brain regions as well. Moreover, the modulation of cortical excitability under and between the electrodes is still under debate and investigation (Kuo, Polanía, & Nitsche, 2016; Nitsche et al., 2008). Therefore, the null finding in our study does not necessarily imply that the M1 is not involved in sequence learning by observation. Instead, our results imply that anodal tDCS over M1 does not facilitate observational practice effects, contrasting the reports on the M1 stimulation effects on physical practice (Ammann et al., 2016; Buch et al., 2016; Hashemirad et al., 2016; Reis & Fritsch, 2011). The discrepancy between the reported positive stimulation effects on physical practice and our null effect on observational practice may suggest that different mechanisms support the two practice types. However, our conclusions are limited by the lack of the physical practice group in our study, which permits a direct comparison of the stimulation effects of the two practice types with exactly equal stimulation parameters.

3.4.2 Inter- and intra-subject variability in cortical excitability

A possibility that M1 was not appropriately stimulated is unlikely. The location of participants' hand motor area was identified by TMS, which is a reliable method for localising the anatomical position of the hand knob (Boroojerdi et al., 1999). However, the stimulation intensity (1 mA) might be too weak to induce a sufficient effect on all participants. There is high interindividual variability in skull thickness and curvature of the hand area that affects stimulation-induced cortical excitability (Opitz et al., 2013). Unlike TMS studies where stimulator output is tailored for each participant, typical tDCS studies, including ours, use fixed stimulation intensity for all participants. A recent study shows that the effect of anodal tDCS over M1 is larger in participants with higher sensitivity to TMS (Labruna et al., 2016). Thus, it is suggested to individually tailor the tDCS parameters based on participant's sensitivity to cortical excitability as measured by TMS (Labruna et al., 2016). Several other factors can also cause high inter-subject as well as intra-subject variability in the tDCS effects. Such factors include hair thickness, skin conductivity (influenced by sweat), circadian, metabolic, and hormonal cycles (Horvath, Carter, & Forte, 2014; Horvath, Vogrin, Carter, Cook, & Forte, 2016; Tremblay et al., 2016). Not all factors were controlled in our study and should be addressed more rigorously in future.

3.4.3 Not the right measure of effect

A previous report on motor skill learning by physical practice showed that anodal tDCS facilitated the learning rate but not the final amount of the learning (Stagg et al., 2011). In the present study, we measured only the post-training outcome of the learning. It is possible that, compared to the sham group, the active stimulation group had a steeper learning rate despite the final amount of learning being the same for both groups. Any possible stimulation effects on learning rate remained uncovered and should be addressed in future studies. It should be noted, though, that measuring the rate of motor skill learning by observation is challenging. One possible solution would be a multiple-group between subject design with a varying observational practice length between groups.

3.4.4 Not an optimal stimulation protocol

Another possibility of the observed null effect in our study is that the tDCS protocol employed was not effective in modulating M1 activity to provide behavioural benefits through observational practice. Future studies should investigate different protocols and electrode montages. For example, several reports demonstrate a powerful effect of dual-M1 stimulation (applying anodal tDCS over the trained hand motor cortex and cathodal tDCS over the untrained hand) on motor learning (Koyama, Tanaka, Tanabe, & Sadato, 2015; Waters-Metenier et al., 2014), which outperforms unilateral M1 stimulation montages (Karok & Witney, 2013; Karok, Fletcher, & Witney, 2017; Mordillo-Mateos et al., 2012; Vines, Cerruti, & Schlaug, 2008). It is suggested that the excitation of the motor performing hand is amplified by inhibiting the opposite hemisphere. Furthermore, the dual-M1 stimulation increases functional connectivity between the area under the anode and intracortical areas involved in the task (Lindenberg, Nachtigall, Meinzer, Sieg, & Flöel, 2013; Lindenberg, Sieg, Meinzer, Nachtigall, & Flöel, 2016; Sehm, Kipping, Schäfer, Villringer, & Ragert, 2013).

3.4.5 Stimulation-related sensation and perception differences

In our study, there were small stimulation-induced sensation differences between active and sham groups. A similar finding was reported by Fertonani et al. (2015) whose sensation questionnaire we adopted. Although the self-reported sensation differences were small and did not compromise our blinding procedure, it is possible that the active stimulation group was more distracted during the training sessions. The self-report on how much performance was affected by the discomforting sensations negatively correlated with the error detection accuracy during the training sessions, adding some support to this idea. Furthermore, the overall error detection accuracy was lower (but not reaching statistical significance) for the active group compared to the sham group. While we do not have any theoretical reason to assume that the anodal tDCS of M1 could negatively affect the error detection accuracy, this possibility cannot be ruled out. Nevertheless, in tDCS studies, it should be a standard procedure not only to ensure an effective blinding but also to record and report sensation differences between active and sham stimulation groups, as we have done in the present study.

3.4.6 Stimulation-related interference on untrained sequence initiation time

To account for the possibility that the stimulation effect on observational training efficacy could be confounded by the active group not being able to learn from the videos as well as the sham group, we performed a secondary, exploratory analysis with the mean error detection accuracy as a covariate when assessing the stimulation effect. The adjusted results indicated that anodal tDCS over M1 during observational practice negatively affects skill generalisation to untrained sequences, specifically regarding the untrained sequence initiation time. This finding could be explained by practice and stimulation-related increase in sequence-specific knowledge that interferes with the general skill transfer to novel sequences (Howard et al., 2004; Müssgens & Ullén, 2015). The sequence initiation time is related to response planning and preparation, processes that are particularly shared between action observation and performance (Prinz, 1997). Although the potential strengthening in sequence-specific knowledge did not provide any performance benefits (when compared to the sham group), this is a potentially important finding supporting M1 involvement in motor sequence learning by observation. The effect should be replicated and further investigated in future studies ensuring comparable sensations and training performance between active and sham stimulation groups.

3.4.7 Conclusions

Our results do not support the hypothesis that anodal tDCS over M1 facilitates keypress sequence learning by observation. The null finding does not necessarily imply that the M1 is not involved in sequence learning by observation, but rather that M1 stimulation, with the parameters employed in our study, does not reliably enhance this function. This finding is important to inform future brain stimulation studies aimed to facilitate learning by observation. Future studies should take special care in minimising inter- and intra-subject variability of the stimulation effect and minimising stimulation-induced discomfort that may interfere with the observational practice effects.

CHAPTER 4

Fluid intelligence and working memory support learning by physical but not by observational practice

4.1 Introduction

Motor skills can be learned by physical practice and by watching another performer. People vary greatly in their ability to acquire new motor skills, but it is unclear if the same factors predict success from physical and observational practice. An extensive amount of research has examined individual differences in motor skill learning through physical practice (Ackerman & Cianciolo, 2000; Kaufman et al., 2010; Reber et al., 1991; Unsworth & Engle, 2005), but little is known about individual differences in motor skill learning through observation. Based on the premise of shared mechanisms between action observation and execution (Gentsch et al., 2016; Rizzolatti & Sinigaglia, 2010), one might expect that the same factors explain individual differences in learning through both types of practice.

In skill acquisition through physical practice, implicit and explicit modes of learning are dissociated. Implicit learning, which occurs subconsciously and unintentionally, is largely independent of effortful cognitive processes and shows little variation across individuals (Kaufman et al., 2010; Reber et al., 1991). Conversely, explicit learning involves conscious awareness of what needs to be learned, requires intentional control and attention, and individual differences in cognitive abilities become more evident (Gebauer & Mackintosh, 2007; Unsworth & Engle, 2005). For example, explicit learning abilities are related to working memory and fluid intelligence (Bo & Seidler, 2009; Christou et al., 2016; Gebauer & Mackintosh, 2007; Janacsek & Nemeth, 2013; Maxwell et al., 2003; Reber et al., 1991; Unsworth & Engle, 2005). Individuals with greater working memory are better at cognitive control (Cowan, 1998; Unsworth & Engle, 2005), whereas individuals with greater fluid intelligence are better at reasoning in novel tasks that cannot be performed automatically or solved simply by short-term memorisation (Gebauer & Mackintosh, 2007; Wang, Ren, & Schweizer, 2017).

When learning a motor skill, working memory supports action pre-planning and goal maintenance (Bo & Seidler, 2009; Unsworth & Engle, 2005; Verwey, Shea, & Wright, 2015), while fluid intelligence supports long-term memory retrieval, reasoning and acquisition of action patterns necessary to perform the motor task (Feldman, Kerr, & Streissguth, 1995; Gebauer & Mackintosh, 2007; Wang et al., 2017). Working memory and fluid intelligence play particularly important roles at the early (cognitive) stage (Fitts & Postner, 1967) of motor skill acquisition and become less important as learning progresses from controlled to automatic processing (Ackerman, 1988; Seidler, Bo, & Anguera, 2012; Serrien, Ivry, & Swinnen, 2007).

As in explicit learning through physical practice, learning by observation relies on high-order cognitive processing, especially at early stages of skill acquisition (Hodges, Ong, Larssen, & Lim, 2011; Lim et al., 2014; Maslovat et al., 2010b; Vogt & Thomaschke, 2007). The cognitive processes that involve understanding action goals and action planning are shared between action execution and observation (Decety & Grèzes, 1999; Prinz, 1997). Furthermore, brain imaging studies show that both action observation and action execution engage common frontoparietal brain regions (Caspers et al., 2010; Gazzola & Keysers, 2009; Molenberghs et al., 2012; Oosterhof et al., 2013; Rizzolatti & Sinigaglia, 2010). Some of these regions are involved in working memory, attention, and intentions (Ikkai & Curtis, 2011; Lückmann et al., 2014). The brain activity in the frontoparietal regions often decreases following both physical and observational practice, which is interpreted as a decrease in cognitive demand as skill acquisition shifts from cognitive to automatic processing (Higuchi et al., 2012; Kelly & Garavan, 2005; Sakreida et al., 2017). The involvement of common cognitive processes in learning through physical or observational practice raises the question whether the same cognitive abilities explain individual differences in both types of skill acquisition.

Here, for the first time, we investigate whether fluid intelligence and working memory explain individual differences in learning both through physical practice and through observation. We hypothesise that higher fluid intelligence and working memory should facilitate both physical and observational practice effects on motor skill acquisition.

In addition to the role of high-order cognitive processes, evidence suggests activation of matching motor representations (internal motor resonance) during action observation, supporting motor skill acquisition beyond just the cognitive stage (Lago-Rodríguez & Cheeran, 2014; Mattar & Gribble, 2005; Naish et al., 2016; Vogt & Thomaschke, 2007). The notion of internal resonance, first experimentally demonstrated in the domain of action (Gallese et al., 1996; Rizzolatti et al., 1996), is thought to extend to broader notion of empathy, and includes "inner imitation" of what others do, think, or feel (Preston & de Waal, 2001). It is suggested that multiple aspects of self-other relations unify under the same basic "mirroring" mechanisms (Gallese, 2001, 2003; Iacoboni, 2009; Leslie, Johnson-Frey, & Grafton, 2004; Preston & de Waal, 2001). If the mechanisms of internal representations of what is perceived and what is experienced generalise across the multiple aspects of self-other relations, then the ability to simulate others' feelings and the ability to simulate others' actions might be interrelated. Brain imaging studies support this view, reporting a relationship between individuals' empathy scores and motor resonance even when perceiving actions with non-emotional content (Gazzola, Aziz-Zadeh, & Keysers, 2006; Kaplan & Iacoboni, 2006; Milston, Vanman, & Cunnington, 2013; Perry, Troje, & Bentin, 2010).

Following this line of reasoning, it is plausible to expect that individual differences in self-other relations might explain variability in motor skill learning by observation. To our knowledge, this question has not been studied before. Therefore, in addition to our main hypothesis, we explore whether individual differences in self-other relations could explain further variability in motor skill learning by observation and how this might compare to learning through physical practice. Finally, we also extend our exploration to broad personality characteristics (McCrae & Costa, 1987), often studied in relation to academic performance and learning (Digman, 1990; Poropat, 2009), but not yet in motor skill learning by observation.

To summarise, the aims of the present study are to (1) investigate whether fluid intelligence and working memory explain individual differences in motor skill learning both through physical practice and through observation; (2) to explore whether self-other relations and broad personality characteristics explain further variability in motor skill learning through observation and how this compares to learning through physical practice.

4.2 Method

4.2.1 Participants

Two hundred twenty-three Bangor University student volunteers took part in the study: 69 males and 154 females, 18 to 37 years old (M = 19.96 years, SD = 3.09). All but one participant were right-handed (based on self-report). The left-handed participant was excluded from the sample. Data of additional 38 participants were also excluded for various reasons (see *4.2.4 Analysis-Data cleaning).* The final sample comprised 184 participants. Participants were randomly assigned to physical (N = 92) or observational (N = 92) practice groups. There were no significant differences between the two groups in terms of demographics and baseline performance (summarised in **Error! Reference source not found.**). Participants provided their written informed consent prior to beginning all experimental procedures. Participation was rewarded with either three course credits or £10. The study was conducted in accordance with the Declaration of Helsinki and all procedures were approved by the Ethics Committee of the School of Psychology at Bangor University (approval number: 2014-11824) and the UK Ministry of Defence Research Ethics Committee.

