Uniwersytet im. Adama Mickiewicza w Poznaniu

Wydział Nauk Społecznych

Instytut Psychologii

Jagna Sobierajewicz

Learning a fine sequential hand motor skill by motor imagery

Uczenie subtelnej, sekwencyjnej umiejętności motorycznej za pomocą symulacji ruchowej

Rozprawa doktorska napisana pod kierunkiem:

dr hab. Roba van der Lubbe

Promotor pomocniczy: dr Anna Przekoracka-Krawczyk

Poznań, 2018

Acknowledgements

First and foremost, I would like to thank my supervisor, Rob van der Lubbe, for being the epitome of a mentor. This work would not have been possible without his encouragement. His excellent guidance, challenging questions, many suggestions, and continuous support provided the basis for the successful completion of my thesis.

I would like to express my gratitude for all the support that I received from my fiancé, my friends and my family. Research is just play. Family is what really matters.

I should also mention other PhD students who shared their experiences with me and discussed everyday issues of the doctoral program. These include Katarzyna Dubas, Monika Wojtczak-Kwaśniewska and Kamila Ciężar. I would like to give special thanks to Monika Czaińska for supporting me through this entire process and for her friendship. My gratitude also goes to numerous other persons and participants whom I cannot mention all in this short piece of acknowledgements – without their time, commitment and courageous engagement, this research simply would not have happened.

After mentioning persons, I feel obliged to mention the institutions that sponsored my work and helped in my studies. The foremost is National Center of Science that provided funding towards my research, together with the Adam Mickiewicz University.

Jagna Sobierajewicz

OŚWIADCZENIE

Ja, niżej podpisana

Jagna Sobierajewicz

…………………………………………………………………………

przedkładam rozprawę doktorską

pt. *Learning a fine sequential hand motor skill by motor imagery*

na Uniwersytecie im. Adama Mickiewicza w Poznaniu
i oświadczam, że przygotowałam ją samodzielnie.

Oznacza to, że przy pisaniu pracy, poza niezbędnymi konsultacjami, nie korzystałam z pomocy innych osób, a w szczególności nie zlecałam opracowania rozprawy lub jej istotnych części innym osobom, ani nie odpisywałam tej rozprawy lub jej istotnych części od innych osób. Wszystkie dane, istotne myśli i sformułowania pochodzące z literatury są opatrzone odpowiednimi odsyłaczami.

Ponadto praca nie zawiera informacji i danych uzyskanych w sposób nielegalny i nie była wcześniej przedmiotem innych procedur urzędowych związanych z uzyskaniem dyplomów lub tytułów zawodowych uczelni wyższej.

Oświadczam również, że egzemplarz pracy dyplomowej w wersji drukowanej jest całkowicie zgodny z egzemplarzem pracy dyplomowej w wersji elektronicznej.

Jednocześnie przyjmuję do wiadomości, że gdyby powyższe oświadczenie okazało się nieprawdziwe, decyzja o wydaniu mi dyplomu zostanie cofnięta.

………………………………………………… ……………………………………………
(miejscowość, data) (podpis)

Table of contents

List of publications

This thesis is based on the work contained in the following three papers, all published in peer-reviewed ISI journals:

Sobierajewicz, J., Przekoracka-Krawczyk, A., Jaśkowski, W., & van der Lubbe, R. (2017). How effector-specific is the effect of sequence learning by motor execution and motor imagery? *Experimental Brain Research, 235*(12), 3757-3769.
doi: 10 1007/s00221-017-5096-z

Sobierajewicz, J., A., Jaśkowski, W., & Van der Lubbe, R. H. J. (2018). Does transcranial direct current stimulation affect the learning of a fine sequential hand motor skill with motor imagery? *Journal of Motor Behavior, 21*:1-15.
doi: 10.1080/00222895.2018.1513395

Sobierajewicz, J., Naskręcki, R., Jaśkowski, W., & Van der Lubbe, R. H. J. (2018). Do musicians learn a fine sequential hand motor skill differently than non-musicians? *PLOS ONE, 13*(11): e0207449.
doi: 10.1371/journal.pone.0207449

List of abbreviations

Abbreviation	Description
BCI	brain computer interface
DSP	discrete sequence production
EEG	electroencephalography/electroencephalogram
EMG	electromyography/electromyogram
ERL	event-related lateralization
ERP	event-related potential
fMRI	functional magnetic resonance imaging
LRP	lateralized readiness potential
MEG	magnetoencephalography/magnetoencephalogram
M1	primary motor area
PET	positron emission tomography
PTSD	posttraumatic stress disorder
SAD	social anxiety disorder
SMA	supplementary motor area
SRT	serial reaction time
tDCS	transcranial direct current stimulation

ABSTRACT

A lot of the time of human life is spent on acquiring new motor skills: starting from walking, writing, using cutlery, driving a car, to practicing sport. Learning motor skills refers to the ability to perform a given task better due to the repetitions of this task; and as a result, a given task is performed faster and more accurately. To learn motor skills, first and foremost, physical training is required. However, motor skills can also be acquired through motor imagery defined as the cognitive process during which motor activity is performed internally by simulating this activity without making any movement.

This thesis was aimed at determining the specificity of acquiring motor skills through motor imagery using the Go/NoGo paradigm, transcranial direct current stimulation (tDCS), and electroencephalography (EEG). First, it was examined whether the learning of a motor skill with motor imagery and motor execution is effector-dependent or not. Results indicated that motor skill learning both with motor execution and motor imagery was not effector-dependent. Next, the influence of increased expertise on learning a motor skill with motor execution and motor imagery was examined by comparing behavioral and EEG results between musicians and non-musicians. Interestingly, the results indicated that learning a fine motor skill depends on increased expertise only in the case of learning with motor execution. Finally, it was investigated whether learning a fine motor skill combined with tDCS would influence the sequence-learning effects. Results revealed that tDCS affects only a-specific learning effects, but not sequence-specific learning effects.

Overall, the results reported in this dissertation indicate that motor imagery has a beneficial effect on acquiring a fine sequential motor skill. The outcome of this thesis increased our understanding of crucial characteristics of motor imagery. Together, the results reported in this thesis have relevant consequences for therapies using motor imagery, for example, for children with cerebral palsy or for patients after stroke. It may also be used to simply enhance specific motor skills (e.g., by musicians or athletes) in the case of inability of physical practice or disease.

STRESZCZENIE

Człowiek podczas swojego życia spędza wiele czasu na nabywaniu nowych umiejętności motorycznych: zaczynając od chodzenia, pisania, używania sztućców, prowadzenia samochodu czy uprawiania sportu. Uczenie się umiejętności motorycznych odnosi się do zdolności wykonywania danego zadania coraz lepiej dzięki wielokrotnemu powtarzaniu tego zadania; w efekcie czego wykonujemy daną czynność szybciej oraz dokładniej. Do nauki umiejętności motorycznych, przede wszystkim, potrzebny jest trening fizyczny. Jednakże umiejętności motoryczne mogą być także nabywane poprzez wyobrażanie ruchowe (*ang. motor imagery*), które definiuje się jako proces poznawczy, podczas którego czynność motoryczna wykonywana jest wewnętrznie poprzez symulację tej czynności bez wykonywania jakiegokolwiek ruchu.

Niniejsza rozprawa doktorska miała na celu określenie specyfiki nabywania umiejętności motorycznych za pomocą wyobrażania ruchowego z wykorzystaniem paradygmatu Go/NoGo, przezczaszkowej stymulacji prądem stałym (tDCS) oraz elektroencefalografii (EEG). Najpierw zbadano, czy uczenie się umiejętności motorycznych jest zależne od efektora, czy też nie. Wyniki wykazały, że uczenie się umiejętności motorycznych zarówno za pomocą wyobrażania ruchowego, jak i fizycznego wykonywania ruchu nie jest zależne od efektora. Następnie zbadano wpływ zwiększonej wiedzy specjalistycznej na uczenie się umiejętności motorycznych, porównując wyniki behawioralne i EEG między muzykami i nie-muzykami. Co ciekawe, wyniki wykazały, że uczenie umiejętności motorycznych zależy od zwiększonej wiedzy tylko w przypadku uczenia się z wykorzystaniem fizycznego wykonywania ruchu. Na koniec zbadano, czy nauka umiejętności motorycznych połączona z tDCS wpłynie na efekty uczenia się sekwencyjnych umiejętności motorycznych. Wyniki wykazały, że tDCS wpływa tylko na efekty uczenia się ogólnego, ale nie na efekty uczenia się specyficznego dla sekwencji.

Podsumowując, wyniki przedstawione w tej rozprawie wskazują, że wyobrażanie ruchowe ma korzystny wpływ na sekwencyjne uczenie się motoryczne. Wyniki przedstawione w tej pracy mają istotne konsekwencje dla terapii wykorzystujących wyobrażanie ruchowe, np. dla dzieci z porażeniem mózgowym lub pacjentów po udarze. Co więcej, wyobrażanie ruchowe może być stosowane po prostu do zwiększenia specyficznych umiejętności motorycznych (np. przez muzyków lub sportowców) w przypadku braku możliwości wykonywania ćwiczeń fizycznych lub choroby.

1. GENERAL INTRODUCTION

Movements are an integral part of our lives. There is hardly any moment, especially when awake, at which we make no movement. The type and complexity of these movements, however, varies widely, from relatively simple (e.g., reaching for a cup), to more complex movements (e.g., lacing one's shoes). Very often these complex movements can be decomposed in a sequence of several simple movements. Since our birth, we are able to develop both fine and gross motor skills. Fine motor skills are small finger or hand movements that are produced by a small group of muscles (Payne & Isaacs, 1987). Hence, movements such as writing, tapping, drawing, or playing a musical instrument can be considered as fine motor skills. Gross motor skills refer to large movements that use muscles in the arms, legs, and torso. At the start of learning a motor skill, movement execution is very difficult and needs a lot of attention, like in the case of walking, eating using cutlery, or driving a car, but with practice they become more and more automatic and require less attention. It is well known that motor skills can be acquired by repeating (i.e., physical practice) a particular movement over and over again. Interestingly, a wide range of experimental studies has provided evidence that learning of a motor skill may already be induced by motor imagery (Jackson, Lafleur, Malouin, & Richards, 2001; Allami, Paulignan, Brovelli, & Boussaoud, 2008; Doussoulin & Rehbein, 2011). The goal of this thesis is to increase our understanding of what motor imagery actually is. Evidence that motor imagery influences the learning of a fine sequential motor skill may support the acquisition of motor skills in the case of inability of physical practice or disease (e.g., stroke), but it may also be used to simply improve performance of a fine motor skill.

In this thesis, I will first present an overview on the nature of motor imagery with special emphasis on the learning of a fine motor skill with motor imagery. In the current chapter, I will present definitions relevant for this dissertation, important paradigms, underlying brain mechanisms, and several research findings in the field of rehabilitation, sports and music. In the subsequent chapters I will report newly acquired results, which deal with the following questions:

- How effector-specific is motor execution and motor imagery?
- Does expertise affect learning of a motor skill with the help of motor imagery?

- To what extent does transcranial direct current stimulation combined with motor imagery may affect learning of a motor skill?

In this dissertation, a modified discrete sequence production (DSP) Go/NoGo paradigm has been used to explore the specificity of the effect of motor imagery on the learning of a fine hand motor skill (De Kleine & Van der Lubbe, 2011). This paradigm in combination with data derived from the electroencephalogram (EEG) enables to examine different phases of the acquisition of motor skills, e.g., motor preparation, motor execution, and motor inhibition. Furthermore, it allows to separate sequence-specific from a-specific learning effects. These different features indicate that this paradigm may be very useful to study the role of motor imagery in learning a fine hand motor skill.

1.1. Definitions

In this section, I will define all relevant terms, which are crucial for a proper understanding of this dissertation, i.e., motor imagery, visual imagery, motor preparation, and motor skill learning. I will especially focus on the distinction between motor imagery and visual imagery as these terms and their respective processes are often misunderstood.