4.2.2 Measures of individual differences

Fluid intelligence and working memory

Fluid intelligence was assessed by a total score of the Analogies, the Number series and the Matrices subtests of The Intelligenz–Struktur–Test 2000R (Amthauer, Brocke, Liepmann, & Beauducel, 2001), as applied before by Beauducel, Brocke, and Liepmann (2001). A computerised version of the subtests was created in MATLAB 8.3.0 (The MathWorks, MA, USA), closely mimicking the paper version of the tests.

Working memory was assessed by a computerised version of the spatial short-term memory test, implemented and validated by Lewandowsky, Oberauer, Yang, and Ecker (2010). Participants had to remember spatial relations between dots in a 10x10 grid.

Personality questionnaires

We used multifaceted empathy, interdependence, narcissism and Big-Five personality measures to assess individuals’ self-other relations and broad personality characteristics. Empathy scores were acquired using the interpersonal reactivity index questionnaire (IRI; Davis, 1980, 1983). The IRI is a 28-item measure of four empathy dimensions: perspective taking (adopting other's point of view), fantasy (self-identification with fictional characters), empathic concern (compassion and concern for others), and personal distress (distress when seeing another's negative experience). Interdependence was assessed by a 24-item Self-Construal scale (Singelis, 1994). The scale measures both interdependence and independence, but in the analysis, we focused only on the interdependence measure. Trait narcissism was measured by a 40-item Narcissistic personality inventory (NPI; Raskin & Terry, 1988). Broad personality characteristics were assessed by a 44-item Big-Five inventory (John, Donahue, & Kentle, 1991; John, Naumann, & Soto, 2008) measuring five domains of personality: openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism. All four questionnaires were created in MATLAB and required forced-choice responses (all questions had to be answered).

4.2.3 Stimuli and procedure

The same keypress sequence learning paradigm was used as in the previous chapters with the same set of stimuli and the same sequence execution and observation trials (*see 2.2.2 Stimuli*).

On arrival, participants were randomly assigned to physical (PP) or observational (OP) practice groups. For each participant, from the set of 12 sequences, one sequence was randomly allocated to the familiarisation with the task, two other sequences to the Trained condition, and two more to the Untrained condition. The motor task required learning two keypress sequences with the left (non-dominant) hand either by a physical practice (PP group) or by watching videos of an actor executing the sequences (OP group).

Familiarisation involved three single sequence execution trials (as in previous chapters, one trial consisted of five continuous repetitions of the same sequence) to ensure participants understand the task. In the pre- and post-training sessions participants executed the two to-be-trained and two untrained sequence trials (one trial per sequence) in a random order. During training, participants practised two sequences by either performing (PP group) or watching (OP group) 36 trials of each sequence. The training session was divided into four sub-sessions. Each sub-session consisted of 9 trials per sequence. For the OP group, one of the 9 trials was an 'error trial' – a video showing at least one incorrect sequence execution. In each sub-session, the error question (see *2.2.2 Stimuli-Sequence observation trial*) was asked randomly 5-7 times. Attention to the observed videos was assessed as a percentage of accurate responses to the 'error question'.

The whole testing procedure lasted approximately two hours and consisted of the following steps: information, consent and instructions; Matrices test; motor task familiarisation; pre-test; 9 blocks of training; Big Five inventory; 9 blocks of training; IRI questionnaire; 9 blocks of training; NPI questionnaire; 9 blocks of training; Self-Construal scale questionnaire; post-test; Analogies test; Numbers test; spatial short-term memory test; debrief.

4.2.4 Analysis

All statistical analyses were performed using R (v3.3.2, 2016-10-31) in RStudio (v1.0.136, 2016-12-21, RStudio, Inc, Boston, MA). Graphs were produced in MS Excel 2016 (Microsoft, Redmond, WA, USA). The Excel files, raw data and scripts with all analysis procedures and for reproducing results are available at https://github.com/dcdace/E1_IndDiff.

The significance threshold for all statistical comparisons was $p < 0.05$. All sample means are reported with their 95% confidence intervals in square brackets. Confidence intervals were calculated as SE*1.99, for 91 degrees of freedom.

Measure of the training effect on sequence-specific learning

Participants’ physical performance was assessed at pre- and post-test, measuring the average sequence execution time of the two trained (to-be-trained) and the two untrained sequences. The sequence execution time was measured as the duration between the first and the fifth keypresses. Incorrectly executed trials were excluded from further analysis.

The effect of training on sequence-specific learning was assessed as a post-training percentage difference between the trained and untrained sequence execution times accounting for possible pre-training percentage differences between the sequences, according to the equation below.

$$Training\ Effect = 100 * \left(\frac{post_{Untrained}ET}{post_{Trained}ET} - 1\right) - 100 * \left(\frac{pre_{Untrained}ET}{pre_{Trained}ET} - 1\right)$$

Data cleaning

One participant who reported being left-handed and 18 participants who did not correctly execute any trials in one (or more) of the four conditions (pre-Trained, pre-Untrained, post-Trained, post-Untrained) were excluded from the analysis. Twelve participants from the OP group were excluded due to the possibility of not paying enough attention to the practice videos. Specifically, the excluded participants had more than 50% error rate to the ‘error question' in the second, third or fourth training sub-session. The exclusion was based on the assumption that the first sub-session was still a familiarisation with the task, but having more than 50% error rate on the following sub-sessions would indicate a lack of attention to the observed videos, thus compromising the practice effect.

From the remaining sample, eight participants were excluded as pre-test outliers. The outliers were defined as pre-Trained or pre-Untrained execution time values being more than two times the interquartile range above the third quartile or below the first quartile.

Hypothesis testing

Our main hypothesis was that fluid intelligence and working memory predict the sequence-specific training effect for both PP and OP groups. We used multiple regression analysis to test this hypothesis. PP and OP groups were analysed separately. All variables were converted to within-group z-scores.

The regression model consisted of the training effect as the dependent measure and three predictor variables: baseline performance (an inverse of the pre-training average of trained and untrained sequence execution times; shorter execution time equals higher performance), fluid intelligence score and working memory score. The baseline performance was included as a predictor because participants who are already skilled at the task may have little benefit from the training compared to participants with poor initial skills (Alexander & Smales, 1997).

Given the sample size of 92 in each group, the test had 80% power to detect predictor effects that are conventionally considered small to medium ($f^2 = 0.12$; Cohen, 1988). The effect size was estimated with a *pwr.f2.test* function in R for a linear regression model with three predictor variables and sample size 92.

Exploratory analysis

In addition to the main hypothesis, we explored whether personality traits further explain the variance of the training effect. As in the main hypothesis testing, PP and OP groups were analysed separately, and all variables were converted to within-group z-scores.

We applied all-subsets regression analysis with 14 predictor variables: baseline performance, fluid intelligence, working memory, perspective taking, fantasy, empathic concern, personal distress, interdependence, narcissism, openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism.

All-subset regression is an alternative to stepwise regression methods for finding the "best" model. Unlike the stepwise approach, all-subsets regression does not presume that a single “best” model exists. Instead, it provides all possible “equally good best” models. All-subsets regression avoids premature termination, which is a limitation of stepwise approaches where some combinations of variables may be missed completely (Brown, 2005; Kuk, 1984). Instead, all-subsets regression uses all possible subsets and combinations of predictor variables and compares the regression models to a chosen statistical criterion, e.g., the Schwarz’s Bayesian information criterion (BIC; Schwarz, 1978). BIC is based, in part, on the likelihood function and uses penalised sum of squares criteria. A model with the lowest BIC is the model with an optimal combination of predictor variables that best explain the variance of the outcome variable.

The all-subsets regression analysis was implemented using the R *regsubsets* function in the *leaps* package, which uses a branch-and-bound algorithm (Furnival & Wilson, 1974; Miller, 2002). The predictor variable subset with the minimum BIC was chosen as the one best explaining the variance in the training effect.

Given the sample size of 92 in each group, the analysis had 80% power to detect predictor effects that are conventionally considered medium to large ($f^2 = 0.23$; Cohen, 1988). The effect size was estimated with a *pwr.f2.test* function in R for a linear regression model with 14 predictor variables and sample size 92.

4.3 Results

4.3.1 Group characteristics

The PP and OP groups were compared using a Chi-square test on the proportion of males and females as well as the number of native English speakers. Participants’ baseline performance, working memory and fluid intelligence scores were compared using an independent measures t-test. Personality questionnaire scores were compared using Mann-Whitney U tests. There were no significant differences between the two groups in terms of demographics, baseline performance or personality measures. Results are summarised in Table 4.1.

Table 4.1 Group characteristics.

	Physical practice (N = 92)	Observational practice (N = 92)	Group difference (p-value)
Demographics			
Gender (male:female)	30:62	30:62	1
Age (years; M ±SD	19.68 ±2.32	19.70 ±2.62	0.976
English 1st language (yes:no)	76:16	80:12	0.538
Baseline performance (M ±SD)			
Pre- Execution time (s)	2.16 ±0.78	2.00 ±0.57	0.113
Personality measures (M ±SD)			
Working memory	196.13 ±15.75	195.18 ±15.17	0.679
Fluid intelligence	31.03 ±8.01	31.78 ±7.22	0.506
Extraversion	3.32 ±0.78	3.2 ±0.73	0.227
Agreeableness	3.76 ±0.67	3.77 ±0.6	0.915
Conscientiousness	3.23 ±0.55	3.29 ±0.65	0.668
Neuroticism	3.14 ±0.8	3.24 ±0.84	0.487
Openness	3.4 ±0.6	3.46 ±0.59	0.359
Perspective taking	18.88 ±4.47	17.96 ±5.35	0.371
Fantasy	18.67 ±6.01	18.74 ±6.08	0.992
Emotional concern	19.03 ±4.56	19.35 ±5.34	0.426
Personal distress	12.36 ±4.8	12.7 ±5.23	0.616
Narcissism	12.41 ±6.27	11.6 ±6.88	0.261
Interdependence	43.3 ±5.83	43.03 ±6.9	0.917

4.3.2 Training effect on sequence-specific learning

Both PP (M = 68% [58%, 78%], $t_{91} = 13.44$, $p < 0.0001$, $d_z = 1.40$) and OP (M = 10% [4%, 16%], $t_{91} = 3.32$, $p = 0.0013$, $d_z = 0.35$) groups showed significant training effects on sequence-specific learning (see Figure 4.1). For the PP group, the training effect was considerably larger than for the OP group (M = 58% [70%, 46%], $t_{149.31} = 9.80$, $p < 0.0001$, $d_z = 1.60$).

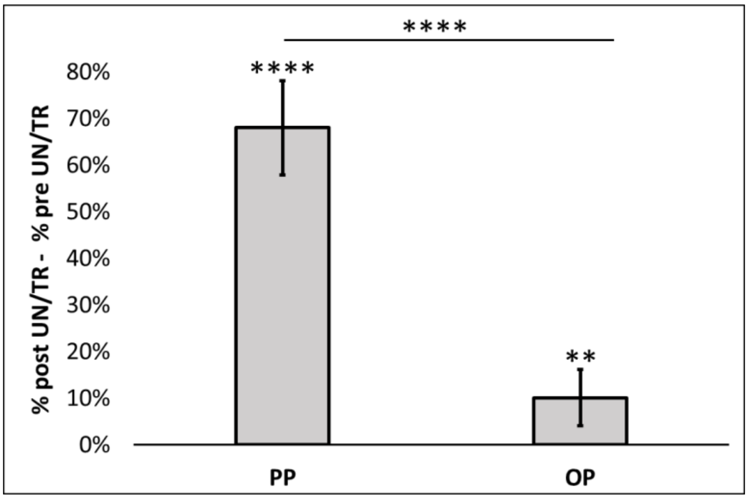


Figure 4.1 Training effect on sequence-specific learning. Error bars: 95% CI, ** p < 0.01, **** p < 0.0001; TR, trained; UN, untrained; PP, physical practice group; OP, observational practice group.

4.3.3 Fluid intelligence and working memory as predictors of the training effects

Primary analysis: sequence-specific learning

We used multiple regression analysis to test whether fluid intelligence and working memory predict the sequence-specific training effect. The baseline performance (an inverse of the pre-training average of trained and untrained sequence execution times) was also included in the model to control for the baseline performance differences which may contribute to the training effect.

All three predictor variables were intercorrelated but not so highly as to suggest multicollinearity. Fluid intelligence and working memory were positively correlated ($r = 0.432$, $p < 0.001$), and both fluid intelligence ($r = 0.423$, $p < 0.001$) and working memory ($r = 465$, $p < 0.001$) were positively correlated with the baseline performance.

The model with the three predictor variables significantly explained sequence-specific training effect variance in the PP group, however, fluid intelligence was the only significant predictor. When controlling for the baseline performance and working memory, the fluid intelligence explained 14% of the training effect variance. Higher fluid intelligence predicted higher sequence-specific training effect. Contrary to our predictions, none of the variables explained variance in the OP group. Results of the regression analyses are summarised in Table 4.2 (see also Appendix 4.3 for raw scatter plots of sequence-specific learning versus fluid intelligence/working memory for OP and PP groups).

Considering the possibility of an interaction between the baseline performance and cognitive abilities, we included interactions between the variables in the regression model. However, none of the interactions for neither PP nor OP group proved to be significant.

Table 4.2. Regression analysis summary of sequence-specific training effects.

	Physical practice			**Observational practice**		
Model	$F_{3,88} = 4.47$, $p = 0.006$, $R^2 = 0.132$			$F_{3,88} = 0.21$, $p = 0.886$, $R^2 = 0.007$		
Coefficients	**β [95% CI]**	**t**	**p**	**β [95% CI]**	**t**	**p**
Intercept	0	0	1	0	0	1
Baseline performance	- 0.203 [-0.456, 0.050]	-1.601	0.112	0.076 [-0.161, 0.313]	0.637	0.526
Fluid intelligence	0.373 [0.149 0.597]	3.312	0.001	0.026 [-0.227, 0.278]	0.202	0.841
Working memory	-0.165 [-0.419, 0.089]	-1.291	0.200	-0.053 [-0.292, 0.185]	-0.446	0.657

Although we were focusing on the sequence-specific training effect, a post-training improvement of untrained sequences (general skill learning) is inevitable (Janacsek & Nemeth, 2013; Meier & Cock, 2014). In our measurement, the sequence-specific learning (the post-training improvement of the trained vs. untrained sequences) was inversely related to the measure of the general skill learning (post-training improvement of the untrained sequences). Inevitably, participants with greater general skill learning would show lower sequence-specific learning. It is also possible that fluid intelligence and working memory have different effects on general compared to sequence-specific learning. It was not the aim of this study to investigate these differences; however, to better understand the relationship between the involved measures, we performed a secondary analysis.

Secondary analysis: general skill learning

In a secondary analysis, we investigated how the baseline performance, fluid intelligence and working memory predict general skill learning. General skill learning was measured as pre/post percentage difference of the untrained sequence execution times.

The model with the three predictor variables significantly explained the general skill learning variance in both PP and OP groups. In the PP group, lower baseline performance and higher working memory significantly predicted higher training effect on general skill learning. Fluid intelligence was not a significant predictor. In the OP group, as well, lower baseline performance predicted higher general skill learning, but neither fluid intelligence nor working memory was a significant predictor. Detailed results of the regression analyses are summarised in Table 4.3.

Table 4.3. Regression analysis summary of general skill learning.

	Physical practice			**Observational practice**		
Model	$F_{3,88} = 6.386$, $p = 0.0006$, $R^2 = 0.179$			$F_{3,88} = 6.582$, $p = 0.0005$, $R^2 = 0.183$		
Coefficients	**β [95% CI]**	**t**	**p**	**β [95% CI]**	**t**	**p**
Intercept	0	0	1	0	0	1
Baseline perf.	-0.514 [-0.760, -0.268]	-4.158	0.00007	-0.434 [-0.650, -0.219]	-4.02	0.0001
Fluid intelligence	-0.268 [-0.245, 0.191]	-0.245	0.807	0.082 [-0.147, 0.311]	0.715	0.476
Working memory	0.384 [0.137, 0.631]	3.089	0.003	-0.072 [-0.288, 0.144]	-0.664	0.508

An integrated visualisation of relationships among the involved measures is presented in Figure 4.2. For each group, in addition to the standardised beta estimates of the two regression models, the figure shows positive correlations among the three predictor variables and a negative correlation between the general skill learning and sequence-specific learning.

Overall, fluid intelligence and working memory were significant predictors of the physical practice effects, but none of the variables predicted observational practice effects. To further investigate what other variables could explain the variance in the physical and observational practice effects, we performed an exploratory analysis with 11 additional predictor variables.

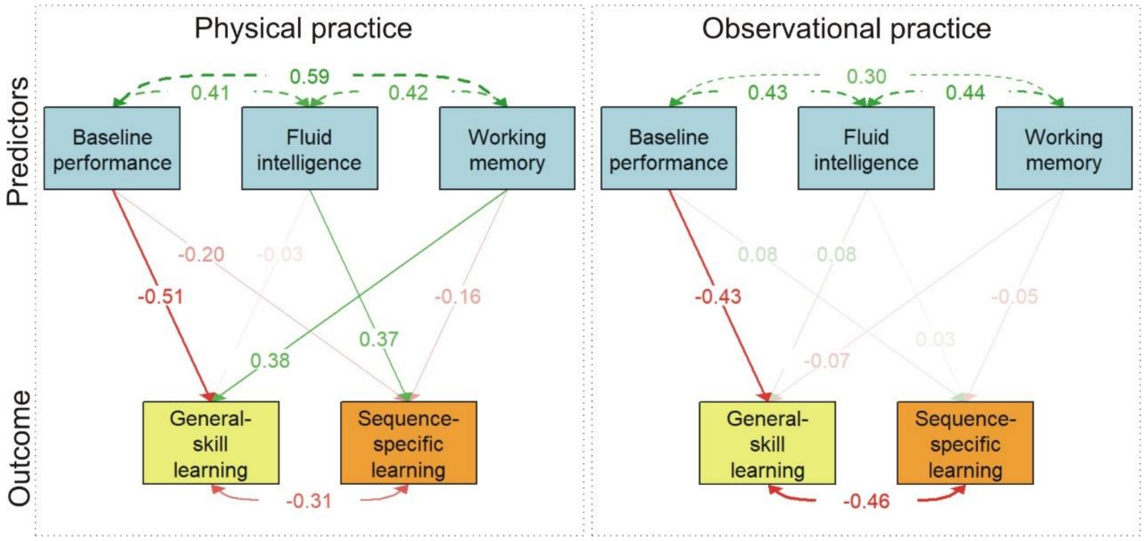


Figure 4.2. An integrated visualisation of relationships among the involved measures. For each group (physical practice and observational practice), the figure shows standardised beta estimates of how baseline performance, fluid intelligence and working memory predict the sequence-specific and general skill learning. In addition, the figure shows the predictor intercorrelation coefficients and outcome intercorrelation coefficients. Green: positive, red: negative, fading reflects significance.

4.3.4 Personality measures as additional predictors of the training effects

In an exploratory analysis, we added 11 additional predictor variables to help further explain the variance in the training effects. As in the main hypothesis testing, PP and OP groups were analysed separately, and all variables were converted to within-group z-scores. Some of the 14 predictor variables were intercorrelated, but not so high as to suggest multicollinearity (Figure 4.3A). For transparency, simple correlations between the training effects and each predictor variable for each group are presented in Figure 4.3B.

Primary analysis: sequence-specific learning

All-subsets regression analysis with BIC for model ranking (see *4.2.4 Analysis-Exploratory analysis*) returned only one subset of predictors that best explains the variance in the training effect on sequence-specific learning. For the PP group, the winning subset included fluid intelligence, working memory and agreeableness, explaining 18.5% of the variance. The winning model and all three predictor variables were significant (see Table 4.4 for detailed results). The result shows that in addition to higher fluid intelligence and lower working memory, higher agreeableness (and not the baseline performance as was reasoned in the primary analysis) is related to better sequence-specific training effects in the PP group. For the OP group, the winning subset included only one predictor variable: openness to experience. However, the winning predictor did not significantly explain the variance of sequence-specific training effect in the OP group (see Table 4.4 for detailed results). All rankings of the two best models for each number of predictors (1-14) for each group are presented in Appendix 4.1.

To investigate the possibility that individual differences in agreeableness might reflect gender differences (Schmitt, Realo, Allik, & Voracek, 2008), we repeated the all-subsets analyses including gender as an additional predictor variable. The repeated analyses did not change the results for either PP or OP group, indicating that there were no significant gender differences in the training effects.

Table 4.4. The winning models for sequence-specific learning.

	Physical practice				**Observational practice**		
Model	$F_{3,88} = 6.635$, $p < 0.001$, $R^2 = 0.185$			**Model**	$F_{1,90} = 1.81$, $p = 0.182$, $R^2 = 0.020$		
Coefficients	**β [95% CI]**	**t**	**p**	**Coefficients**	**β [95% CI]**	**t**	**p**
Intercept	0	0	1	**Intercept**	0	0	1
Fluid intelligence	0.395 [0.180, 0.611]	3.641	0.0005	**Openness**	0.140 [-0.067, 0.348]	1.345	0.182
Working memory	-0.329 [-0.545, -0.113]	-3.037	0.003				
Agreeableness	0.286 [0.089, 0.482]	2.888	0.005				

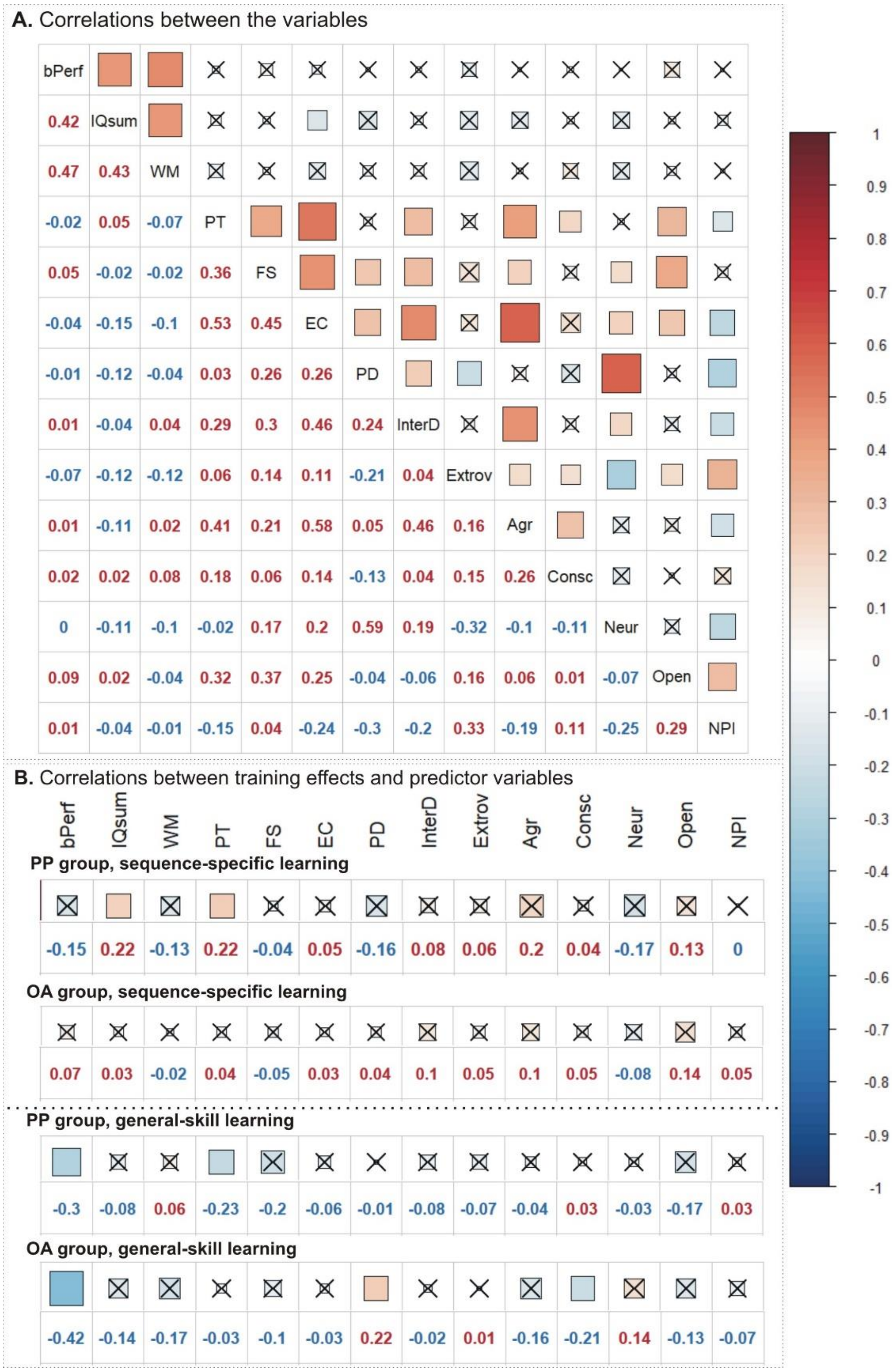
Secondary analysis: general skill learning

For the training effects on general skill learning, none of the personality measures helped further explain the variance in the PP group. The all-subsets regression analysis with BIC for model ranking returned baseline performance and working memory as the best predictors of the physical practice effects (see Table 4.5 for detailed results).