In various studies, motor imagery is denoted as “mental training”, “mental movements”, “mental practice”, “mental imagery”, “mental rehearsal”, “imagined actions”, etc. (Jeannerod, 2006; Schuster, et al., 2011). A precise definition of motor imagery seems crucial to differentiate this process from visual imagery, visual-motor imagery or the internal observation of a movement (Neuper, Scherer, Reiner, & Pfurtscheller, 2005). Jeannerod (1995) defined motor imagery as the cognitive process during which motor actions are internally simulated without producing an overt action (i.e., the mental simulation of a movement). In other words, Jeannerod (2001) claimed that “covert actions are in fact actions, but they are simply not executed”. Maillet et al. (2013) pointed out that motor imagery is related with the recall of feelings perceived during movement execution. However, motor imagery should be differentiated from other covert actions, which also activate the motor system, e.g., observation of an action performed by others, learning by observation, or action in dreams (Jeannerod & Frak, 1999). For example, Rizzolatti et al. (1996) found activation in the macaque monkey`s premotor cortex during observed action. They identified neurons within the premotor cortex that become activated both during performing particular goal-directed actions and during the observation of an action. These neurons were called *mirror neurons* and a similar type of neurons was found in humans (Oberman, Pineda, & Ramachandran, 2007; Fabbri-Destro & Rizzolatti, 2008). It has been shown that the motor system (especially the premotor cortex) is activated when someone observes another individual performing an action. The observer is thought to be able to build a representation of the action, which is carried out by another person (Gallese & Goldman, 1998; Jeannerod, 2006). So, one is able to understand and to anticipate the observed action. It has been argued that mirror neurons are involved in motor imagery as the observer also imagines performing the observed action (Kosslyn, Ganis, & Thompson, 2001). Several studies revealed that the observer might engage in action observation and motor imagery simultaneously (for reviews see: (Vogt, Di Rienzo, Collet, Collins, & Guillot, 2013; Taube, et al., 2015; Eaves, Riach, Holmes, & Wright, 2016)).

If motor imagery is understood as the mental representation of a movement without making a body movement, then it seems that motor imagery may involve the whole body, but it may also be limited to a part of the body (Guillot & Collet, 2005). Moreover, motor imagery is associated with the conscious activation of brain regions which are also involved in movement preparation and its execution, accompanied by a voluntary withhold of the actual movement (e.g., the prefrontal cortex, the premotor cortex, the supplementary motor area, and the parietal cortex), (Mulder, 2007). “It is also clear that a great deal of motor activity is normally unconscious and automatic and is therefore unlikely to feature in motor imagery which, is, by definition, conscious” (Annett, 1995, p. 1411). Jeannerod (1995) claimed that conscious motor imagery and unconscious motor preparation share common mechanisms and are functionally equivalent. For example, it has been shown in the study of Sobierajewicz et al. (2016) that participants who did not perform any overt or covert actions (i.e., control group) executed the sequences as fast and accurately as participants who had to imagine the execution of motor sequence. It can be explained by the fact that participants in the control group could also imagine (even unconsciously) a sequence movement during the preparation interval (before the Go/NoGo signal). During motor preparation, performance of a movement is anticipated as one can imagine performing a movement before executing it. Henry and Rogers (1960) defined motor preparation as the representation of “establishing a state of readiness to make a specific planned movement”. In other words, during motor preparation prior information about required movement parameters is integrated (e.g., the spatial and temporal aspects of a movement). These spatial and temporal aspects appear to be related with the concept of a motor program. A motor program can be defined as an abstract representation of a movement that organizes the details of an intended movement in advance (Schmidt, 1975). So, the similarity between motor imagery and motor preparation may be due to the fact that both processes involve activation of a motor program.

Based on the previous views, it seems clear that motor imagery should not be understood as the simply suppression of an action (i.e., response inhibition), but as the conscious, mental simulation of a motor response. Response inhibition is defined as the ability to suppress irrelevant or interfering stimuli (Garavan, Ross, & Stein, 1999). In the case of motor inhibition, motor responses should be withheld; whereas in the case of motor imagery, motor responses should be mentally carried out, but without flexing the muscles. Nevertheless, it has been argued that motor imagery also requires a process of inhibition as the overt movement should not be executed (Jeannerod, 1995). Jeannerod gave two possible explanations of the presence of inhibition during imagery (Jeannerod, 2006). First, it may be hypothesized that transfer of the information produced at a cortical level (e.g., in the premotor cortex or in the prefrontal cortex) is blocked before entering the primary motor cortex (M1). Deiber et al. (1998) observed decreased activation in the inferior prefrontal cortex, suggesting that this area may be related with motor inhibition during motor imagery (Deiber, et al., 1998), which is in line with other findings (Brass, Zysset, & von Cramon, 2001). However, there is evidence that M1 is also activated during motor imagery (Lotze, et al., 1999; Geradin, et al., 2000; Miller, Schalk, Fetz, Ojemann, & Rao, 2010), which refutes this hypothesis. The second hypothesis suggests that the process of inhibition might be localized at the spinal cord. Jeannerod proposed a dual mechanism, which operates at the spinal level, including an increased corticospinal activation during the preparation of a movement, and the suppression of overt movement in muscles (Jeannerod, 2001; Jeannerod, 2006). In some previous studies motor imagery and motor inhibition were not contrasted (Caldara, et al., 2004; Allami, Paulignan, Brovelli, & Boussaoud, 2008; Zhang, et al., 2011). However, in the study of Sobierajewicz et al. (2017) it was examined to what extent motor imagery resembles motor execution, by comparing it with motor execution as well as with motor inhibition. Behavioral results revealed that learning of a fine sequential motor skill can by induced not only by physical practice, but also by motor imagery. To obtain more evidence for the notion that motor imagery resembles motor execution rather than motor inhibition, EEG activity was also examined during learning a motor skill. Results revealed maximal activity above central sites which are related to motor processes during motor execution and motor imagery relative to motor inhibition. Additionally, ERLs revealed similarities between motor imagery and motor execution, because more negativity was present for these condition as compared with motor inhibition. In the case of motor inhibition, a polarity reversal was observed indicating the inhibition of activity in the contralateral motor cortex. These results provide evidence that motor imagery induces motor skill learning (by improving response time and accuracy of a motor sequence), which is related with similar activation of brain areas during motor skill learning with both motor execution and motor imagery.

1.1.1. Visual imagery vs. motor imagery

To better understand what is meant with the term of motor imagery, it seems relevant to indicate in what way it can be distinguished from visual imagery (Solodkin, Hlustik, Chen, & Small, 2004). In general, imagery may incorporate all our sensory modalities: vision, audition, olfaction, gustation, and kinesthetic (Jackson, Lafleur, Malouin, & Richards, 2001; Gregg & Clark, 2007). Although motor imagery and visual imagery may have several features in common (Jeannerod, 2001), they are thought to refer to quite different processes (Solodkin, Hlustik, Chen, & Small, 2004; Mizuguchi N., Nakata, Uchida, & Kanosue, 2012). In the case of visual imagery, visual representations are assumed to be involved (see, Solodkin et al., 2004), whereas in the case of kinesthetic imagery, this is thought to involve the mental simulation of a movement. By employing EEG, it has been demonstrated that during motor imagery central cortical motor areas are activated, while during visual imagery posterior visual brain areas are activated (Kosslyn, Ganis, & Thompson, 2001; Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). Visual imagery requires self-visualization of a movement, whereas kinesthetic imagery requires to “feel” a movement - one is able to imagine the feeling of the body as it moves (Guillot & Collet, 2005; Dun & Burton, 2005). In other words, visual imagery implies a third person perspective - the person sees him/herself performing the movement, whereas kinesthetic imagery implies a first person perspective - the person imagines to perform a movement him/herself (Mulder, 2007; Gaggioli, Morganti, Mondoni, & Antonietti, 2013; Maillet, et al., 2013). During visual imagery, the participant is more like a spectator, while during kinesthetic imagery, the participant is more like a performer. Another distinction between visual imagery and kinesthetic imagery is associated with the idea that visual imagery is more easily accessible to verbal processes, whereas kinesthetic imagery is not (Jeannerod, 1995; Solodkin, Hlustik, Chen, & Small, 2004). Studies investigating the effectiveness of mental practice revealed distinct functions of motor and visual imagery. For example, motor imagery turned out to be more effective for tasks that require more advanced motor control, i.e., during acquisition of the precise timing and coordination of a particular movement (Neuper, Scherer, Reiner, & Pfurtscheller, 2005). Depending on the manner of how a participant performs a required task, the relative contribution of various aspects involved in motor imagery, such as movement intention, motor planning, or kinesthetic representations may vary (Neuper, Scherer, Reiner, & Pfurtscheller, 2005).

1.1.2. Motor skill learning

A precise definition of learning itself seems crucial to understand what motor skill learning is. Skill learning can be defined as the improvement in perceptual, cognitive or motor performance following practice (Debarnot, Sperduti, Di Rienzo, & Aymeric, 2014). The official definition of learning by UNESCO (ISCED 2011) is known as: “individual acquisition or modification of information, knowledge, understanding, attitudes, values, skills, competencies or behaviors through experience, practice, study or instruction”. The term *learning* suggests a relatively permanent change in a person’s performance of a skill (Wulf, Shea, & Lewthwaite, 2010).

Motor skill learning may involve three different types of learning: *procedural* (implicit), *declarative* (explicit), and *stimulus-response (S-R) associative* learning (Graf & Schacter, 1985). Procedural learning refers to the obtaining the ability to acquire motor or cognitive skill gradually, with practice, without any knowledge about rules needed to perform a required skill (i.e., implicit learning), (Cohen & Squire, 1980). This type of learning is associated with the acquisition of skills such as walking, reading or writing (Chambaron, Berberian, Delbecque, Ginhac, & Cleeremans, 2009). Declarative learning (related with episodic and semantic memory) refers to the ability to remember factual knowledge about objects, places, or events that can be consciously recalled (Tulving, 1972). This type of learning requires attention and awareness. The third type of learning, associative learning, is the process of learning by simple association between stimulus and response and is based on the notion that experiences can reinforce one another

(Passingham, Toni, & Rushworth, 2000; Holland, 2008). In this dissertation, the emphasis is on sequence learning which refers to acquiring the skill to produce a sequence of actions as fast and accurate as possible, which might be acquired implicitly and explicitly (Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003; Verwey & Wright, 2014).

Many researchers have made a distinction between various phases during the learning of a motor skill. According to Anderson (1982), three phases can be distinguished, which are responsible for separate processes*: a cognitive phase, an associative phase, and an autonomous phase* (Fitts, 1964; Anderson, 1982). First, *a cognitive phase* (called also: a verbal-cognitive phase) is responsible for the decision what movement should be made. In this phase, the role of attention is significant (Čoh, Jovanović-Golubović, & Bratić, 2004). The second phase is *an associative phase,* in which one chooses the most effective strategy and can make some corrections if there is any need for that. In the third, *autonomous phase,* the skill becomes more automatic in a sense that it lacks interference from any particular secondary task (Lotze, Scheler, Tan, Braun, & Birbaumer, 2003; de Kleine, 2009). In this phase, one can focus on other aspects of performance, e.g., on the emotional aspects of a movement (Chaffin & Logan, 2006). This third phase is actually never completely finished, and usually it lasts for several years (Čoh, Jovanović-Golubović, & Bratić, 2004).

Another model of staged motor learning was proposed by Hikosaka (1999) who distinguished between two streams of information processing: a *spatial processing stream* and a *motor processing stream* (Hikosaka, et al., 1999). In the early phase of training, information about the movement is spatially encoded, and in a later phase motor programs are formed. For more complex movements, these two different streams probably operate in parallel (Luft & Buitrago, 2005).

Verwey et al. (2015) proposed that two different representational levels may be involved while learning to produce a sequence of movements. *A cognitive level* is related to spatio-temporal aspects of the motor sequence and this level is thought to develop already with limited practice. A second *motoric level* relates to the involved muscles or muscle groups (Verwey, Groen, & Wright, 2016), but representation at this level only develops after extended practice (Verwey & Wright, 2004). It has been argued that representations at a cognitive level develop faster (especially in the initial phase of learning of a motor sequence) than motor or muscle-specific representations. Based on this notion, the development of sequence representation at different levels can differ due to an increased expertise (e.g., between professional musicians and non-musicians). It may be hypothesized that spatial representation of sequence representation will develop among novices, whereas both spatial and motor representations can be developed among professionals due to an increased expertise (e.g., among musicians). As a consequence, the potential benefit of musicians during learning a motor skill may be related to the processing of a motor sequence at both cognitive and motor level due to long-term practice and expertise, while for non-musicians a motor sequence would be reinforced only at a cognitive level, which will be detailed in *Chapter 3*.

The involvement of representations at two different levels is also related with the notion that motor skill learning transfers from an effector-independent stage to an effector-dependent stage. Different views have been forwarded with respect to effector-dependency of learned motor skills. For example, previous research showed that learning is effector-dependent, which implies that training of one group of muscles does not generalize to another group of muscles (Bapi, Doya, & Harner, 2000; Verwey & Wright, 2004; Osman, Bird, & Heyes, 2005; Verwey & Clegg, 2005). However, it has also been argued that motor skill learning is initially effector-independent and may become effector-dependent with extensive practice (Hikosaka, et al., 1999). Considering these results, it might be questioned how effector-specific the effect of learning a sequential motor skill by motor execution and motor imagery is. This aspect will be further explored in *Chapter 2*.

Previous studies suggest that motor imagery is beneficial for learning a motor skill (Doussoulin & Rehbein, 2011; Wriessnegger, Steyrl, Koschutnig, & Müller-Putz, 2014; Xu, et al., 2014; Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). Results from these studies revealed that training with motor imagery is more beneficial in the early stages of learning relative to later stages of learning (Doussoulin & Rehbein, 2011). It has been shown that not only motor imagery may enhance motor skill learning. Observational practice, the learner`s focus on attention, feedback, and self – controlled practice are also influential methods, which are assumed to play a role in motor skill learning (Wulf, Shea, & Lewthwaite, 2010). Wulf et al. (2010) pointed out that information about the outcome (either about the performance or about the results) or giving specific instructions to the performer, which directs attention to particular movements, may facilitate learning a motor skill. They also underlined that effectiveness of a certain practice depends on the motivational state of a learner, which has an impact on later effects of motor skill learning.

In this dissertation, the influence of motor imagery on a sequence-specific learning effects was investigated. Sequence-specific learning can be determined in tasks like the SRT (Abrahamse & Verwey, 2008), the DSP task, (Abrahamse, Ruitenberg, de Kleine, & Verwey, 2013), or the Go/NoGo DSP task (de Kleine & Van der Lubbe, 2011) which will be described in more detail below.

1.2. How to study motor imagery?

A highly relevant principle for the examination of motor imagery is Fitts`s law, because it provides information about the mechanisms underlying motor execution and possibly motor imagery as well. The main rule of Fitts`s law is the notion that there is an inverse relationship between the difficulty of a movement and its speed (Decety & Jeannerod, 1996; Lotze & Halsband, 2006). Hence, when the difficulty of a task increases the speed of the movement decreases. In accordance with the notion that similar brain mechanisms are involved in motor imagery as in motor execution (Jeannerod, 2001), it has been investigated whether Fitts`s law also applies to motor imagery. Studies detailed below examined whether motor execution and motor imagery indeed involve the same processes. Most often movement time or reaction time paradigms have been used to examine the relation between motor imagery and actual movement execution (Stevens, 2005). Examples of the employed tasks to study motor imagery are the walking task, the writing task, and the hand laterality judgment (HLJ) task. Below there is a detailed description of these different tasks. Next, I will separately describe the DSP Go/NoGo task, as this task was used in all the empirical chapters of this dissertation.

1.2.1. The walking task and the writing task

Decety and Jeannerod (1996) investigated whether Fitts`s law is also applicable to motor imagery. They created a task in which participants were asked to form a mental image of themselves while walking through gates of different widths at different distances. There were gates at three different distances (3 m, 6 m, or 9 m), with three different widths (45 cm, 90 cm, 135 cm). Each participant watched one of the gates on the track for five seconds, which was presented with a virtual reality system. Next, participants were instructed to imagine themselves walking through the different gates. Mental walking time was measured from a Go signal (a sound) until participants gave a sign by opening their hand, which indicated that they finished walking. Results revealed an increase in mental walking time with increasing gate distance and decreasing gate width. This rule was present for all participants. Moreover, in this experiment, participants were asked to estimate their subjective sensation of effort with respect of the gates width and gate distance. They reported that their "sense of effort" during this task was affected more by the gate distance compared with the gates widths, but both variables affected the time needed to imagine the movement (Decety & Jeannerod, 1996).

Papaxanthis et al. (2002) examined the timing correspondence between actual execution and motor imagery of a writing and a walking task. In the writing task, participants were asked to write (or imagine writing) one sentence: "2 Rue de la Libération". In the walking task, they were asked to walk (or imagine walking) a distance of 6 m at a comfortable speed. Participants were divided into two groups. In the first group, participants first imagined a movement and next they executed a real movement. In the second group the order of task conditions was reversed, so they had to imagine the movement preceding its actual execution. All participants measured their time using an electronic stopwatch on their own. The results revealed that the duration of imagined movements was very similar to those of real execution of movement for both tasks. This may arise from the notion that the brain mechanisms partially overlap during executed and imagined action, though they are not identical (Jeannerod, 2001).

Another variant of the walking task was created by Decety et al. (1989) in order to measure the effectiveness of mental imagery. They compared the duration of walking at targets which were placed at different distances with the same task but during mental simulation (Decety, Jeannerod, & Prablanc, 1989). Various distances were used: 5 m, 10 m, and 15 m. Participants were asked to switch on a stopwatch when they started to walk (actually or mentally), and to switch it off when they finished. The time needed to execute (real walk) and to simulate (imagined walk) was similar. In this study participants were additionally asked to carry a heavy (25 kg weight) load on their shoulders. Walking time was measured during actual walking and mental walking, in 10 trials for each of the three target distances (60 trials per subject). The time needed in the mental task with load was significantly longer for all participants. During actual movement, the times were in the same range as those measured during previous experiment. Researchers gave some explanation of the difference between physical and mental walk related with the different loads: “the subjects who carried the load generated centrally a greater force to overcome the resistance produced by the load” (Decety, Jeannerod, & Prablanc, 1989). Another variation of this task, was the mental simulation of walking along beams varied in width, but having the same length. In this situation, the beam width was assumed to be a factor of difficulty of the task. The result of this examination showed that walking on a narrower beam was longer in both conditions: in an actual and a mental walking task (Decety, 1991). Another study focused on a graphic task (Decety & Jeannerod, 1996), in which participants were asked to write or to imagine a short sentence with their right hand. The time needed to execute the task in both situations was similar. Results also showed similar time of execution for the left hand, and for writing the text in large letters and in small letters. Taken together, the time needed to execute and imagine a variety of tasks increases with difficulty of the task.

1.2.2. The hand laterality judgement task

Another task which is thought to involve motor imagery processes is the hand laterality judgment task. Participants are asked to differentiate between the right or left hand from pictures of the hands, which are presented in different orientations (an upright orientations - 0º, rotated counter clockwise, rotated clockwise, and upside down - 180º). Previous studies of Parsons suggested that participants, when asked to judge the laterality of a rotated image of hand, imagined their own hand moving from its current position into the presented stimulus orientation (i.e., motor imagery was implicitly used to solve this task), (Parsons, 1987; Parsons, 1994). The fact that participants use motor imagery can be inferred from the behavioral performance or neuroimaging studies (de Lange, 2008; Zapparoli, et al., 2014). For example, in the study of Jongsma et al. (2013), three conditions were used with different hand positions (hands positioned 45° inward; hands positioned 45°outward; control condition: hands straight position). So, the hand picture was rotated laterally or dorsally by 45 degrees. Participants were instructed to decide whether the hand picture on the screen was a right hand or a left hand. Results showed that participants took longer to correctly judge hand laterality when they were presented with laterally compared to medially rotated pictures of hands (Jongsma, et al., 2013). It has been proposed that motor imagery was more involved, depending on difficulty of the task, in this case, of the number of axes of rotation (Jongsma, et al., 2013). In other words, the time to give a motor response reflected the degree of mental rotation needed to bring one`s hand in a position adequate for achieving the task (Jeannerod & Frak, 1999). These behavioral effects observed while executing the hand laterality judgment task are reflected at the neuronal level. Studies using fMRI revealed that during executing the hand laterality judgment task, brain areas involved in motor imagery (e.g., the premotor area, the supplementary motor area) were activated (de Lange, Hagoort, & Toni, 2005; Zapparoli, et al., 2014). In accordance with the previous studies of Parsons (1987, 1994), it has been shown that participants engaged motor imagery to solve the hand laterality judgment task as they internally simulated movement of the hand.

To summarize, motor imagery is thought to engage similar cognitive processes as in the case of physical motor execution. The limitation of the above-mentioned tasks concerns the fact that participants could either use visual imagery instead of motor imagery, or they could simply report that they imagined a movement during carrying out a task. Nevertheless, substantial evidence demonstrates a close correspondence between temporal features of executed and imagined movements (Decety, Jeannerod, Germain, & Pastene, 1991; Guillot & Collet, 2005).

1.2.3. The Go/NoGo DSP paradigm

A paradigm that may be very useful to study the learning of a fine hand motor skill is the Go/NoGo DSP task (de Kleine & Van der Lubbe, 2011). This task can be considered as a modified version of Rosenbaum`s S1-S2 paradigm (Rosenbaum, 1980). In a typical DSP task (Verwey, 2003), specific placeholders are displayed on a computer screen where each placeholder spatially corresponds to a particular key on the keyboard. Participants are asked to press these corresponding keys when a placeholders lights up, which often concerns a sequence of different stimuli (Abrahamse, Ruitenberg, de Kleine, & Verwey, 2013).

De Kleine and van der Lubbe (2011) developed a modified version of the DSP task – the Go/NoGo DSP task, in which participants respond only after presenting the full stimulus sequence. This usually requires responding to a series of three to six key – specific stimuli. As a consequence, this implies that the whole sequence has to be memorized before it can be carried out. In the case of a Go signal, participants are instructed to execute a required sequence by pressing the corresponding buttons on a keyboard, and in the case of a NoGo signal the response should not be executed.

This version of the DSP task enables to examine processes underlying the preparation phase and the motor execution separately, while in Verwey `s version motor execution and motor preparation might occur simultaneously. The advantage of having a clear start- and end-point allows for measuring and distinguishing particular stages of brain activation during the acquisition of motor skills, i.e., encoding of the stimuli, memorizing the sequence, response preparation, and response execution. Moreover, in the context of learning a fine hand motor skill, the use of the DSP task allows to examine two different phases: an initial practice phase, and a final test phase which may include unfamiliar (new) sequences as a control condition (Abrahamse, Ruitenberg, de Kleine, & Verwey, 2013). Importantly, these unfamiliar sequences in the test phase enable to determine sequence-specific learning effects instead of unspecific learning effects. In the case of learning a motor skill, it seems quite relevant to make a distinction between a-specific learning and sequence-specific learning. Sequence-a-specific learning involves the development of a sequencing skill in general, while sequence-specific learning concerns the learning of a particular sequence. So, a-specific learning effects are associated with familiarization with the task. For example, learning effects may be due to an improved ability to decode stimuli or relate stimuli with responses, or due to improved motor control, spatial attention, spatial memory, etc. Sequence-specific learning is assumed to be based on sequence-specific representations at the central and motor processing levels, so called symbolic sequence representations and motor chunks (Verwey, 2015), which will be described in *Behavioral measures*.