In the OP group, baseline performance and agreeableness best explained the variance of the training effect on general skill learning. Both lower baseline performance and lower agreeableness predicted higher general skill learning, however, agreeableness did not reach statistical significance (see Table 4.5 for detailed results). Adding gender as an additional predictor variable did not change the results for either the PP or OP group.

Table 4.5. The winning models for general skill learning.

	Physical practice				**Observational practice**		
Model	$F_{2,89} = 9.651$, $p < 0.001$, $R^2 = 0.160$			**Model**	$F_{2,89} = 11.81$, $p < 0.001$, $R^2 = 0.192$		
Coefficients	**β [95% CI]**	**t**	**p**	**Coefficients**	**β [95% CI]**	**t**	**p**
Intercept	0	0	1	**Intercept**	0	0	1
Baseline perf.	-0.521 [-0.711 -0.331]	-4.341	0.00004	**Baseline perf.**	-0.431 [-0.619, -0.243]	-4.569	0.00002
Working memory	0.377 [0.138, 0.615]	3.139	0.002	Agreeableness	-0.182 [-0.370, 0.006]	-1.929	0.057



A. Correlations between the variables

bPerf	□	□	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
0.42	IQsum	□	☒	☒	□	☒	☒	☒	☒	☒	☒	☒	☒
0.47	0.43	WM	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
-0.02	0.05	-0.07	PT	□	□	☒	□	☒	□	□	☒	□	□
0.05	-0.02	-0.02	0.36	FS	□	□	□	☒	□	☒	□	□	☒
-0.04	-0.15	-0.1	0.53	0.45	EC	□	□	☒	□	☒	□	□	□
-0.01	-0.12	-0.04	0.03	0.26	0.26	PD	□	□	☒	☒	□	☒	□
0.01	-0.04	0.04	0.29	0.3	0.46	0.24	InterD	☒	□	☒	□	☒	□
-0.07	-0.12	-0.12	0.06	0.14	0.11	-0.21	0.04	Extrov	□	□	□	□	□
0.01	-0.11	0.02	0.41	0.21	0.58	0.05	0.46	0.16	Agr	□	☒	☒	□
0.02	0.02	0.08	0.18	0.06	0.14	-0.13	0.04	0.15	0.26	Consc	☒	☒	☒
0	-0.11	-0.1	-0.02	0.17	0.2	0.59	0.19	-0.32	-0.1	-0.11	Neur	☒	□
0.09	0.02	-0.04	0.32	0.37	0.25	-0.04	-0.06	0.16	0.06	0.01	-0.07	Open	□
0.01	-0.04	-0.01	-0.15	0.04	-0.24	-0.3	-0.2	0.33	-0.19	0.11	-0.25	0.29	NPI

B. Correlations between training effects and predictor variables

	bPerf	IQsum	WM	PT	FS	EC	PD	InterD	Extrov	Agr	Consc	Neur	Open	NPI
PP group, sequence-specific learning	☒	□	☒	□	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	-0.15	0.22	-0.13	0.22	-0.04	0.05	-0.16	0.08	0.06	0.2	0.04	-0.17	0.13	0
OA group, sequence-specific learning	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	0.07	0.03	-0.02	0.04	-0.05	0.03	0.04	0.1	0.05	0.1	0.05	-0.08	0.14	0.05
PP group, general-skill learning	□	☒	☒	□	☒	☒	☒	☒	☒	☒	☒	☒	☒	☒
	-0.3	-0.08	0.06	-0.23	-0.2	-0.06	-0.01	-0.08	-0.07	-0.04	0.03	-0.03	-0.17	0.03
OA group, general-skill learning	□	☒	☒	☒	☒	☒	□	☒	☒	☒	□	☒	☒	☒
	-0.42	-0.14	-0.17	-0.03	-0.1	-0.03	0.22	-0.02	0.01	-0.16	-0.21	0.14	-0.13	-0.07

Figure 4.3. Simple correlations between the variables. The figure shows correlation coefficient values and their representations as squares. Positive correlations are displayed in red and negative correlations in blue colour. Colour intensity and size of the squares are proportional to the magnitude of the correlation. Crossed squares represent non-significant ($p < 0.05$) correlations. **bPerf**, baseline performance; **IQsum**, fluid intelligence; **WM**, working memory; **PT**, perspective taking; **FS**, fantasy; **EC**, empathic concern; **PD**, personal distress; **InterD**, interdependence; **Extrov**, extraversion; **Agr**, agreeableness; **Consc**, conscientiousness; **Neur**, neuroticism; **Open**, openness to experience; **NPI**, narcissism. **A.** Correlations between all 14 predictor variables. **B.** Correlations between the training effects and predictor variables.

4.3.5 Working memory predicts general skill learning but not sequence-specific learning in the PP group

In the PP group, the observed negative relationship between working memory and sequence-specific learning is likely due to individuals with higher working memory being better at general skill learning, and the general skill learning measure being inversely related to the sequence-specific learning measure. To examine this possibility, we included the post-training performance of untrained sequences as an additional regressor to the winning model of the sequence-specific learning and repeated the regression analysis. As before, the model significantly explained the variance of the sequence-specific training effect in the PP group ($F_{4,87} = 6.555$, $p = 0.0001$, $R^2 = 0.232$). Fluid intelligence ($\beta = 0.441$, $p = 0.0001$) and agreeableness ($\beta = 0.280$, $p =0.005$) were still significant positive predictors; the post-training performance of untrained sequences was a significant negative predictor ($\beta = 0.262$, $p = 0.023$; higher sequence-specific learning was related to poorer performance of the untrained sequences post-training); but working memory was not a significant predictor anymore ($\beta = -0.201$, $p = 0.080$).

Accordingly, the overall results indicate that working memory does not play a significant role in physical practice effects on sequence-specific learning, but is a significant predictor of general skill learning.

4.3.6 Fluid intelligence and working memory as predictors of perceptual improvements

It is important to emphasise that during the practice sessions the OP group had to engage in two parallel tasks: learning the motor sequence and detecting errors in the observed model's performance. Because error detection was an explicit task that the OP group was asked to perform, we were interested to see whether fluid intelligence and working memory are related to the perceptual improvements.

Across the four observational practice sub-sessions (runs), the mean error detection accuracy in the OP group was 89% [87%, 91%]. There was a significant improvement from run 1 to run 2 ($t_{91} = 3.99$, $p = 0.0001$) with no significant improvements in the following runs ($p > 0.380$; see Figure 4.4A).

We excluded run 1 from the subsequent analysis assuming that during the first sub-session error detection accuracy reflected not only participants' perceptual abilities but largely also a general unfamiliarity with the task. Therefore, observational practice-related perceptual improvement was measured as error detection accuracy difference between run 4 and run 2 (results of run 4 vs. run 1 instead are included in Appendix 4.2.). Although on average there was no significant difference between the two runs, it was still worth investigating individual differences in participants' perceptual improvements. Importantly, we were able to measure only the general (pre- to post- training improvement) not the sequence-specific perceptual improvement as participants were never asked to watch the untrained sequences. An investigation of sequence-specific perceptual improvements should be carried out in future studies.

The error detection accuracy at run 2 (as a baseline performance), fluid intelligence, and working memory measures were z-scored and included in a multiple regression analysis to test whether they predict the error detection accuracy improvement from run 2 to run 4. The regression model significantly explained the variance in the perceptual improvement measure, with lower baseline performance and higher working memory as significant predictors (see Table 4.6 and Figure 4.4B). Note that a similar result was found for the general motor skill learning in the PP group (Table 4.3). Overall, in the OP group, working memory was a significant predictor for general perceptual improvements but not for the motor skill learning.

Further, we investigated whether the error detection accuracy would help explain motor skill learning in the OP group. To do so, we repeated the all-subsets analyses (as in section 4.3.4) including the mean error detection accuracy (the mean across all four runs and the mean of runs 2 to 4) as an additional predictor variable. The repeated analyses did not change the results for either the sequence-specific nor general skill learning in the OP group, implying that error detection ability did not significantly influence motor skill acquisition through observation.

Table 4.6. OP group perceptual improvement (from run 2 to run 4) regression analysis summary.

	Run4 – Run2 accuracy		
Model	$F_{3,88} = 16.56$, $p < 0.0001$, $R^2 = 0.334$		
Coefficients	**β [95% CI]**	**t**	**p**
Intercept	0	0	1
Run2 accuracy	-0.588 [-0.765, -0.411]	-6.618	< 0.0001
Fluid intelligence	0.144 [-0.052, 0.341]	1.463	0.147
Working memory	0.203 [0.014, 0.393]	2.133	0.036

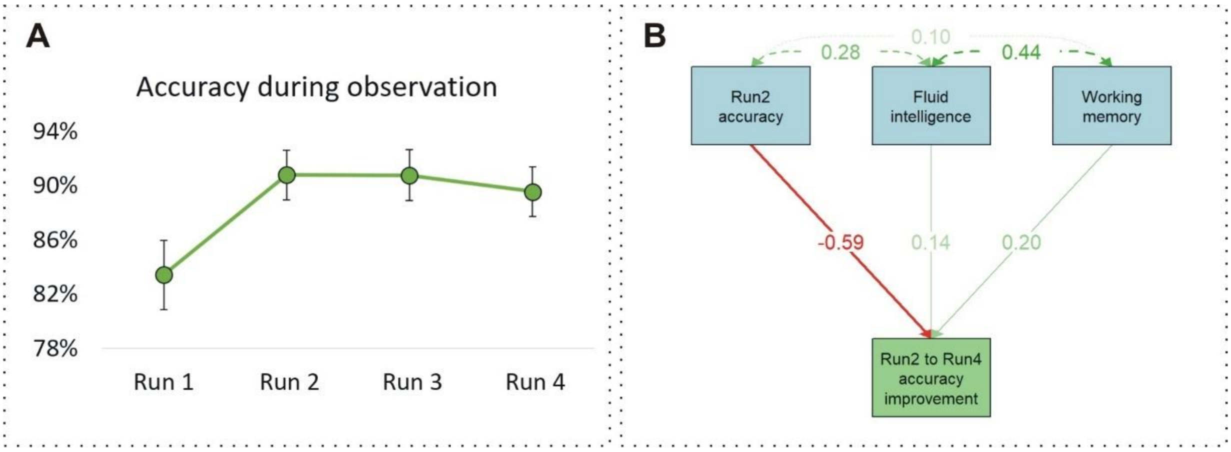


Figure 4.4. Error detection accuracy and perceptual improvement predictors. A. Group-averaged accuracy in response to the error question during observational training. Error bars represent within-subject (Cousineau, 2005) 95% CI. **B.** Perceptual improvement predictor variables. The figure shows standardised beta estimates of how error detection accuracy in run 2, fluid intelligence, and working memory predict the perceptual improvement from run 2 to run 4. In addition, the figure shows the predictor intercorrelation coefficients. Green: positive, red: negative, fading reflects significance.

4.4 Discussion

Based on the premise of shared mechanisms between action observation and execution (Gentsch et al., 2016; Rizzolatti & Sinigaglia, 2010), we examined whether the same factors explain individual differences in learning through physical and observational practice. We hypothesised that individuals' cognitive abilities, specifically fluid intelligence and working memory, would positively predict both physical and observational practice effects (Aim 1, see *4.1 Introduction*), as both types of learning involve high-order cognitive processes. In addition, we explored whether individuals' self-other relations and broad personality characteristics further explain the variance in observational practice effects and how this compares to physical practice (Aim 2). In general, we found that both physical and observational practice facilitated motor skill acquisition. Fluid intelligence, working memory, and agreeableness were significant predictors of the physical practice effects. However, contrary to our predictions, none of our measures of interest explained variance for the observational practice effects.

4.4.1 Individual differences in physical practice effects on skill acquisition

In line with previous reports (Bo & Seidler, 2009; Christou et al., 2016; Gebauer & Mackintosh, 2007; Janacsek & Nemeth, 2013; Maxwell et al., 2003; Reber et al., 1991; Unsworth & Engle, 2005), we found that both higher working memory and fluid intelligence support learning through physical practice. Furthermore, although working memory and fluid intelligence were correlated, they also supported different processes, as reported previously

(Ackerman, Beier, & Boyle, 2005; Kane, Hambrick, & Conway, 2005; Shipstead, Harrison, & Engle, 2016; Wang et al., 2017). Specifically, working memory contributed to general skill learning, while fluid intelligence contributed to sequence-specific learning.

General skill learning refers to an overall faster execution of both trained and untrained sequences due to familiarity with the task and increased tapping speed. Sequence-specific learning refers to acquiring knowledge of the sequence structure, enabling fast and smooth sequence execution. Our aim was not to compare the two types of learning, *per se*. Instead, we were primarily interested in sequence-specific learning, as it better reflects the actual sequence skill learning over general performance improvements (Janacsek & Nemeth, 2013; Wong, Lindquist, Haith, & Krakauer, 2015). However, in our measurement, the sequence-specific learning was inversely related to the measure of the general skill learning. Inevitably, participants with greater general skill learning would show lower sequence-specific learning. Furthermore, it is possible that fluid intelligence and working memory have different effects on general compared to sequence-specific learning. Therefore, to better understand the relationship between the involved measures, we examined individual differences in both general skill and sequence-specific learning.