1.2.4. Recent findings with the Go/NoGo DSP paradigm

Previous studies that examined motor imagery with the Go/NoGo DSP paradigm focused on the following questions (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017):

- Does motor imagery resemble motor execution?

  In the study of Sobierajewicz et al. (2017), the question addressed concerned the resemblance between motor imagery and motor execution. As mentioned before, motor imagery is considered as mental simulation of a motor response, which can be easily misunderstood with the simply suppression of an action (i.e., response inhibition). In the case of motor inhibition, the motor response should be withheld; whereas in the case of motor imagery, the motor response should be mentally carried out (without flexing the muscles). Thus, to understand the nature of motor imagery, motor imagery was compared not only with physical execution but also with motor inhibition. By employing the Go/NoGo DSP task, it was possible to examine whether motor imagery really resembles motor execution or whether motor imagery is more similar to motor inhibition. Behavioral results from this study revealed that learning of a fine sequential motor skill can by induced not only by physical practice, but also by motor imagery. To obtain evidence for the notion that motor imagery resembles motor execution rather than motor inhibition, EEG activity was examined during learning a motor skill. EEG results revealed maximal activity above central sites which are related to motor process during motor execution and motor imagery relative to motor inhibition. Additionally, ERLs revealed similarities between motor imagery and motor execution, because more negativity was present for these conditions as compared with motor inhibition. In the case of motor inhibition, a polarity reversal was observed indicating the inhibition of activity in the contralateral motor cortex. These results provided evidence that motor imagery induces motor skill learning (by improving response time and accuracy of a motor sequence), which is related with similar activation of brain areas during motor skill learning with motor execution and motor imagery. Although the effect of motor imagery was less strong relative to motor execution, we revealed that motor imagery resembles motor execution rather than motor inhibition.

- To what extent can motor imagery replace learning by executing a motor skill?

  In the study of Sobierajewicz et al. (2016), the main issue to be addressed concerned the extent to which learning a fine motor skill by motor imagery can replace motor execution. The notion that motor imagery may replace to some extent motor execution has relevant consequences for therapies using mental practice, for example, for patients after stroke (who are not able to execute a movement physically). In order to establish to what extent motor execution can be replaced by motor imagery, different proportions of executed and imagined movement sequences were employed, and two groups of participants took part in this experiment (including a control group in which participants were asked to withhold executing the movement instead of mentally imagine the movement sequence). Results showed that motor imagery induces motor learning - especially the accuracy of a movement was improved, although to reach a maximal speed of execution it was shown that it required at least 75% of physical execution. Therefore, this study revealed that a combination of mental imagery with a high rate of physical practice is beneficial for the acquisition of a motor skill.

- Is motor imagery comparable to motor preparation?

  In the study described above (Sobierajewicz et al., 2016), we could also investigate whether motor imagery is comparable to motor preparation. In this experiment, in the case of a NoGo signal, participants either had to imagine carrying out the response sequence (the motor imagery group), or the response sequence had to be withheld (the control group). Participants in the control group were instructed to withhold executing the sequence, what indicates that until the Go/NoGo signal the required task was the same for both groups. Interestingly, similar learning effects were observed in both groups (including the control group) suggesting that the presence of mere motor preparation may be sufficient to acquire a motor skill. It can be explained by the fact that participants in the control group could also imagine a motor response during preparation intervals, as a consequence they could also mentally practice a required sequence. Furthermore, even EEG results demonstrated similar lateralized activity for motor preparation between two groups of participants. However, wavelet analyses revealed different patterns for the alpha band between motor imagery and motor preparation (decreased contralateral power with an initial parietal focus that became more occipital at the end of the time interval; an initial occipital focus that became more parietal at the end of the time interval, respectively), (Van der Lubbe, Sobierajewicz, Jongsma, & Przekoracka-Krawczyk, 2017). The current findings suggest that motor imagery and motor preparation are not identical, although both seem to be sufficient to learn a motor skill.

1.3. Behavioral measures

In all presented studies (chapters 2-4) in this dissertation, RT and PC were calculated to determine sequence-learning effects. A Go/NoGo discrete sequence production (DSP) task was employed, wherein a five-stimulus sequence presented on each trial indicated the required sequence of finger movements. Participants either had to imagine carrying out the response sequence or the response sequence had to be physically executed by pressing appropriate keys on the keyboard, or the response sequence had to be withheld. RT and PC were calculated for sequences which were physically executed in both the practice phase and the test phase (which also included unfamiliar sequences). The great advantage of using the Go/NoGo DSP and the DSP task is that sequence-specific learning effects can be established in the final test phase by comparing RT and PC from sequences that were practiced before (executed, imagined, or inhibited) with unfamiliar sequences (unpracticed).

Response time (RT) was defined as the time between the onset of the Go signal (an informative cue indicating that the cued sequence had to be executed) and depression of the first key, and as the time between two consecutive key presses within a sequence (de Kleine & Van der Lubbe, 2011; Ruitenberg, De Kleine, Van der Lubbe, Verwey, & Abrahamse, 2011). It has been revealed that the time to initiate a sequence is typically longer than the time needed to execute other key presses. It can be explained by the fact that the initiation time is related with the selection and preparation of a whole sequence or a limited number of responses which are called *motor chunks*. These motor chunks represent several responses which are carried out if they are a single response. In the case of longer sequences (more than four key presses), it has been observed that the sequence is segmented in several motor chunks. Abrahamse et al. (2013) indicated that during the execution of these motor chunks there may be a *concatenation point*, which is related with the preparation for an upcoming motor chunk. This concatenation point is manifested by a slower response, which indicates the transition from one motor chunk to another (Abrahamse, Ruitenberg, de Kleine, & Verwey, 2013).

The percentage of correct responses (PC) were analyzed after performing an arcsine transformation to stabilize variances (Abrahamse & Verwey, 2008). PC indicated the percentage of correct responses. It has been observed that the number of incorrect responses during the initial phase of learning reduces and stabilizes with practice. The improvement was much slower during the subsequent blocks (latter phases of learning) as compared with this initial phase of learning.

1.4. Psychophysiological measures

Once there were only few methods which allowed to examine how specific functions are implements in the brain, e.g., by studying the brain *post mortem,* or by observing the behavior of people who had some specific head injuries (like Phineas Gage) or who had a brain operation (H.M.). These methods gave useful information about the probable functions of specific brain areas. Nowadays, many neuroimaging techniques are available to gain more insight in the processes of the living brain. Methods like positron emission topography (PET) or functional magnetic resonance imaging (fMRI) are suitable for addressing the question *where* different areas in brain are activated during the execution of a required task. To answer the question *when* specific cortical areas are involved, electroencephalography (EEG) seems to be a more suitable method. Electro - and also magnetoencephalography (MEG) allows to measure the electrical/magnetic activity generated by the brain on a sub-millisecond time scale. However, an important disadvantage of these methods is the low spatial resolution, as activity at a specific electrode does not directly relate to a specific underlying brain area. To optimize the spatial resolution, source localization analyses techniques have been used, but with these methods the resolution is about 1 to 3 cm (Slotnick, 2004). Thus, fMRI has a very good spatial resolution but a low temporal resolution, while EEG has a high temporal resolution but a low spatial resolution.

The good temporal resolution of EEG enables to measure and separate the various phases of acquisition a motor skill (i.e., stimulus encoding, memorization, response preparation and response execution/imagery). As a result, the advantage of having good temporal resolution in the case of EEG allows for assessing whether motor imagery is governed by the same rules as motor execution.

1.4.1. EEG

Nowadays, EEG is a standard method for studying cognitive processes, for example: memory, attention, perception or motor processes etc. (Harmon-Jones & Amodio, 2012). EEG is a non-invasive and completely painless imaging technique that reads scalp electrical activity after being picked up by Ag/AgCl electrodes (Luck, 2014). The EEG provides a real-time measure of the brain`s electrical activity. Application of EEG allows not only to examine the timing of specific processes (e.g., during motor imagery or motor execution), but also based on observed topography it can be established whether potential learning effects are more likely due to motor or visual imagery. Nevertheless, the most important advantage of EEG is the above-mentioned high temporal resolution.

Specific methods have been developed to examine brain activation within fractions of a second after a stimulus has been presented, e.g., event-related potentials (ERPs) or event-related lateralizations (ERLs). ERPs provide information about the averaged brain electrical activity in response to a stimulus or an event and enable to follow the time course of processes preceding the actual execution of a movement sequence (Kuperberg, 2004; de Kleine & Van der Lubbe, 2011). Furthermore, EEG enables to isolate activity that depends on the relevant side while any other activity is cancelled out, i.e., ERLs. The ERL method is commonly applied to all symmetrical electrodes above the left and right hemisphere (Wascher & Wauschkuhn, 1996), and can be viewed as an extension of the lateralized readiness potential (LRP) method which is only applied to central electrodes (Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988; De Jong, Wierda, & Mulder, 1988). ERPs and ERLs enable to gain a better insight into the processes associated with motor imagery and motor execution.

During measurement of the EEG, signal distortions called artefacts may appear. Teplan (2002) divided artefacts into two groups. First, called participant-related, such as: any minor body movements, electromyography, pulse, pace-maker, eye movements or sweating. The second group related with technical problems, e.g., impedance fluctuations, cable movements, broken wire contacts, too much electrode paste/jelly or dried pieces or low battery (Teplan, 2002). For example, in order to use EEG in sport, scientists have to resolve these inconveniences by using for instance portable amplifiers, but still there is a problem with patient-related artefacts, e.g., body movement or sweating. Thomson, Steffert, Ros, Leach, and Gruzelier (2008) pointed out the fact that muscle artefacts can completely obscure EEG activity. In order to avoid muscle artefacts during motor execution, motor imagery seems to be an optimal method as a substitute of motor execution for measurement of brain activity during motor performance (Thomson, Steffert, Ros, Leach, & Gruzelier, 2008).

1.4.2. EMG

EMG (electromyography) is a technique that records electrical activity produced by muscles. In this dissertation, EMG was recorded to control for muscular activation especially during motor imagery and motor inhibition. Mulder (2007) defined motor imagery as "… the mental execution of a movement without any overt movements or without any peripheral (muscle) activation". He pointed out that motor imagery is a cognitive process without even tightening the muscles. Thus, in order to confirm that a specific effect is really due to motor imagery, the possibility that the effect is caused by any overt movements or peripheral (muscle) activation should be ruled out.

However, previous brain imaging studies have shown that although the fMRI signal increases during motor imagery of finger movements, it is not related to the degree of EMG activation (Neuper, Scherer, Reiner, & Pfurtscheller, 2005). Some researchers suggested that weak EMG activity may be present in some participants during the motor imagery task (Neuper, Scherer, Reiner, & Pfurtscheller, 2005; Lotze & Halsband, 2006). However, participants should avoid any movements of the target muscles during motor imagery, and this is exactly controlled by EMG electrodes. In many studies, EMG is recorded to exclude other explanation of the effects of motor imagery (Stephan & Franckowiak, 1996; Lotze, Scheler, Tan, Braun, & Birbaumer, 2003; Caldara, et al., 2004; Papadelis, Kourtidou-Papadeli, Bamidis, & Albani, 2007; Kranczioch, Mathews, Dean, & Sterr, 2009). However, some studies did not check EMG activity (Stecklow, Infantosi, & Cagy, 2010; Machado, et al., 2013; Allami, et al., 2014). As a consequence, it is difficult to assess whether participants really used motor imagery as they may have flexed their muscles during mental execution of a task.

Concluding, EMG seems an appropriate technique to record muscular activity during motor performance. EMG enables either to provide evidence that motor imagery is not accompanied by the muscle activity, but also to control whether only required movements (i.e., button presses) are carried out during motor execution.

1.5. Transcranial direct current stimulation

The possibility that transcranial direct current stimulation (tDCS) affects motor skill learning induced by motor imagery seems relevant for different disciplines associated with motor functions: neurorehabilitation, physiotherapy, sport psychology, and specific training programs for athletes and musicians. The combined approach of using motor imagery together with brain stimulation may provide relevant data for the development of novel therapeutic tools, as motor imagery represents an alternative approach for rehabilitation.

One of the major interests for modern neuroscience is to investigate the plastic changes that occur in brain structures when people participate in motor and/or mental training. Brain plasticity refers to the putative changes in neural organization that accounts for the diverse forms of short-lasting or enduring behavioral modifiability. Currently, the challenge is to explore in greater detail the processes of neuroplasticity and how to modulate them in order to achieve the best behavioral outcome. Both motor imagery and tDCS are thought to induce plastic changes in the brain. Results from previous studies are inconsistent and therefore, it should be clarified what stimulation method leads to a desirable outcome (Nitsche & Paulus, 2000; Quartarone, et al., 2004). This aspect will be further explored in *Chapter 4.*

tDCS is presumed to strengthen synaptic connections through a mechanism similar to long-term potentiation (LTP) and long-term depression (LTD) - cellular mechanisms that underlie learning (Cuypers, et al., 2013). Thus, tDCS might improve motor skill learning by augmenting the neural plasticity within primary motor cortex (Fritsch, et al., 2010). The study conducted by Cuypers et al. (2013) showed that a combination of motor learning and 1.5 mA of anodal stimulation over the primary motor cortex contralateral to the dominant hand performing the motor task, leads to improved motor performance as compared to sham stimulation. This study showed that anodal tDCS of the motor cortex can be effective in augmenting learning effects in a sequence learning task. The research revealed that even five minutes of weak (1mA) tDCS may induce a short lasting significant variation of cortical excitability in humans. In particular, anodal tDCS to the primary motor cortex resulted in an increase of cortical excitability, whereas cathodal tDCS had an opposite effect (Nitsche & Paulus, 2000; Ang K., et al., 2015). However, the findings of Quartarone et. al (2004) showed that cathodal stimulation with tDCS can induce long lasting effects on cortical excitability during motor imagery, while anodal tDCS induces the opposite effect (Quartarone, et al., 2004). Nitsche and Paulus (2000) reported that the size and endurance of excitability's changes after anodal tDCS depended on stimulation duration and current intensity. However, there is a speculation whether larger current intensity leads to increased strengthening of learning-related synaptic connections, thus resulting in improved performance.

In conclusion, it has been revealed that transcranial direct current stimulation (tDCS) indeed affects motor learning. The question remains open whether tDCS combined with motor imagery above the primary motor cortex also influences sequence-specific learning of a fine hand motor skill.

1.6. Brain mechanisms

In the previous section, different measures were described which allow to examine the brain mechanisms underlying motor imagery and motor execution. There are also other sources, from which information about underlying brain mechanisms may come, i.e., brain metabolism, patients with brain lesions or studies on changes in brain excitability (Jeannerod & Frak, 1999), but in this dissertation I will focus only on research findings based on EEG and fMRI studies.

Recent studies have revealed that almost the same cortical regions that are active during the execution of a movement are also active during motor imagery (Parsons, 1994; Parsons, et al., 1995; Geradin, et al., 2000; Stevens, 2005; Xu, et al., 2014). Moreover, it has been proposed that motor imagery may be similar to the preparation phase of the motor action, because the brain areas which are activated during preparation and planning the motor action are also activated during motor imagery. Previous studies using fMRI or PET confirmed the notion that motor imagery activates similar cortical areas during planning and execution of motor movement (Miller, Schalk, Fetz, Ojemann, & Rao, 2010).

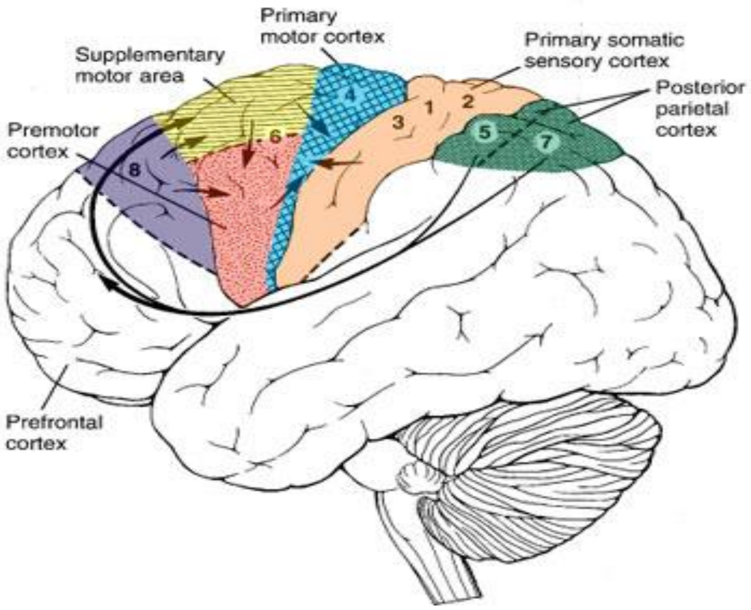

Figure 1. The motor areas of the cerebral cortex (http://brainmind.com/FrontalMotorAreas.html).

The prefrontal cortex

Jeannerod (2001) pointed out that the prefrontal cortex is activated when a decision must be taken about details of the movement. So the activation of this area is actually observable during a preparation phase of both the executed and the imagined action. Moreover, the prefrontal areas are associated with working memory and they are involved in planning, memory of actions and acquisition of new movements. It has been revealed that during mental simulation the prefrontal cortex is activated, for the simple reason that participants must engage working memory and executive attention (with the extent of this activation depending on the nature of the imaging task), (Dietrich, 2008). Meta-analysis of Grèzes et al. (2001) confirmed the notion about an equivalent activation of those areas both during motor execution and motor imagery, because for these two processes planning of details of a motion is needed.

Motor skill learning, in the initial stage, requires attentional processes, so the prefrontal cortex is also highly active (Halsband & Lange, 2006). This area is also associated with explicit learning which requires awareness of performance (Hikosaka, Nakamura, Sakai, & Nakahara, 2002). Therefore, with practice this part of the brain becomes less active, which is combined with automatization of a motor skill. Moreover, the prefrontal cortex has been associated with a number of functions that could contribute to sequence learning: working memory, action planning, memory for temporal order, and inhibition of extraneous information (Curran, 1995). So another function of the prefrontal cortex is the motor inhibition during mental simulation (Dietrich, 2008). This may be associated with making decision what should be done, or with simply inhibition during mental simulation.

The premotor cortex

It has been shown that the premotor area is involved in planning, programming, initiation, guidance and execution of simple and skilled motor tasks (Grèzes & Decety, 2001). The function of this area is to plan a more complex and coordinated movement, regardless of whether it is a covert or an overt action (Grèzes & Decety, 2001). The premotor area is divided into dorsal and ventral parts. Decety et al. (1994) found a large activation in both these parts of lateral premotor area during imagined hand movements. Importantly, a lot of research showed that the premotor area (especially the ventral premotor cortex) is associated with mirror neurons in humans (Halsband & Lange, 2006), which are also assumed to play a role in motor imagery.

The supplementary motor area

The supplementary motor area (SMA) is divided into pre-supplementary motor area (pre-SMA) and proper supplementary area (SMA), and each of them is associated with specific functions. Grèzes et al. took notice that the SMA and pre-SMA are involved in: simple vs. complex tasks, execution vs. selection, automatic performance vs. initial stage of skill acquisition, respectively (Grèzes & Decety, 2001). A previous meta-analysis showed that during execution, simulation and observation the SMA is more active, whereas the pre-SMA is more associated with mental simulation and observation with the aim to imitate (Grèzes & Decety, 2001). Moreover, the SMA plays a role in planning and selection of particular movement, so it is involved in the motor preparation of a movement (Dietrich, 2008). The pre-SMA is mainly active during movement selection, preparation and initiation of both imagined and executed action. The SMA is also involved in motor control, because of its ability to regulate the motor performance and to collaborate with other regions such as: the primary motor cortex or the somatosensory cortex (Xu, et al., 2014).

It is assumed that the pre-SMA also plays a role in the acquisition of sequential movements – it has been shown that neurons in this area are more activated during learning of new sequences as compared with the performance of learned sequences (Hikosaka, Nakamura, Sakai, & Nakahara, 2002). As another function of the pre-SMA is temporally segmenting the movement and anticipating its successive steps (Jeannerod, 2001), the special meaning of this area is during the early stages of motor skill acquisition as compared with later stages of motor learning. Furthermore, the SMA proper is more involved in implicit learning as compared with pre-SMA which is more active during explicit learning, (Halsband & Lange, 2006). Nevertheless, it has been proposed that the SMA and the pre-SMA work together to produce sequential movements (Tanji, 2001). However, neurons in the pre-SMA are more activated during learning of new sequences, but not during the performance of learned sequences (Nakamura, Sakai, & Hikosaka, 1998).

The primary motor cortex

There is a lot of discussion concerning the involvement of M1 during motor imagery. Some research has confirmed that M1 is activated during motor imagery (fMRI studies: (Leonardo, et al., 1995; Porro, et al., 1996)), but some other studies did not (PET studies: (Roland, Larsen, Lassen, & Skinhoj, 1980; Decety, et al., 1994)). This discrepancy could be due to the different neuroimaging methods employed as they have different temporal resolutions. Solodkin et al. (2004) pointed out that there should be lack of activation of M1 during motor imagery, because overt movements during mental simulation are avoided. However, results from the study of Miller and colleagues (2010) are inconsistent with this notion. They examined the activation of M1 using electrocorticogram measuring of cortical surface potentials during overt action and during imagery of the same motor action. This study revealed that the magnitude of imagery-induced cortical activity changed about 25% of that associated with the overt action (Miller, Schalk, Fetz, Ojemann, & Rao, 2010). Furthermore, the study of Geradin (2000) showed that the amount of about 30% of the activation of M1 present during motor execution is also observed during motor imagery. Lotze and Halsband (2006) suggested that the level of the activation of M1 depends on intensity and threshold of imagined movement. These results are in agreement with the previous studies indicating the activation of M1 during motor imagery is present, but in reduced proportion as compared to motor execution (Caldara, et al., 2004; Lotze & Halsband, 2006). The more complex an imagined action is, the higher the activation of M1. Not only has it been revealed that magnitude of M1 during motor imagery is much lower, but also that the time of its activation is shorter than during motor execution. These results clearly showed that M1 is involved in motor imagery, which suggests that its functions are not restricted to the mere motor execution (Lotze, et al., 1999). Furthermore, previous studies using functional neuroimaging methods showed that M1 also participates in motor preparation and motor skill learning (Richter, Andersen, Georgopoulos, & Kim, 1991; Kawashima, Roland, & O'Sullivan, 1994; Georgopoulos, 1995; Zang, et al., 2003).

The parietal cortex

Another brain area that is involved in motor execution, is the parietal cortex, which integrates visual and somatosensory information and transforms objects spatially. Hence, it is involved in higher spatial aspects of the motion, but it has been shown that its activation is smaller during motor imagery of simple movements (Lotze, et al., 1999; Dietrich, 2008). The parietal cortex is also involved in motor skill learning. As the prefrontal cortex is more activated during early stages of motor skill learning, the parietal cortex is activated at later stages of acquisition of new skills (Hikosaka, Nakamura, Sakai, & Nakahara, 2002).

1.7. Application of motor imagery

Exploring the neural mechanisms underlying motor imagery and investigating training strategies for both motor skill learning and motor function rehabilitation have been the focus of many scientists. Discovery that motor imagery involves similar neural pathways to those involved in actual movement (as detailed above) gave an opportunity to investigate the influence of motor imagery on learning motor skills. Moreover, it has been suggested that motor imagery may result in the same plastic changes (which refers to the changes in neuronal organization) in the motor system as actual physical practice (Mulder, 2007; Debarnot, Sperduti, Di Rienzo, & Aymeric, 2014). In other words, the structure of brain may be affected by the people's activation (either it is mental or actual). As Jeannerod (2001) underlined that "the presence of activity in the motor system during imagined action would put this action representation in a true *motor* format, it would be regarded by the motor system as a real action" (Jeannerod, 2001).