Participants' baseline performance and working memory (but not their interaction or fluid intelligence) significantly predicted physical practice effects on general skill learning. Individuals who performed well already at the beginning of the experiment benefited less from physical practice than individuals with poor initial performance. However, even though individuals with higher working memory performed better at the baseline measure, they also exhibited greater general skill learning than individuals with lower working memory. Contrary, higher fluid intelligence and agreeableness predicted beneficial effects of physical practice on sequence-specific learning. However, neither working memory, nor baseline performance, nor their interaction played a significant role in sequence-specific learning.

It has been suggested before that working memory might be more related to general skill learning rather than sequence-specific learning (Janacsek & Nemeth, 2013; Rhodes et al., 2004). Working memory is important in supporting attention and maintaining task goals (Unsworth & Engle, 2005). These abilities are essential for general task performance, which relies on short-term memorisation of the cued sequence and fast execution of discrete keypresses. By contrast, sequence-specific skills, in addition to general task performance, involve long-term memory retrieval of the trained sequence and integration of its discrete keypresses into a unified sequence representation (Abrahamse et al., 2013; Verwey, 1996).

Long-term memory retrieval has been linked to intelligence (Alexander & Smales, 1997), and, consistent with our findings, previous reports show that fluid intelligence predicts learning and retrieval processes beyond the influence of working memory (Wang et al., 2017).

Besides fluid intelligence, agreeableness explained an additional 8% of the variance in sequence-specific learning by physical practice. Individuals who score highly on agreeableness are characterised as being cooperative and exhibiting high self-control to comply with external demands (McCrae & Löckenhoff, 2010). In the context of learning, agreeable individuals are more motivated and willing to make an effort at performing the task at hand (Bidjerano & Dai, 2007; Vermetten, Lodewijks, & Vermunt, 2001). Thus, it is plausible to suggest that the higher motivation and engagement with the task, as demonstrated by agreeable individuals, can facilitate motor skill acquisition through physical practice.

4.4.2 Individual differences in observational practice effects on skill acquisition

As in learning through physical practice, learning through observation involves high-order cognitive processes (Hodges et al., 2011; Lim et al., 2014; Maslovat et al., 2010b; Vogt & Thomaschke, 2007). Therefore, we hypothesised that the same cognitive abilities (fluid intelligence and working memory) should explain individual differences in both types of skill acquisition. However, our results did not support this hypothesis.

Previous research shows that fluid intelligence and working memory are significant predictors for explicit, but not implicit, learning. Under explicit conditions, individuals engage in intentional cognitive processes of attention and executive control. It is suggested that intentional control processes facilitate learning through hypothesis-testing strategies (Maxwell et al., 2003; Norman, Price, & Duff, 2006; Unsworth & Engle, 2005). Namely, the performer is constantly establishing and monitoring how their motor output matches the desired outcome (e.g., through internal inverse and forward models of motor control; Wolpert & Ghahramani, 2000). Such hypothesis-testing is not possible in implicit (unintentional) learning, as the performer is not consciously aware of what the desired outcome is. When learning by observation, although the desired outcome is known, direct monitoring of the motor output is not possible, making the hypothesis-testing impossible as well. Perhaps although deliberate cognitive processes are involved in observational learning, the limited aspect of hypothesis-testing makes observational learning itself more implicit than explicit in its nature.

The experimental procedure employed in our study might have further contributed to the implicit nature of sequence learning in the OP group. During the practice sessions the OP group had to engage in two parallel tasks: watch and learn the motor sequence, and watch and detect errors in the model's performance. The error detection was an explicit task that the OP group was asked to perform, making the sequence learning itself a rather secondary task. In contrast, the main task for the PP group was a fast and accurate execution of the cued sequences, receiving constant feedback, thus encouraging performance improvement. In retrospect, we acknowledge that physical practice *without* feedback would have been more appropriate for comparing the effects of learning by physical and observational practice. This adjustment should be considered in future studies, as has been advocated by Kirsch and Cross (2015). Furthermore, follow-up research efforts may wish to exclude the attention (error detection) task during observational practice, to avoid sequence learning becoming a secondary task. For example, eye tracking could be applied instead to assess participants' attention during observational practice.

Our results support the notion of the explicit/implicit nature of the two parallel tasks the OP group was performing. Specifically, we found that working memory was a significant predictor of the error detection accuracy improvement (the explicit task), but not for the motor skill learning through observation (the implicit task). We speculate that in the present study, sequence-learning by observation was indeed rather implicit in nature, explaining why cognitive abilities and personality measures did not emerge as reliable predictors of practice effects. Previous research shows that implicit learning has little variation across individuals[1] (Kaufman et al., 2010; Reber et al., 1991). To our knowledge, only age (Howard & Howard, 1997; Howard et al., 2004) and self-report measures of openness (Kaufman et al., 2010) relate to individual differences in implicit learning. We did not include age as a predictor variable because our participant sample was rather homogeneous regarding age[2]. Perhaps of most interest, among all 14 predictor variables, openness was the one that best explained the variance in observational practice effects on sequence-specific learning (even though it did not reach statistical significance).

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[1] Noteworthy, in our study too the OP group overall had less variation in the training effects across participants than in the PP group (smaller CI range; see Figure 4.1 and Appendix 4.3).

[2] In fact, out of curiosity, we checked the results with age included as an additional predictor variable in our exploratory all-subsets regression analyses (as in section 4.3.4). Indeed, despite our homogenous sample, age explained the sequence-specific learning variance in the OP group slightly better than openness, however it was still not significant. Age was not related to any other measure, neither baseline performance nor PP effects on skill acquisition.

We reasoned that the existence of motor resonance during action observation and possible common mechanisms between motor resonance and affective resonance (encompassing a broader notion of empathy that includes “inner imitation” of what others do, think, or feel), would support a link between self-other relations and motor learning through observation. However, our results did not support this reasoning. Although some evidence exists of a relationship between individuals’ empathy scores and motor resonance during action observation (Gazzola et al., 2006; Kaplan & Iacoboni, 2006; Milston et al., 2013; Perry et al., 2010), the effects might be too small to contribute to behavioural differences discernible in a task like that used in the present study. For example, Gazzola et al. (2006) showed higher motor resonance for individuals with higher perspective taking scores, but behavioural differences were not observed. In addition, reports of positive (Gazzola et al., 2006; Kaplan & Iacoboni, 2006), negative (Milston et al., 2013; Perry et al., 2010), and nonexistent (for a review, see Baird, Scheffer, & Wilson, 2011) relationships between empathy and motor resonance exist. While the link between self-other relations and motor resonance might exist, its direction and contribution to observational learning success is likely context-dependent and possibly depends on other factors that we did not measure in the present study.

4.4.3 Conclusions

Our results do not support the hypothesis that fluid intelligence and working memory explain individual differences in motor skill acquisition through both physical and observational practice. Although consistent with previous reports, higher working memory and fluid intelligence predicted physical practice effects, they did not play a significant role in learning by observation. Furthermore, neither self-other relations nor broad personality characteristics explained variance in observational practice effects. We speculate that the limited aspect of hypothesis-testing makes observational learning more implicit than explicit in nature. Unlike explicit learning, implicit learning has little variation across individuals. Besides, possibly the rather homogeneous sample of college students contributed to the null findings of personality differences in motor skill acquisition in our study.

CHAPTER 5

General discussion

Previous research suggests that mechanisms that underlie the ability to learn by observation are similar to the mechanisms of learning through physical practice (for a review, see Chapter 1). However, it remains poorly understood to what extent observational practice changes the neural representations of the acquired skill, and whether observational learning is influenced by the same factors as learning by doing. Employing a keypress sequence learning paradigm and brain imaging, brain stimulation, and behavioural methods we investigated three parallel questions to help to provide a more comprehensive and integrative perspective on motor skill learning through observation and how it compares to previous findings on learning by doing.

5.1 A summary of the main findings

5.1.1 Specificity of internal action representations

In Study 1 (Chapter 2) we investigated whether action observation establishes movement-sequence-specific neural representations that become more distinct with observational practice like reported in the physical practice study by Wiestler and Diedrichsen (2013). We found that, indeed, action observation evoked sequence-specific neural representations in multiple frontoparietal brain areas. However the representations were not more distinct for the observationally trained compared to the untrained sequences.

Nevertheless, for the first time, we show that mere observation of kinematically matched keypress sequences establishes sequence-specific representations (brain activity patterns) in the observer’s parietal and premotor brain regions. The finding suggests that the observed keypresses were encoded as unified actions at an abstract level of motor hierarchy which is likely shared with planning one’s own actions (Prinz, 1997). Furthermore, we found decreased activity in the frontoparietal brain regions and their increased coupling with the secondary somatosensory area (parietal operculum) when watching the sequences again after four days of observational practice. The brain activity and connectivity changes likely indicate reduced cognitive demand and greater neural efficiency following practice (Kelly & Garavan, 2005). Similar brain activity changes have been linked to more established neural representations of physically trained sequences (Wiestler & Diedrichsen, 2013). However, our results did not show more distinct representations for the observation of trained compared to untrained sequences. Possibly, internal representations of observed, compared to executed sequences, are less distinct. Consequently, the differences between trained and untrained sequence representations of observed actions might be subtler and more difficult to detect than representations of executed actions. In addition, brain areas with more specialised representations of the trained sequences might not be covered with our analysis, for example, cerebellum and basal ganglia.

5.1.2 Feasibility of non-invasive brain stimulation to facilitate observational practice effects

In Study 2 (Chapter 3) we investigated whether non-invasive brain stimulation could facilitate observational practice effects, as reported for learning through physical practice. We found no beneficial effects of the brain stimulation on motor skill acquisition through observation.

Previous reports show that anodal transcranial direct current stimulation (tDCS) of the primary motor cortex (M1) facilitates motor skill learning through physical practice (for reviews, see Ammann et al., 2016; Buch et al., 2016; Hashemirad et al., 2016; Reis & Fritsch, 2011). We too chose to stimulate M1, although M1 is not typically considered a part of the human mirror system. We decided based on the growing evidence that M1 plays an important role in observational learning and that M1 activity during observational practice might be critical for the learning success (Aridan & Mukamel, 2016). However, our results did not support the hypothesis that observational practice coupled with the anodal tDCS over M1 would have beneficial effects compared to observational practice alone. The null finding does not necessarily imply that M1 is not critically involved in motor skill learning by observation, although this possibility cannot be ruled out.

Our brain imaging results from Study 1 revealed potential target areas for future investigations of brain stimulation effects on observational practice. For example, the parietal operculum (secondary somatosensory area) might be of special interest. Our results showed that the frontoparietal brain areas that exhibited observational practice-related activity decreases were stronger coupled with the contralateral parietal operculum when watching trained compared to untrained sequences. The parietal operculum has been implicated in the memory storage and retrieval of movement sequence representations and planned actions (Jubault et al., 2007; Valyear & Frey, 2015). The parietal operculum also emerged as an area that showed sequence-specific neural representations following observational practice. Observational practice-related increase in coupling with the frontoparietal brain areas and formation of sequence-specific action representations indicate that parietal operculum plays an important role in motor skill acquisition through observation.

5.1.3 Individual differences in learning through observation

In Study 3 (Chapter 4) we investigated whether individual differences in learning through observation are explained by the same cognitive abilities and personality characteristics as in learning by physical practice. In line with previous reports (Bo & Seidler, 2009; Christou et al., 2016; Gebauer & Mackintosh, 2007; Janacsek & Nemeth, 2013; Maxwell et al., 2003; Reber et al., 1991; Unsworth & Engle, 2005), we found that fluid intelligence and working memory were significant predictors of the physical practice effects on the motor skill acquisition. However, neither fluid intelligence or working memory, nor any of the personality measures helped explain the variance of motor skill learning through observation. We speculate that the limited aspect of hypothesis-testing strategies for motor control makes observational learning more implicit than explicit in nature.

5.2 Observational practice facilitates motor skill acquisition

Behavioural results from all three studies contribute to the evidence (Bird & Heyes, 2005; Heyes & Foster, 2002; Lago-Rodríguez & Cheeran, 2014; Vogt & Thomaschke, 2007) that motor skills can be learned by observation without overt physical practice. In our behavioural measures, we controlled for various aspects to ensure that the reported motor skill improvements reflect observational practice effects as closely as possible.

In all three studies, before undergoing observational training, participants physically performed both observationally trained and untrained sequences. Consequently, the post-training performance improvement, at least partly, could be driven by the consolidation of the initial physical performance (Censor et al., 2012). To account for this factor and to capture the observational practice effects as accurately as possible, we focused our analyses on sequence-specific learning, measuring the post-training difference between trained and untrained sequences. In addition, we accounted for unwanted differences in the difficulty of trained and untrained sequences. Hence, it is plausible to assume that the sequence-specific performance improvement reported in our studies was achieved merely through the observational practice. Furthermore, we posit that the observational practice-related motor skill improvement in our studies cannot be explained solely by memorising the digit sequence or by the familiarity with the spatiotemporal pattern of the sequence obtained by stimulus observation. Although we did not control for it in our studies, previous reports show that observing the actual action performed by an actor contributes to performance improvement (Boutin et al., 2010; Van Der Werf et al., 2009).