As a result, motor imagery (also added to physical practice) might be beneficial either in recovery after neurological damages, e.g. after stroke, cerebral, spinal or peripheral damage, or in healthy condition to improve motor skills per se, e.g., in education, sport, or music (Schuster, et al., 2011). But the greatest value of motor imagery seems to be in rehabilitation for all patients who are not able to physically practice, e.g., patients with hemiplegia. Moreover, it has been proposed that a combination of tDCS with motor imagery may increase the effects of rehabilitation, which will be examined in *Chapter 4* in detail.

Several factors may influence motor imagery regardless of a field of interest: ability of imagery, skill level and type of the action, motivation or specific area of lesion with neurological patients etc. (Gregg & Clark, 2007). The imagery ability refers to the vividness and precision of the evoked images or sensations. “The ability to generate imagined movements is necessary for motor imagery to be most effective” (Lopes Abbas, Lucas, Teixeira, & Paes, 2011). Furthermore, the ability of motor learning, and thereby the ability of motor learning with motor imagery can differ between individuals. Differences among participants can be caused by differences in degree of motor experience, and may depend on the perception of information, motivation, disease, age or the capacity of short-term and long-term memory (Čoh, Jovanović-Golubović, & Bratić, 2004; Wulf, Shea, & Lewthwaite, 2010; Maillet, et al., 2013). Thus, it is assumed that personal factors affect both motor imagery, and physical practice (i.e., mood, personal distractors, sickness, even the level of hunger or fatigue), (Batson, Feltman, & Waring, 2007). Motor imagery`s ability might be measured by the several questionnaires, for example by the Movement Imagery Questionnaire or the Vividness of Movement Imagery Questionnaire. Many researchers have employed these questionnaires to control motor imagery`s ability in their studies (Meister, et al., 2004; Stecklow, Infantosi, & Cagy, 2010; Gaggioli, Morganti, Mondoni, & Antonietti, 2013; Frank, Land, Pop, & Schack, 2014).

Because a relationship between age and imaging ability is unclear, several studies have investigated the effects of development and aging on motor imagery ability (Mizuguchi, Nakata, Uchida, & Kanosue, 2012). Of course, it is important to establish at what age the optimal imaging ability is reached and when it begins to decrease in order to determine the optimal conditions of training with motor imagery (Mizuguchi, Nakata, Uchida, & Kanosue, 2012). Previous studies revealed that elderly are less accurate than young subjects (Verwey, Abrahamse, Ruitenberg, Jiménez, & de Kleine, 2011). For example, it has been shown that they make more errors in extra personal space during motor imagery as compared with young participants (Lopes Abbas, Lucas, Teixeira, & Paes, 2011). Nevertheless, Fansler et al. (1985) revealed that mental practice can also improve performance even in elderly and it can be used as a complementary form of training (Fansler, Poff, & Shepard, 1985).

In the next subsections, I will concentrate on the importance and application of motor imagery in rehabilitation, sport and music, as many experiments focused on these fields.

1.7.1. Rehabilitation

Motor imagery receives more and more in neurological rehabilitation practices. Previous studies have investigated the use of mental practice through motor imagery to enhance functional recovery of patients. Solodkin et al. (2004) suggested that motor imagery may play a crucial role in the improvement of motor skill learning in healthy subjects, but also in recovery after neurological damage (Solodkin, Hlustik, Chen, & Small, 2004).

Many researchers have proposed motor imagery as a cost-efficient tool in neurorehabilitation after the damage to the central nervous system (Mulder, 2007; Lopes Abbas, Lucas, Teixeira, & Paes, 2011; Maillet, et al., 2013). Green et al. (1997) underlined beneficial effects of motor imagery in rehabilitation, especially in the case of exercises which are difficult, painful or simply impossible to perform. Therefore, patients can “exercise” mentally in order to prevent the changes that take place as a result of inactivity and disuse (Mulder, 2007). The possibility to use motor imagery as a recovery technique can be very relevant in situations where physical practice may be limited by expense, time constraints, fatigue or potential for injury (Hird, Landers, Thomas, & Horan, 1991). “When the neurological condition does not allow patients to perform movements, motor imagery is needed in order to keep the neural networks active and also to promote cortical reorganization, so that the motor preparation facilitates future executions of specific movements during the rehabilitation program” (Lopes Abbas, Lucas, Teixeira, & Paes, 2011). Even if a patient is able to move, one can improve its recovery using motor imagery, as a complementary technique to physical practice. Furthermore, motor imagery as a treatment technique is attractive because it encourages patients to assume some of the responsibility for their recovery (Fansler, Poff, & Shepard, 1985).

Moreover, Moran et al. (2015) testified that motor imagery can be used as a therapeutic tool in three clinical conditions: posttraumatic stress disorder (PTSD), personality disorder and social anxiety disorder (SAD), (Moran, Bramham, Collet, Guillot, & MacIntyre, 2015). Moran pointed out that processes of imagery (either motor or visual imagery) are also relevant and helpful in the treatment of psychopathology. Yet, little is known about the application of motor imagery in clinical disorders. It seems the imagery perspective is also relevant for the treatment of these disorders (first vs. third perspective), (see: (McIsaac & Eich, 2015)).

Neuropsychological studies have revealed that different brain lesions may lead to distinct forms of mental imagery impairments. Especially, in the acute phase after stroke, motor imagery therapy seems useful as an alternative for a standard, physical therapy (Tangwiriyasakul, Mocioiu, van Putten, & Rutten, 2014). Motor imagery can be used for training of gait (Lee, Song, Lee, Cho, & Lee, 2011; Cho, Kim, & Lee, 2013); when combined with physiotherapy it can offer functional benefits after stroke (Schuster, Butler, Andrews, Kischka, & Ettlin, 2012). It is assumed that brain damage affecting the execution of an action may also affect the ability to mentally simulate the action. It has been argued that patients with damage to the right parietal cortex are impaired in motor imagery and loose the capacity to predict the duration of a movement during mental simulation (Lotze & Halsband, 2006). Thus, lesions in the parietal lobe can impair motor imagery, because the parietal lobe is known to be responsible for the generation of mental representations of a movement (Lopes Abbas, Lucas, Teixeira, & Paes, 2011). As a consequence, these patients may have difficulties in imagining a movement. Moreover, the location of the lesion may affect different aspects of motor imagery. Patients suffering from Parkinson's disease (caused by a dysfunction of basal ganglia and the frontal cortex) have been reported to have difficulties with mentally simulating finger movement sequences or mental rotations of the hand. “The performance deficits of movement disorders may be caused not only by the brain lesions themselves, but also by the abnormal connectivity between motor regions” (Xu, et al., 2014). For example, patients with a corticospinal lesion with hemiplegia are still able to generate imagined movements with their affected limb, but for patients, for instance, with Parkinson`s disease, it is more problematic, the imagined movement is impaired or is slower, the same as real executed movements (Jeannerod, 2001).

Motor imagery is also used for brain computer interfaces (BCIs), (Alonso-Valerdi, Salido-Ruiz, & Ramirez-Mendoza, 2015). A BCI is an important medical device for patients who have lost their motor abilities, as it enables to control a computer with patient`s brain activity (Morash, Bai, Furlani, Lin, & Hallett, 2008). BCI enables to communicate with the environment, to restore motor control, and to recover motor functions. For example, there are several studies of BCI using motor imagery on stroke patients (for review see: (Ang, et al., 2011; Ang & Guan, 2013)).

In conclusion, motor imagery provides an opportunity to increase the number of repetitions[1] without undue physical fatigue in case of patient`s disability. When physical practice is impossible or difficult, motor imagery seems to be a useful tool to train different motor functions (Warner & McNeill, 2013). A therapy with motor imagery can be easily incorporated into the patient`s home rehabilitation (Fansler, Poff, & Shepard, 1985). Although motor imagery can be a very useful tool for rehabilitation, there are no general guidelines, specific parameters about weekly frequency, duration or adequate moment to start the therapy with motor imagery (Lopes Abbas, Lucas, Teixeira, & Paes, 2011; Malouin, Jackson, & Richards, 2013). Future research should focus on identifying these parameters, which may affect the effectiveness of training with motor imagery.

1.7.2. Sports

Recently, motor imagery has been used as a technique for influencing learning a motor skill in sport disciplines. In the context of sport, motor imagery is more often called as “mental rehearsal” (Solodkin, Hlustik, Chen, & Small, 2004). It is assumed that imagery is a mental skill, which is more frequently incorporated to everyday training of athletes (Dun & Burton, 2005). For example, the benefit of motor imagery has been shown during specific aerobic training sessions in tennis players (Guillot, et al., 2015). It is worth to notice that in the case of application of motor imagery in sport, more complex actions were examined, e.g., golf putting, lay-up shots (Gaggioli, Morganti, Mondoni, & Antonietti, 2013).

---

[1] Some research even investigated benefit of motor imagery on the development of surgical skills (Hall, 2002; Sanders, Sadoski, Bramson, Wiprud, & Van Walsum, 2004; Cocks, Moulton, Luu, & Cil, 2014).

Motor imagery can also be used for motivation, self-confidence and anxiety reduction (Malouin, Jackson, & Richards, 2013). So, mental imagery in sports can not only enhance performance but also can be used as motivational tool to reach goals, to name them and motivate to reach them. Very often, a training program with a motor imagery should include three pieces of information: the imagery ability of the athlete, the effect of imagery on performance, and the motive for using imagery (Dun & Burton, 2005).

In the case of sport disciplines motor imagery might be misunderstood as visual imagery (i.e., visualization). However, Mizuguchi et al. (2016) suggest that if a person lacks a motor representation for a difficult whole-body movement (thus, motor-related regions of the brain are not involved), visual imagery is involved unintentionally. In their fMRI study, they revealed an activation in the primary visual cortex during motor imagery of difficult whole body movements (Mizuguchi, Nakata, & Kanosue, 2016). Nevertheless, sports psychologists recommend that imagined performances should be felt as well as visualized (Annett, 1995).

Motor imagery allows to familiarize with the environment or action itself, and can be also used as a reminder of the key elements of the performance requiring attention or to facilitate warm up (Annett, 1995). The mental representation of the movement can be used during mental simulation to cue the learner on temporal and spatial elements of the skill, so it can be used to monitor and to improve the physical performance (Gaggioli, Morganti, Mondoni, & Antonietti, 2013). Another great advantage of motor imagery in sport, is its facility and accessibility, so it can be used in risky sport, where conditions of training are demanding (e.g., jumps into the water, wing suit flying).

In the field of sport psychology there are two questionnaires of kinesthetic imagery: Vividness of Kinesthetic Imagery (VKI) and the Control of Kinesthetic Imagery (CKI), which are used by trainers. Although they still require refinement, they can be supportive for trainers to establish the ability of athletes to mentally simulate the motor action (Dun & Burton, 2005).

To summarize, motor imagery seems to be a useful adjunctive technique in sport disciplines. It has been shown that motor imagery may enhance skill acquisition and facilitate the actual performance of a learnt skill (Warner & McNeill, 2013). Taken together, motor imagery has been applied in various sport disciplines, revealing benefits in speed, performance accuracy, movements dynamics, balance or coordination (Gaggioli, Morganti, Mondoni, & Antonietti, 2013).

1.7.3. Music

Most of the prior studies that aimed to investigate motor learning with motor imagery have shown that training with motor imagery can significantly promote the learning of a novel motor skill, but such training needs to be very intensive (Pascual-Leone, et al., 1995; Jackson, Lafleur, Malouin, Richards, & Doyon, 2003; Allami, Paulignan, Brovelli, & Boussaoud, 2008). Here, I would like to focus on studies, which investigated the effect of motor imagery on music performance. It is known that professional musicians use additional strategies of mental imagery of music performance. It has been suggested that auditory, motor and visual imagery may facilitate many aspects of music performance, e.g., pitch accuracy, tempo or movement velocity. Moreover, *musical imagery* has been differentiated and defined as multimodal process associated with auditory, visual, kinesthetic and tactile properties of music-related movements (Keller, 2012).

In study of Brown and Palmer (2013) pianists' pitch accuracy was measured to examine how auditory and motor imagery abilities affect learning and recall of novel melodies. Pianists learned melodies either by performing without sound (motor learning) or by listening without performing (auditory learning). Although results revealed that pitch accuracy was higher after auditory learning than after motor learning, both auditory and motor imagery skills improved pitch accuracy. Another recent study of Bernardi et al. (2013) questioned whether mental practice may optimize movement timing by employing expert pianists who performed difficult music sequences either with mental practice or with physical practice. Changes in performance were observed in movement velocity, timing and coordination. These results revealed an improvement in performance after mental practice, although better results were obtained after physical practice (Bernardi, De Buglio, Trimarchi, Chielli, & Bricolo, 2013).

Modern neuroimaging techniques provide the opportunity to investigate the brains of living musicians while performing a piece of music. Investigation of the cerebral network with the use of fMRI has revealed the activation of a frontoparietal network during execution and imagery of musical performance (Meister, et al., 2004). As compared with non-musicians, fMRI studies have revealed decreased motor activation within the SMA, the premotor cortex and the ipsilateral primary motor cortex during the performance of sequential finger movements in professional musicians (Jäncke, Shah, & Peters, 2000). However, Baumann et al. (2007) revealed that musicians engage sensorimotor regions (i.e., dPMC, SMA) more than non-musicians when imagining the motor movements associated with music performance (Baumann, et al., 2007). Nevertheless, it is has been proposed that highly trained individuals (as compared to novices) are characterized by a decrease in the overall volume of brain activation (e.g., fronto-parietal network) with increased activation of specific brain areas involved in the execution of the task (e.g., the primary motor cortex, the primary somatosensory cortex, the supplementary motor area), (Jäncke, Shah, & Peters, 2000; Lotze, Scheler, Tan, Braun, & Birbaumer, 2003; Debarnot, Sperduti, Di Rienzo, & Aymeric, 2014). Lotze et al. (2003) compared brain activation of professional and amateur violinists during actual and imagined performance. They revealed that professionals demonstrated more focused activation patterns during imagined musical performance as opposed to amateurs. These results showed that musical production engaged not only the motor areas, but also the somatosensory, auditory, emotional and memory networks. Moreover, these findings also revealed that prolonged musical training is associated with increased efficiency and reduced effort.

Neuroimaging studies revealed that the activation of brain areas differs depending on the expertise level (for a review see: Debarnot, Sperduti, Di Rienzo, & Aymeric, 2014). Considering these results together with several studies focusing on motor skill learning, it may be proposed that electrophysiological activity may be stronger in the case of non-musicians as opposed to professional pianists. This aspect will be further explored in *Chapter 3*.

1.8. Questions to be addressed in this thesis

This thesis addresses several aspects of the role of motor imagery for learning a fine hand motor skill. In this chapter, I gave an overview of the most recent literature on motor imagery. A definition of motor imagery and a relationship between motor imagery and motor skill learning was specified. Different paradigms were described, in particular including a DSP Go/NoGo task, as this paradigm allows to determine sequence-specific learning effects. Furthermore, different aspects of the mechanisms underlying motor imagery were presented. Next, the results of the recent studies were presented in the field of rehabilitation, sport and music.

In the following empirical chapters (*Chapter 2 to 4*), the influence of motor imagery on the learning of a sequential motor skill will be further specified. The following questions will be addressed:

Does motor imagery help to learn a fine hand motor skill?

All the studies (*Chapters 2-4*) presented in this dissertation concern the question whether motor imagery helps to learn a fine motor skill.

How effector-specific is motor imagery?

In *Chapter 2,* I focused on performance using either only an index finger or four fingers to focus on the learning of a spatial pattern rather than on the learning of a specific motor pattern. This study allows to determine how effector-specific the effect of motor imagery is, by varying the execution mode while learning a motor skill (i.e., the practice phase) and during a final test phase.

Does expertise affect learning of a motor skill with the help of motor imagery?

In *Chapter 3,* behavioral results and electrophysiological activation of professional musicians and non-musicians during learning a fine motor skill with motor execution, motor imagery and motor inhibition were examined. Comparison of these two groups enabled to determine whether expertise affects learning of a motor skill with motor imagery.

Does transcranial direct current stimulation affect the learning of a fine sequential hand motor skill with motor imagery?

In *Chapter 4*, it was investigated whether learning a fine motor skill with motor execution and motor imagery combined with tDCS would influence the sequence-learning effects.

The answers to the abovementioned questions will be summarized in the final *Chapter 5*, where a more integrative discussion of the various findings from chapters 2 to 4 will be presented. This chapter ends with some final conclusions and some possible paths along which the currently presented research may be further developed.

References

Abrahamse, E. L., & Verwey, W. B. (2008). Context dependent learning in the serial RT task. *Psychological Research*, *72*(4), 397–404.

Abrahamse, E. L., Ruitenberg, M. F. L., de Kleine, E., & Verwey, W. B. (2013). Control of automated behavior: insights from the discrete sequence production task. *Frontiers in Human Neuroscience, 7*, 82.

Allami, N., Brovelli, A., Hamzaoui, E. M., Regragui, F., Paulignan, Y., & Boussaoud, D. (2014). Neurophysiological correlates of visuo-motor learning through mental and physical practice. *Neuropsychologia, 55*, 6-14.

Allami, N., Paulignan, Y., Brovelli, A., & Boussaoud, D. (2008). Visuo-motor learning with combination of different rates of motor imagery and physical practice. *Experimental Brain Research, 184*(1), 105-113.

Alonso-Valerdi, L. M., Salido-Ruiz, R. A., & Ramirez-Mendoza, R. A. (2015). Motor imagery based brain–computer interfaces: An emerging technology to rehabilitate motor deficits. *Neuropsychologia*, *79*, 354-363.

Anderson, J. R. (1982). Acquisition of cognitive skill. *Psychological Review, 89*(4), 369-406.

Ang, K.K.; Guan, C., Phua, K.S., Wang, C., Zhao, L., Teo, W.P., Chen, C., Ng, Y.S., Chew, E. (2015). Facilitating effects of transcranial direct current stimulation on motor imgery brain-computer interface with robotic feedback for stroke rehabilitation. *Archives of Physical Medicine and Rehabilitation, 96*, 79-87.

Ang, K. K., & Guan, C. (2013). Brain-Computer Interface in Stroke Rehabilitation. *Journal of Computing Science and Engineering, 7*(2), 139-146.

Ang, K. K., Guan, C., Chua, K. S., Ang, B. T., Kuah, C. W., Wang, C., . . . Zhang, H. (2011). A Large Clinical Study on the Ability of Stroke Patients to Use an EEG-Based Motor Imagery Brain-Computer Interface. *Clinical EEG and neuroscience, 42*(4), 253-258.

Annett, J. (1995). Motor imagery: perception or action? *Neuropsychologia, 33*(11), 1395-1417.

Batson, G., Feltman, R., & Waring, J. (2007). Effect of mental practice combined with physical practice on balance in the community-dwelling elderly. *Activities, Adaptation & Aging, 31*, 1-18.

Baumann, S., Koeneke, S., Schmidt, C. F., Meyer, M., Lutz, K., & Jancke, L. (2007). A network for audio–motor coordination in skilled pianists and non-musicians. *Brain research, 1161*, 65-78.

Bernardi, N. F., De Buglio, M., Trimarchi, P. D., Chielli, A., & Bricolo, E. (2013). Mental practice promotes motor anticipation: evidence from skilled music performance. *Frontiers in Human Neuroscience, 7*, 451.

Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The Inhibition of Imitative Response Tendencies. *NeuroImage, 14*(6), 1416-1423.

Caldara, R., Deiber, M.-P., Andrey, C., Michel, C. M., Thut, G., & Hauert, C.-A. (2004). Actual and mental motor preparation and execution: a spatiotemporal ERP study. *Experimental Brain Research, 159*(3), 389-399.

Chaffin, R., & Logan, T. (2006). Practicing perfection: How concert soloists prepare for performance. *Advances in Cognitive Psychology, 2*, 113-130

Chambaron, S., Berberian, B., Delbecque, L., Ginhac, D., & Cleeremans, A. (2009). Implicit motor learning in discrete and continuous tasks: Toward a possible explanation of discrepant results. In L. T. Pellegrino, *Handbook of Motor Skills: Development, Impairment, and Therapy* (pp. 139-155). New York: Nova Science Publishers.

Cho, H., Kim, J., & Lee, G. (2013). Effects of motor imagery training on balance and gait abilities in post-stroke patients: a randomized controlled trial. *Clinical rehabilitation, 27*(8), 675-680.

Cocks, M., Moulton, C.-A., Luu, S., & Cil, T. (2014). What surgeons can learn from athletes: mental practice in sports and surgery. *Journal of surgical education, 71*(2), 262-269.

Čoh, M., Jovanović-Golubović, D., & Bratić, M. (2004). Motor learning in sport. *Physical Education and Sport, 2,* 45-59.

Cohen, N. J., & Squire, L. R. (1980). Preserved learning and retention of pattern analyzing skills in amnesia: Dissociation of knowing how and knowing that. *Science, 210,* 207–210.

Curran, T. (1995). On the neural mechanisms of sequence learning. *Psyche: An Interdisciplinary Journal of Research on Consciousness, 2*(12).

Cuypers, K., Leenus, D., van den Berg, F. E., Nitsche, M. A., Thijs, H., Wenderoth, N., & Meesen, R. L. (2013). Is Motor Learning Mediated by tDCS Intensity? *PLoS ONE, 8*(6):e67344.

de Jong, R., Wierda, M., & Mulder, L. (1988). Use of partial information in responding. *Journal of Experimental Psychology: Human Perception and Performance, 14*(4), 682-692.

de Kleine, E. (2009). *Cognitive control of sequential behavior.* Ipskamp, Enchede.

de Kleine, E., & Van der Lubbe, R. H. (2011). Decreased load on general motor preparation and visual-working memory while preparing familiar as compared to unfamiliar movement sequences. *Brain and Cognition, 75*(2), 126-134.

de Lange, F. P. (2008). *Neural mechanisms of motor imagery.*

de Lange, F. P., Hagoort, P., & Toni, I. (2005). Neural topography and content of movement representations. *Journal of cognitive neuroscience, 17*(1), 97-112.

Debarnot, U., Sperduti, M., Di Rienzo, F., & Aymeric, G. (2014). Experts bodies,experts minds: How physical and mental training shape the brain. *Frontiers in Human Neuroscience, 8,* 280.

Decety, J. (1991). Motor information may be important for updating the cognitive processes involved in mental imagery of movement. *Cahiers de Psychologie Cognitive/Current Psychology of Cognition, 11*(4), 415-426.

Decety, J., & Jeannerod, M. (1996). Mentally simulated movements in virtual reality: does Fitts`s law hold in motor imagery? *Behavioural Brain Research, 72,* 127-134.

Decety, J., Jeannerod, M., & Prablanc, C. (1989). The timing of mentally represented actions. *Behavioural Brain Research, 34*(1-2), 35-42.

Decety, J., Jeannerod, M., Germain, M., & Pastene, J. (1991). Vegetative response during imagined movement is proportional to mental effort. *Behavioural Brain Research, 42*(1), 1-5.

Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., . . . F. F. (1994). Mapping motor representations with positron emission tomography. *Nature, 371*, 600-602.