Our results across the three studies indicate that multiple days of observational practice have no advantage over a single practice day. In Study 1 and Study 2 participants underwent four days of training and practised four sequences, while in Study 3, they only had a single day of training and practised two sequences. To see whether multiple days of observational training provide larger effect than a single day of training, we compared the results across all three studies[1]. We found no significant difference among the three studies in terms of the observational practice effects on sequence-specific learning ($F_{1,157} = 0.544$, $p = 0.582$; see Figure 5.1). The finding may imply that multiple day training, compared to a single day training, has no advantage on skill acquisition through observation. Such conclusion would contradict previous findings showing that as with physical practice, a longer period of observational practice leads to better skill acquisition (Andrieux & Proteau, 2013). Although this possibility cannot be ruled out, it is more likely that learning four sequences in Study 1 and Study 2 was more demanding than learning only two sequences in Study 3. Thus, unfortunately, we cannot reliably compare the training effects across the three studies. The question about the multiple versus single day training effects on observational learning should be investigated in more detail in future studies.

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[1] Originally, the training effects in each study were calculated in slightly different ways. Here for simplicity we calculated the observational training effects on sequence-specific learning as an absolute difference between trained and untrained sequence execution times post-training, not accounting for possible per-training differences. In this comparison, from Study 2 both sham and active stimulation group participants were included, but from Study 3 only participants from the observational practice group were included.

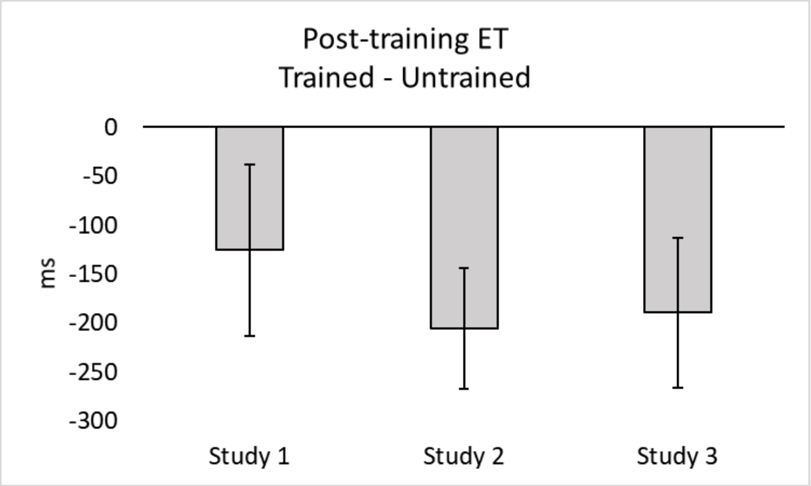

Figure 5.1 Observational training effect on sequence-specific learning across the three studies. In Study 1 and Study 2 participants practised four sequences for four days, while in Study 3, two sequences in a single day. Error bars: 95% CI. ET, Execution time.

5.3 Role of cognitive processes in learning through observation

In Study 1 we found that activity in the frontoparietal brain regions reduced when participants watched trained compared to untrained sequences. These regions are part of a frontoparietal network involved in a wide range of processes, including working memory, attention, and mental imagery (Ikkai & Curtis, 2011; Lückmann et al., 2014; Rottschy et al., 2012), as well as action observation and execution (Caspers et al., 2010; Gazzola & Keysers, 2009; Molenberghs et al., 2012; Oosterhof et al., 2013; Rizzolatti & Sinigaglia, 2010). Reduced activity in the frontoparietal brain regions has been reported both following physical as well as observational practice implying a decrease in cognitive demand as skill acquisition shifts from cognitive to automatic processing (Higuchi et al., 2012; Kelly & Garavan, 2005; Sakreida et al., 2017).

Observing the sequences was a cognitively demanding task. According to the task instructions, participants had to engage in multiple parallel tasks: holding in memory the cued sequence, paying attention to the videos to detect errors in the model's performance, and to learn the observed motor sequences. Decreased brain activity in the frontoparietal areas following observational practice may indicate lower cognitive demand when watching the trained sequences. We wonder, which aspect of the task would became less cognitively demanding? Was the lower cognitive demand reflecting less effort in memorising the cued sequence, less effort in detecting the model's errors, or less effort due to the acquired motor skill?

In Study 3 we hypothesised that due to the high-order cognitive processing in learning by observation, individuals' cognitive abilities, such as working memory and fluid intelligence, would be related to the motor skill acquisition through observation. However, our results did not confirm this hypothesis. Motor skill acquisition through observation was not related to either working memory nor fluid intelligence. Instead, we found that working memory was a significant predictor of improved ability to detect the model’s errors. Improved action discrimination, following observational practice, has been reported before (Black & Wright, 2000; Lago-Rodriguez et al., 2013; Maslovat et al., 2010b), and it is acknowledged that observational practice facilitates both action discrimination and motor learning (for a review, see Lago-Rodríguez & Cheeran, 2014).

The relationship between working memory and improved perceptual abilities reported in Study 3, indicate that the brain activity decrease in Study 1 was likely more related to the attention task (the error detection) and not to the motor skill acquisition. We speculate that motor skill acquisition was rather an implicit process running in parallel to the explicit and cognitively demanding error detection task. The implicit nature of the motor skill acquisition through observation could explain why cognitive abilities and personality measures did not emerge as reliable predictors of practice effects as previous research shows that implicit learning has little variation across individuals (Kaufman et al., 2010; Reber et al., 1991).

We speculate that cognitive processes involved in learning through physical practice are directed towards hypothesis-testing strategies (Maxwell et al., 2003; Norman et al., 2006; Unsworth & Engle, 2005). Explicitly, establishing and monitoring how the motor output matches the desired outcome (e.g., through internal inverse and forward models of motor control; Wolpert & Ghahramani, 2000). Contrary, the cognitive processes involved in learning through observation might be directed towards explicit perceptual processing and attention, but may not be critical for motor skill acquisition. Although both physical practice and observational practice may engage in the internal feedforward models of motor control (Flanagan et al., 2003; Friston et al., 2011; Iacoboni, 2005; Oztop et al., 2006), perhaps observational practice is more about hypothesis building while physical practice is more about hypothesis testing. Future studies should investigate these possibilities.

5.4 Limitations

5.4.1 Lack of physical practice groups/conditions in Study 1 and Study 2

A weakness of the thesis is the lack of physical practice groups in Study 1 and Study 2 limiting our conclusions on how learning by observation compares to learning by doing. Consequently, we could only refer to the previously published reports on learning by physical practice and provide an indirect comparison of the two learning types.

We decided to only have an observational practice group and observational practice condition in the Study 1 and Study 2 due to both practical and methodological considerations. Introducing a second, physical practice group, would have doubled the sample size. Because in both studies each participant had to attend six sessions, doubling the sample size was not feasible due to the time constraints of the thesis.

A possible solution could have been to have participants practice one set of sequences by observation and another set by physical practice in a within-subjects design. Such an approach was used, for example, by Higuchi et al. (2012). However, we decided against a within-subject design due to the high likelihood of skill transfer between physical and observational practice conditions. Possibly transfer effects are less concerning for different types of guitar chords used by Higuchi and colleagues. However, for the continuous multi-finger sequences used in our study, significant transfer effects are inevitable because the 12 sequences used in the paradigm shared a substantial proportion of movement transitions between specific finger pairs (Wiestler & Diedrichsen, 2013). In the original study of the paradigm, Wiestler and Diedrichsen (2012; also Wiestler et al., 2014) acknowledged considerable transfer effects (general skill learning) from trained to untrained sequences. All three studies of the present thesis also showed post-training improvement of untrained sequences. As with the skill transfer from trained to untrained sequences, similarly, there would be some skill transfer from physically to observationally practised sequences and vice versa. Consequently, a clear separation of physical practice and observational practice effects in the post-training performance measurements would not be possible.

For the same reason, we did not use novel sequences at the post-training test of untrained sequence performance in our studies. Instead, we used the same set of untrained sequences at the pre-training and post-training tests. In this context, it is useful to recall that in our studies, to assess the baseline performance, participants physically performed all trained and untrained sequences prior to the observational practice phase. Accordingly, post-training performance improvement of the trained sequences could be both a result of the observational practice and the consolidation of the initial physical performance (Censor et al., 2012). However, because untrained sequences were also physically performed before the training phase, we could separate the physical performance and observational practice effects by assessing the post-training performance difference of trained and untrained sequences. Moreover, this approach allowed us to also separate the observational practice effects of sequence-specific skill learning from the general skill learning (transfer of the observational practice effects to the untrained sequences).

We argue that our approach is a more robust way to assess observational practice effects on motor skill learning compared to within-subjects designs of physical and observational practice conditions. For future studies, we advocate for independent physical practice and observational practice groups (as in our Study 3) because within-subject physical practice and observational practice conditions would not allow clear separation of physical and observational practice effects.

5.4.2 Differences between physical and observational practice conditions

The physical performance (pre-test and post-test phases in all studies) and physical practice (in Study 3) phases in our studies corresponded closely to the original Wiestler and Diedrichsen (2012) paradigm. However, the observational practice phase (in all studies) differed not only in the mode of practice (watching instead of doing) but in two additional essential aspects: lack of continuous performance feedback and the secondary task to detect the model’s errors.

Performance feedback during physical practice

In the physical practice trials, participants continuously received feedback on their performance speed and accuracy. The feedback may motivate participants to continuously improve their performance and facilitate skill acquisition (Wulf & Prinz, 2001). Such feedback on how well a participant has learned the practised sequence and the feedback-based performance updating is not possible during observational practice. Certainly, performance feedback and feedback-based performance updating are distinguishing learning by doing and learning by observation in natural learning environments. However, in experimental settings, comparing rather basic mechanisms of physical versus observational practice, physical practice without feedback would have been more appropriate. This adjustment should be considered in future studies, as has been advocated by Kirsch and Cross (2015).

An additional task during observational practice

During the observational practice phases participants had to engage in two parallel tasks: watch and learn the motor sequence, and watch and detect errors in the model's performance. The error detection task was introduced to keep participants focused on the videos and to monitor participants' attention. However, the error detection task possibly made the sequence learning itself rather an implicit secondary task. In other words, participants were likely more focused on detecting the model's errors instead of fully concentrating on sequence learning. Follow-up research efforts may wish to exclude the attention (error detection) task during observational practice, to avoid sequence learning becoming a secondary task. For example, eye tracking could be applied instead to assess participants' attention during observational practice. A drawback of such a passive assessment method would be that it would no longer provide an incentive for the participants to keep their attention on the videos.

5.4.3 Model's performance speed

Another potential limitation of our work is the model's performance speed. The choice of a model is an essential methodological consideration. Previous reports show that a model's characteristics are a critical factor for the achievement of favourable training effects (for a review, see Maslovat et al., 2010a).

We decided for an intermediate beginner speed of the model's performance with the primary concern that faster performance might be too difficult to process visually. We determined the intermediate beginner's performance level from behavioural pilot test results, where the average correct sequence execution time at the baseline was 2.29 seconds (N = 17, M = 2.29 s, SE = 0.14). In fact, this performance was on average significantly slower (t_{249} = 5.65, $p < 0.001$) than the baseline performance of our participants across all three studies (N = 250, M = 2.05 s, SE = 0.04) with 68% of participants performing faster at the baseline than the model on average. Perhaps the observational practice participants in our study were not sufficiently challenged by the comparatively slow model performer. For example, Aridan and Mukamel (2016) reported better motor skill learning via observation if the observed model's performance was faster than the observer's performance at baseline.

Future studies, using our paradigm, should adjust the model's sequence execution speed at least to the average of 2.05 seconds (determined by the large sample size of 250 across our studies). Moreover, it would be beneficial to test the observational practice effects with a more advanced model's performance. For example, a model could perform at a level in between of a beginner and expert. Based on our results, the average sequence execution time at this level would be 1.76 seconds[1]. Visual processing of the model's behaviour might be challenging at this speed and would require prior assessment via pilot tests. However, in our experience, participants' ability to follow and discriminate the model's keypresses improves over time and should not be an issue if a model performs 23% faster than in our paradigm.

5.5 Conclusions

Previous research suggests that learning through observation and physical practice involve similar mechanisms and processes. Across the three studies, we found some similarities and some differences in learning by observation and how it compares to previously published reports on learning by doing. Specifically, we found that same as physical practice, observational practice provides behavioural benefits on motor skill acquisition. Furthermore, same as physical performance (Wiestler & Diedrichsen, 2013), action observation establishes distinguishable sequence-specific activity patterns in premotor and parietal brain areas. However, unlike following physical practice, the sequence-specific activity patterns did not become more specialised following observational practice. Moreover, unlike with physical practice, anodal tDCS of M1 during observational practice provided no benefits for motor skill acquisition by observation. In addition, it appears that cognitive processes play a different role in learning by observation than in learning by doing. Perhaps although deliberate cognitive processes are involved in observational learning, the limited aspect of hypothesis-testing makes observational learning itself more implicit than explicit in its nature.

And finally, punting is indeed not as easy as it looks, but the more you watch, the easier it gets! Watching with a brain stimulation cap on, might not be very feasible, though.

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[1] Determined as an average of the mean sequence execution time at the baseline (N = 250, M = 2.05 s, SE = 0.04) and the mean sequence execution time following observational practice (N = 158, M = 1.48 s, SE = 0.04).

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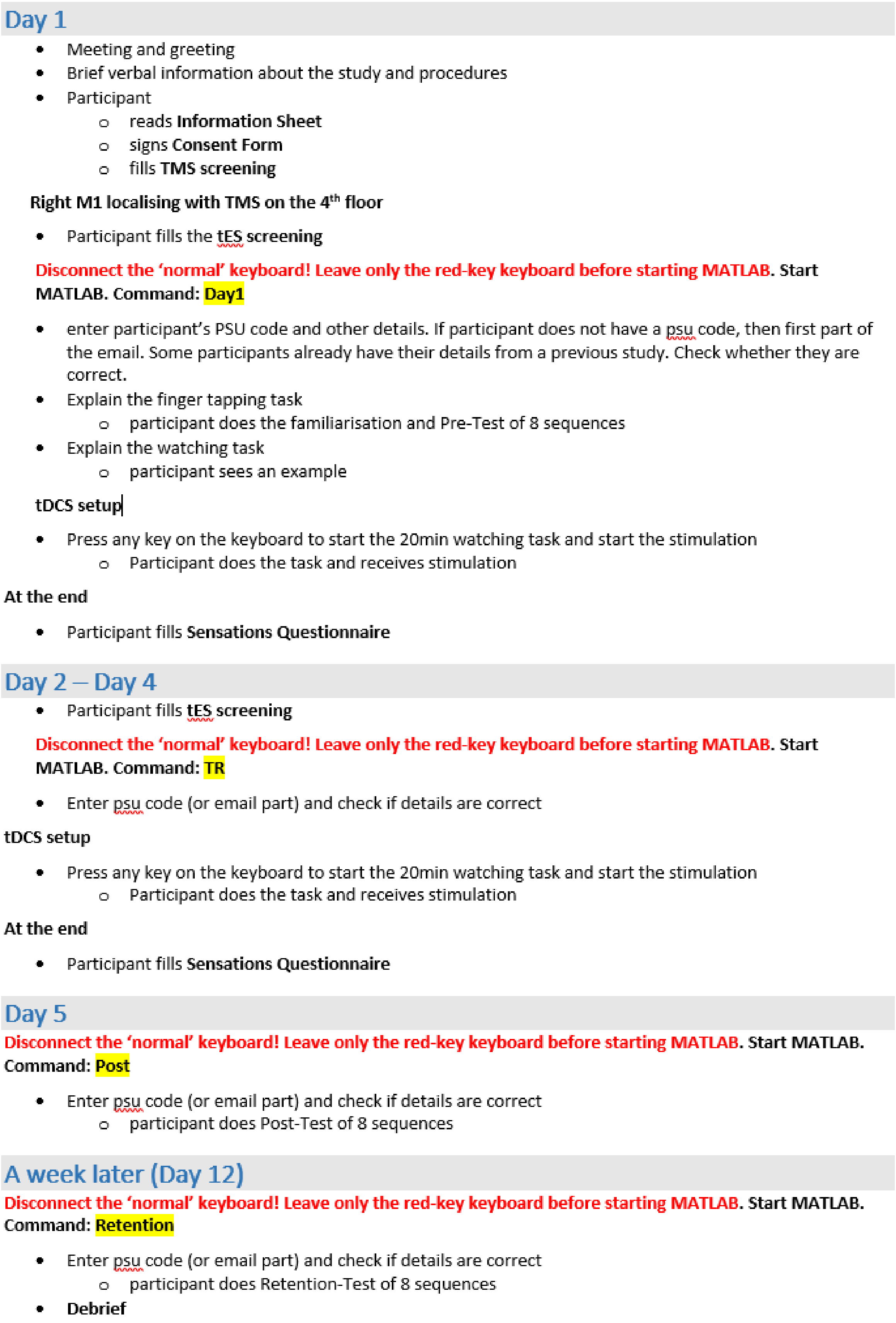
Appendices

Appendix 3.1 Experimental procedure



Day 1

- Meeting and greeting
- Brief verbal information about the study and procedures
- Participant
    - reads **Information Sheet**
    - signs **Consent Form**
    - fills **TMS screening**

Right M1 localising with TMS on the 4th floor

- Participant fills the **tES screening**

Disconnect the 'normal' keyboard! Leave only the red-key keyboard before starting MATLAB. Start MATLAB. Command: Day1

- enter participant's PSU code and other details. If participant does not have a psu code, then first part of the email. Some participants already have their details from a previous study. Check whether they are correct.
- Explain the finger tapping task
    - participant does the familiarisation and Pre-Test of 8 sequences
- Explain the watching task
    - participant sees an example

tDCS setup

- Press any key on the keyboard to start the 20min watching task and start the stimulation
    - Participant does the task and receives stimulation

At the end

- Participant fills **Sensations Questionnaire**

Day 2 – Day 4

- Participant fills **tES screening**

Disconnect the 'normal' keyboard! Leave only the red-key keyboard before starting MATLAB. Start MATLAB. Command: TR

- Enter psu code (or email part) and check if details are correct

tDCS setup

- Press any key on the keyboard to start the 20min watching task and start the stimulation
    - Participant does the task and receives stimulation

At the end

- Participant fills **Sensations Questionnaire**

Day 5

Disconnect the 'normal' keyboard! Leave only the red-key keyboard before starting MATLAB. Start MATLAB. Command: Post

- Enter psu code (or email part) and check if details are correct
    - participant does Post-Test of 8 sequences

A week later (Day 12)

Disconnect the 'normal' keyboard! Leave only the red-key keyboard before starting MATLAB. Start MATLAB. Command: Retention

- Enter psu code (or email part) and check if details are correct
    - participant does Retention-Test of 8 sequences
- **Debrief**

Appendix 3.2 Results without and with the nine non-TMS localised participants

Observational practice effects and tDCS effects on sequence-specific learning with nine non-TMS localised participants excluded. For comparison of results with all 50 participants, see the table below (a copy of the Table 3 from the main text).

		Observational training effect (trained vs. untrained performance)		**tDCS effect (group difference)**	**tDCS effect, accounted for the accuracy during training sessions**
		Sham (N = 15)	**Active (N = 26)**		
Initiation time	**Post**	$t_{13} = 1.95$, $p = 0.073$, $B_0 = 11\%$, $d_z = 0.50$.	$t_{24} = 4.02$, $p < 0.001$, $B_0 = 24\%$, $d_z = 0.79$.	$t_{38} = 1.50$, $p = 0.141$, $d = 0.49$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.76/1.31$).	$t_{37} = 2.69$, $p = 0.011$, $d = 0.89$, substantial evidence for the effect ($BF_{10}/BF_{01} = 3.44/0.29$).
	Ret.	$t_{13} = 2.67$, $p = 0.019$, $B_0 = 25\%$, $d_z = 0.69$.	$t_{24} = 2.87$, $p = 0.008$, $B_0 = 21\%$, $d_z = 0.56$.	$t_{38} = -0.35$, $p = 0.729$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.33/3.00$).	$t_{37} = -0.29$, $p = 0.773$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.34/2.97$).
Execution time	**Post**	$t_{13} = 2.42$, $p = 0.031$, $B_0 = 10\%$, $d_z = 0.62$.	$t_{24} = 4.75$, $p < 0.001$, $B_0 = 14\%$, $d_z = 0.93$.	$t_{38} = 0.16$, $p = 0.876$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.31/3.18$).	$t_{37} = -0.07$, $p = 0.943$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.32/3.16$).
	Ret.	$t_{13} = 2.40$, $p = 0.032$, $B_0 = 9\%$, $d_z = 0.62$.	$t_{24} = 3.99$, $p = 0.001$, $B_0 = 10\%$, $d_z = 0.78$.	$t_{38} = -0.47$, $p = 0.64$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.35/2.84$).	$t_{37} = -0.42$, $p = 0.678$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.35/2.82$).
Error rate	**Post**	$t_{13} = 1.90$, $p = 0.079$, $B_0 = 6\%$, $d_z = 0.49$.	$t_{24} = 2.89$, $p = 0.008$, $B_0 = 9\%$, $d_z = 0.57$.	$t_{38} = 0.69$, $p = 0.497$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.38/2.63$).	$t_{37} = 0.43$, $p = 0.667$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.36/2.82$).
	Ret.	$t_{13} = 2.13$, $p = 0.053$, $B_0 = 8\%$, $d_z = 0.55$.	$t_{24} = 1.45$, $p = 0.161$, $B_0 = 4\%$, $d_z = 0.28$.	$t_{38} = -0.72$, $p = 0.476$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.38/2.61$).	$t_{37} = -1.00$, $p = 0.322$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.46/2.20$).

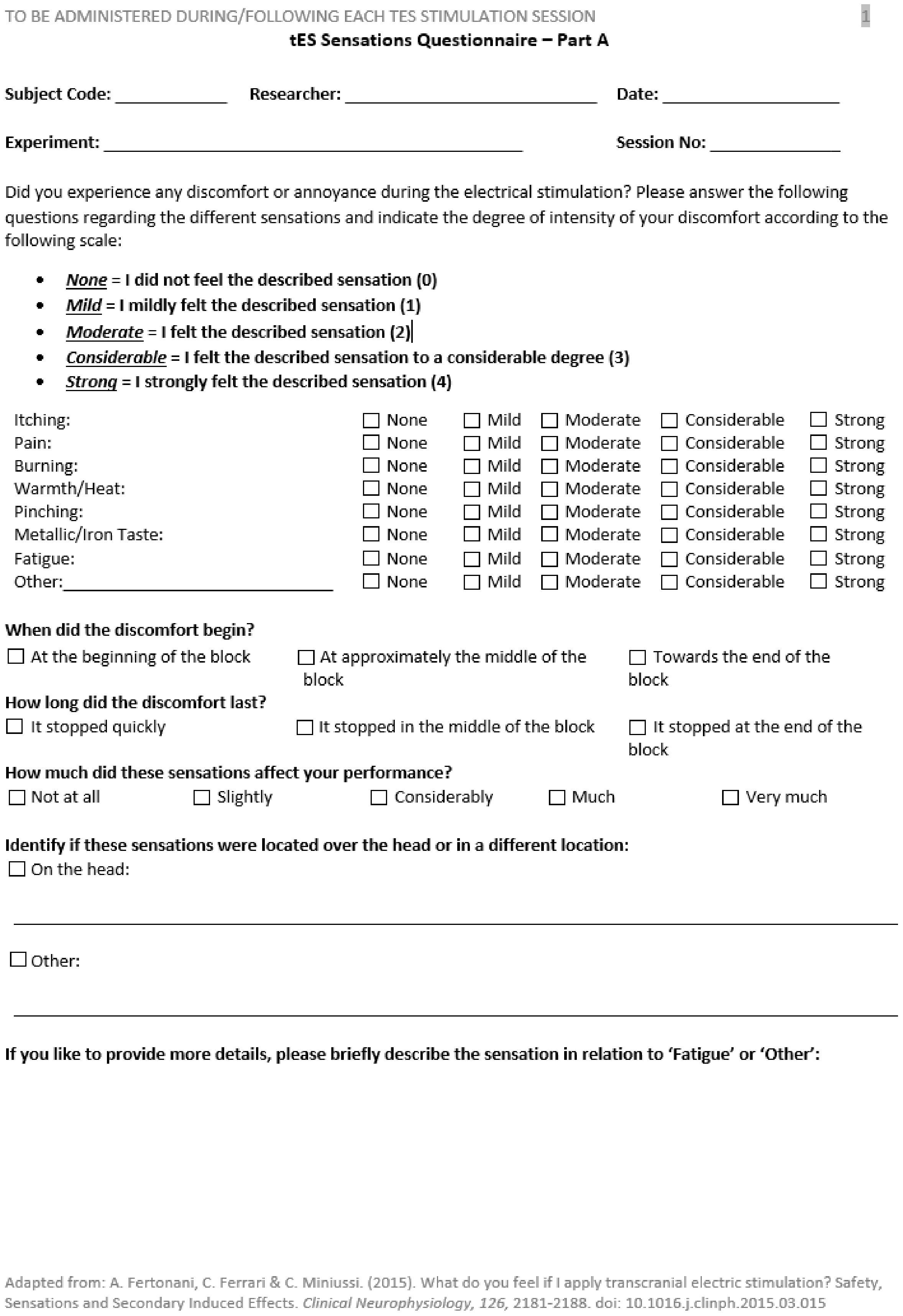
Shaded fields highlight non-significant effects.

Observational practice effects and tDCS effects on sequence-specific learning with all 50 participants

		Observational training effect (trained vs. untrained performance)		**tDCS effect (group difference)**	**tDCS effect, accounted for the accuracy during training sessions**
		Sham (N = 24)	**Active (N = 26)**		
Initiation time	**Post**	$t_{22} = 2.65$, $p = 0.015$, $B_0 = 13\%$, $d_z = 0.54$.	$t_{24} = 4.02$, $p < 0.001$, $B_0 = 24\%$, $d_z = 0.79$.	$t_{47} = 1.50$, $p = 0.141$, $d = 0.44$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.70/1.43$).	$t_{46} = 2.48$, $p = 0.017$, $d = 0.73$, anecdotal evidence for the effect ($BF_{10}/BF_{01} = 2.41/0.41$).
	Ret.	$t_{22} = 3.21$, $p = 0.004$, $B_0 = 21\%$, $d_z = 0.66$.	$t_{24} = 2.87$, $p = 0.008$, $B_0 = 21\%$, $d_z = 0.56$.	$t_{47} = 0.05$, $p = 0.961$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.29/3.49$).	$t_{46} = 0.01$, $p = 0.992$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.29/3.45$).
Execution time	**Post**	$t_{22} = 5.02$, $p < 0.001$, $B_0 = 15\%$, $d_z = 1.02$.	$t_{24} = 4.75$, $p < 0.001$, $B_0 = 14\%$, $d_z = 0.93$.	$t_{47} = -0.37$, $p = 0.710$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.30/3.31$).	$t_{46} = -0.49$, $p = 0.624$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.31/3.20$).
	Ret.	$t_{22} = 4.02$, $p = 0.001$, $B_0 = 10\%$, $d_z = 0.82$.	$t_{24} = 3.99$, $p = 0.001$, $B_0 = 10\%$, $d_z = 0.78$.	$t_{47} = -0.06$, $p = 0.950$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.28/3.55$).	$t_{46} = -0.02$, $p = 0.984$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.29/3.43$).
Error rate	**Post**	$t_{22} = 2.56$, $p = 0.018$, $B_0 = 7\%$, $d_z = 0.52$.	$t_{24} = 2.89$, $p = 0.008$, $B_0 = 9\%$, $d_z = 0.57$.	$t_{47} = 0.47$, $p = 0.644$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.31/3.20$).	$t_{46} = 0.20$, $p = 0.845$, substantial evidence against the effect ($BF_{10}/BF_{01} = 0.31/3.28$).
	Ret.	$t_{22} = 2.99$, $p = 0.007$, $B_0 = 7\%$, $d_z = 0.61$.	$t_{24} = 1.45$, $p = 0.161$, $B_0 = 4\%$, $d_z = 0.28$.	$t_{47} = -0.81$, $p = 0.420$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.37/2.71$).	$t_{46} = -1.05$, $p = 0.298$, anecdotal evidence against the effect ($BF_{10}/BF_{01} = 0.44/2.27$).

Shaded fields highlight non-significant effects.

Appendix 3.3 tDCS sensations questionnaire



TO BE ADMINISTERED DURING/FOLLOWING EACH TES STIMULATION SESSION 1

tES Sensations Questionnaire – Part A

Subject Code: ____________ **Researcher:** ____________________________ **Date:** ____________________

Experiment: ____ **Session No:** ______________

Did you experience any discomfort or annoyance during the electrical stimulation? Please answer the following questions regarding the different sensations and indicate the degree of intensity of your discomfort according to the following scale:

- ***None*** **= I did not feel the described sensation (0)**
- ***Mild*** **= I mildly felt the described sensation (1)**
- ***Moderate*** **= I felt the described sensation (2)**
- ***Considerable*** **= I felt the described sensation to a considerable degree (3)**
- ***Strong*** **= I strongly felt the described sensation (4)**

Itching:	☐ None	☐ Mild	☐ Moderate	☐ Considerable	☐ Strong
Pain:	☐ None	☐ Mild	☐ Moderate	☐ Considerable	☐ Strong
Burning:	☐ None	☐ Mild	☐ Moderate	☐ Considerable	☐ Strong
Warmth/Heat:	☐ None	☐ Mild	☐ Moderate	☐ Considerable	☐ Strong
Pinching:	☐ None	☐ Mild	☐ Moderate	☐ Considerable	☐ Strong
Metallic/Iron Taste:	☐ None	☐ Mild	☐ Moderate	☐ Considerable	☐ Strong
Fatigue:	☐ None	☐ Mild	☐ Moderate	☐ Considerable	☐ Strong
Other:____________________________	☐ None	☐ Mild	☐ Moderate	☐ Considerable	☐ Strong

When did the discomfort begin?

☐ At the beginning of the block ☐ At approximately the middle of the block ☐ Towards the end of the block

How long did the discomfort last?

☐ It stopped quickly ☐ It stopped in the middle of the block ☐ It stopped at the end of the block

How much did these sensations affect your performance?

☐ Not at all ☐ Slightly ☐ Considerably ☐ Much ☐ Very much

Identify if these sensations were located over the head or in a different location:

☐ On the head:

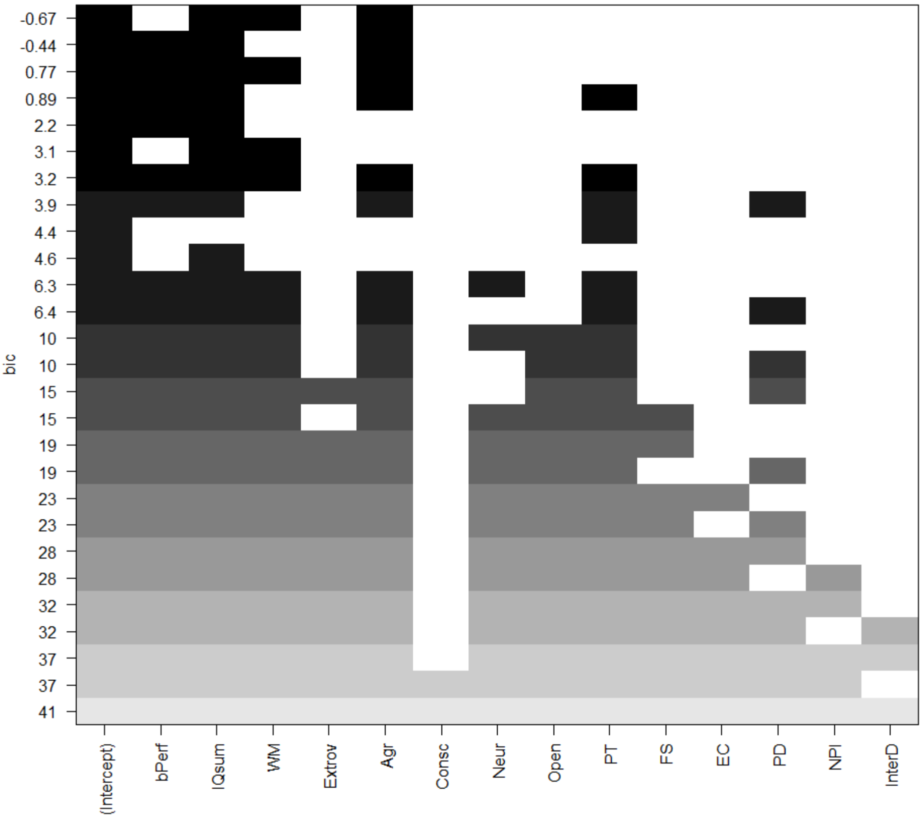
☐ Other:

If you like to provide more details, please briefly describe the sensation in relation to 'Fatigue' or 'Other':

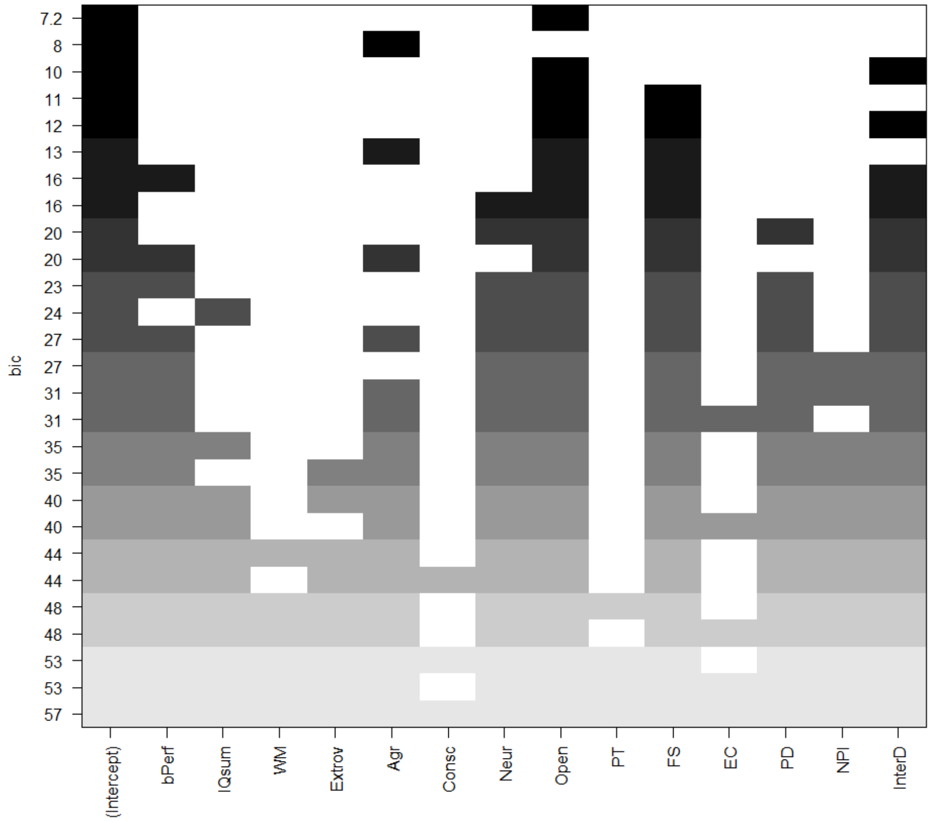
Adapted from: A. Fertonani, C. Ferrari & C. Miniussi. (2015). What do you feel if I apply transcranial electric stimulation? Safety, Sensations and Secondary Induced Effects. *Clinical Neurophysiology, 126,* 2181-2188. doi: 10.1016.j.clinph.2015.03.015

Appendix 4.1 Model rankings

PP group

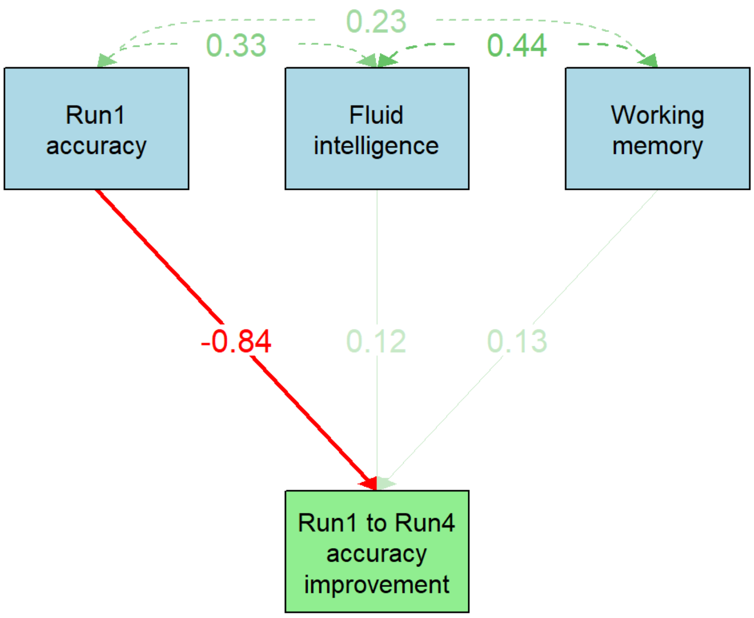


OA group



Appendix 4.2 Fluid intelligence and working memory as predictors of perceptual improvements (from run 1 to run 4)

Perceptual improvement predictors



Perceptual improvement regression analysis summary

	Run4 – Run1 accuracy		
Model	$F_{3,88} = 51.03$, $p < 0.0001$, $R^2 = 0.623$		
Coefficients	**β [95% CI]**	**t**	**p**
Intercept	0	0	1
Run1 accuracy	-0.842 [-0.979, -0.706]	-12.269	< 0.0001
Fluid intelligence	0.124 [-0.024, 0.273]	1.670	0.098
Working memory	0.131 [-0.013, 0.275]	1.815	0.073

Appendix 4.3 Raw scatter plots of sequence-specific learning versus fluid intelligence/working memory for OP and PP groups