Deiber, M., Ibanez, V., Honda, M., Sadato, N., Raman, R., & Hallett, M. (1998). Cerebral processes related to visuomotor imagery and generation of simple finger movements studied with positron emission tomography. *NeuroImage, 7(2)*, 73-85.

Dietrich, A. (2008). Imaging the imagination: The trouble with motor imagery. *Methods, 45*(4), 319-324.

Doussoulin, A., & Rehbein, L. (2011). Motor imagery as a tool for motor skill triaing in children. *Motricidade, 7*(3), 37-43.

Dun, K., & Burton, L. (2005). Kinaesthetic Imagery: Does it exist and how can we measure it? *11th World Congress of Sport Psychology, Sydney, Australia*, 1-4.

Eaves, D. L., Riach, M., Holmes, P. S., & Wright, D. J. (2016). Motor Imagery during Action Observation: A Brief Review of Evidence, Theory and Future Research Opportunities. *Frontiers in Neuroscience*, *10*, 514.

Fabbri-Destro, M., & Rizzolatti, G. (2008). Mirror Neurons and Mirror Systems in Monkeys and Humans. *Physiology, 23*, 171-179.

Fansler, C. L., Poff, C. L., & Shepard, K. F. (1985). Effects of mental practice on balance in elderly women. *Physical therapy, 65*(9), 1332-1338.

Fitts, P. M. (1964). Perceptual-motor skill learning. In *Categories of human learning (Melton AW, ed)* (pp. 243-285). New York: Academic.

Frank, C., M. Land, W., Pop, C., & Schack, T. (2014). Mental Representation and Mental Practice:Experimental Investigation on the Functional Links between Motor Memory and Motor Imagery. *PLoS ONE, 9*(4): e95175.

Fritsch, B., Reis, J., Martinowich, K., Schambra, H. M., Ji, Y., Cohen, L. G., & Lu, B. (2010). Direct current stimulation promotes BDNF-dependent synaptic plasticity: Potential implications for motor learning. *Neuron, 66*(2), 198-204.

Gaggioli, A., Morganti, L., Mondoni, M., & Antonietti, A. (2013). Benefits of combined mental and physical training in learning a complex motor skill in basketball. *Psychology, 4*, 1-6.

Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in cognitive sciences, 2*(12), 493-501.

Garavan, H., Ross, T. J., & Stein, E. A. (1999). Right hemispheric dominance of inhibitory control: An event-related functional MRI study. *Proceedings of the National Academy of Sciences of the United States of America*, *96*(14), 8301–8306.

Georgopoulos, A. P. (1995). Current issues in directional motor control. *Trends in Neurosciences, 18*(11), 506-510.

Geradin, E., Sirigu, A., Lehéricy, S., Poline, J.-B., Gaymard, B., Marsault, C., . . . Le Bihan, D. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex, 10*(11), 1093-1104.

Graf, P., & Schacter, D. (1985). Implicit and explicit memory for new association in normal and amnestic subjects. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *11*(3), 501-518.

Gratton, G., Coles, M. G., Sirevaag, E. J., Eriksen, C. W., & Donchin, E. (1988). Pre- and post-stimulus activation of response channels: a psychophysiological analysis. *Journal of Experimental Psychology: Human Perception and Performance, 14*(3), 331-344.

Gregg, M. J., & Clark, T. (2007). Theoretical and practical applications of mental imagery. *International Symposium on Performance Science*, 295-300.

Grèzes, J., & Decety, J. (2001). Functional Anatomy of Execution, Mental Simulation, Observation, and Verb Generation of Actions: A Meta-Analysis. *Human Brain Mapping, 12*(1), 1-19.

Guillot, A., & Collet, C. (2005). Contribution from neurophysiological and psychological methods to the study of motor imagery. *Brain Research Reviews, 50*(2), 387-397.

Guillot, A., Di Rienzo, F., Pialoux, V., Simon, G., Skinner, S., & Rogowski, I. (2015). Implementation of motor imagery during specific aerobic training session in young tennis players. *PLoS ONE, 10*(11): e0143331.

Hall, J. C. (2002). Imagery practice and the development of surgical skills. *The American Journal of Surgery, 184*(5), 465-470.

Halsband, U., & Lange, R. K. (2006). Motor learning in man: A review of functional and clinical studies. *Journal of Physiology, Paris, 99*(4-6), 414-424.

Harmon-Jones, E., & Amodio, D. M. (2012). Electroencephalographic methods in psychology. In H. Cooper, *APA Handbook of Research Methods in Psychology: Vol.1. Foundations, Planning, Measures, and Psychometrics* (pp. Chapter 26, 1-20). American Psychological Association.

Hikosaka, O., Nakahara, H., Rand, M. K., Sakai, K., Lu, X., Nakamura, K., . . . Doya, K. (1999). Parallel neural networks for learning sequential procedures. *Trends in Neurosciences, 22*(10), 464-471.

Hikosaka, O., Nakamura, K., Sakai, K., & Nakahara, H. (2002). Central mechanisms of motor skill learning. *Current Opinion in Neurobiology, 12*(2), 217-222.

Hird, J. S., Landers, D. M., Thomas, J. R., & Horan, J. J. (1991). Physical practice is superior to mental practice in enhancing cognitive and motor task performance. *Journal of sport & exercise psychology, 13*(3), 281-293.

Holland, P. C. (2008). Cognitive versus stimulus-response theories of learning. *Learning & Behavior, 36*(3), 227–241.

Jackson, P. L., Lafleur, M. F., Malouin, F., & Richards, C. (2001). Potential Role of Mental Practice Using Motor Imagery in Neurologic Rehabilitation. *Archives of Physical Medicine and Rehabilitation, 82*(8), 1133-1141.

Jackson, P., Lafleur, M., Malouin, F., Richards, C., & Doyon, J. (2003). Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. *NeuroImage, 20*(2), 1171-1180.

Jäncke, L., Shah, N., & Peters, M. (2000). Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Cognitive Brain Research, 10*(1-2), 177-183.

Jeannerod, M. (1995). Mental imagery in the motor context. *Neuropsychologia, 33*(11), 1419-1432.

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage, 14*(1), 103-109.

Jeannerod, M. (2006). Motor cognition: What actions tell the self. New York: Oxford University Press.

Jeannerod, M., & Frak, V. (1999). Mental imaging of motor activity in humans. *Current Opinion in Neurobiology, 9*(6), 735-739.

Jongsma, M. L., Meulenbroek, R. G., Okely, J., Baas, C., van der Lubbe, R. H., & Steenbergen, B. (2013). Effects of hand orientation on motor imagery-event related potentials suggest kinesthetic motor imagery to solve the hand laterality judgment task. *PLoS ONE, 8*(9): e76515 1-10.

Kawashima, R., Roland, P. E., & O'Sullivan, B. T. (1994). Fields in Human Motor Areas Involved in Preparation for Reaching, Actual Reaching, and Visuomotor Learning: A Positron Emission Tomography Study. *Journal of Neuroscience, 14*(6), 3462-3474.

Keele, S. W., Ivry, R., Mayr, U., Hazeltine, E., & Heuer, H. (2003). The Cognitive and Neural Architecture of Sequence Representation. *Psychological Review, 110*(2), 316–339.

Keller, P. E. (2012). Mental imagery in music performance: underlying mechanisms and potential benefits. *Annals Of The New York Academy Of Sciences, 1252,* 206-213.

Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2001). Neural foundations of imagery. *Nature Reviews. Neuroscience, 2*(9), 635-642.

Kranczioch, C., Mathews, S., Dean, P. J., & Sterr, A. (2009). On the equivalence of executed and imagined movements: evidence from lateralized motor and nonmotor potentials. *Human Brain Mapping, 30*(10), 3275-3286.

Kuperberg, G. R. (2004). Electroencephalography, Event-Related Potentials, and Magnetoencephalography. In D. D. Dougherty, S. L. Rauch, & J. Rosenbaum, *Essentials of neuroimaging for clinical practice* (pp. 117-127). American Psychiatric Press.

Lee, G., Song, C., Lee, Y., Cho, H., & Lee, S. (2011). Effects of motor imagery training on gait ability of patients with chronic stroke. *Journal of Physical Therapy Science, 23*(2), 197-200.

Leonardo, M., Fieldman, J., Sadato, N., Campbell, G., Ibanez, V., Cohen, L., . . . Hallet, M. (1995). A functional magnetic resonance imaging study of cortical regions associated with motor task execution and motor ideation in humans. *Human Brain Mapping, 3*(2), 83-92.

Lopes Abbas, A., Lucas, M. F., Teixeira, S., & Paes, F. (2011). Motor imagery and stroke neurorehabilitation: an overview of basic concepts and therapeutic effects. *Neuroscience International, 2*(2), 59-64.

Lotze, M., & Halsband, U. (2006). Motor imagery. *Journal of Physiology, 99*, 386-395.

Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., . . . Grodd, W. (1999). Activation of Cortical and Cerebellar Motor Areas during Executed and Imagined Hand Movements: An fMRI Study. *Journal of Cognitive Neuroscience, 11*(5), 491–501.

Lotze, M., Scheler, G., Tan, H.-R., Braun, C., & Birbaumer, N. (2003). The musician`s brain functional imaging of amateurs and professionals during performance and imagery. *NeuroImage, 20*(3), 1817-1829.

Luck, S. J. (2014). *An introduction to the event-related potential technique.* London, England: MIT press.

Luft, A. R., & Buitrago, M. M. (2005). Stages of motor skill learning. *Molecular Neurobiology, 32*(3), 205-216.

Machado, S., Arias-Carrión, O., Paes, F., Ribeiro, P., Cagy, M., Piedade, R., … Nardi, A. E. (2013). Changes in Cortical Activity During Real and Imagined Movements: an ERP Study. *Clinical Practice and Epidemiology in Mental Health: CP & EMH, 9,* 196–201.

Maillet, A., Fraix, V., Thobois, S., Derost, P., Bloem, B., Pollak, P., & Debû, B. (2013). Kinesthetic imagery of gait in advanced Parkinson`s disease. *Movement &Sport Sciences - Science & Motricité, 82,* 115-128.

Malouin, F., Jackson, P. L., & Richards, C. L. (2013). Towards the integration of mental practice in rehabilitation programs. A critical review. *Frontiers in Human Neuroscience, 7*, 576.

McIsaac, H. K., & Eich, E. (2015). Vantage Point in Traumatic Memory. *Psychological Science, 15*(4), 248-253.

Meister, I., Krings, T., Foltys, H., Boroojerdi, B., Müller, M., T. R., & Thron, A. (2004). Playing piano in the mind - an fMRI study on music imagery and performance in pianists. *Cognitive Brain Research, 19*(3), 219-228.

Miller, K. J., Schalk, G., Fetz, E. E., den Nijs, M., Ojemann, J. G., & Rao, R. P. N. (2010). Cortical activity during motor execution, motor imagery, and imagery-based online feedback. *Proceedings of the National Academy of Sciences of the United States of America, 107*(9), 4430–4435.

Mizuguchi, N., Nakata, H., & Kanosue, K. (2016). Motor imagery beyond the motor repertoire: activity in the primary visual cortex during kinesthetic motor imagery of difficult whole body movements. *Neuroscience, 315,* 104-113.

Mizuguchi, N., Nakata, H., Uchida, Y., & Kanosue, K. (2012). Motor imagery and sport performance. *The Journal of Sports Medicine and Physical Fitness, 1,* 103-111.

Moran, A., Bramham, J., Collet, C., Guillot, A., & MacIntyre, T. E. (2015). Motor imagery in clinical disorders: importance and implications. *Frontiers in Psychiatry, 6,* 23.

Morash, V., Bai, O., Furlani, S., Lin, P., & Hallett, M. (2008). Classifying EEG Signals Preceding Right Hand, Left Hand, Tongue, and Right Foot Movements and Motor Imageries. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology, 119*(11), 2570–2578.

Mulder, T. (2007). Motor imagery and action observation: cognitive tools for rehabilitation. *Journal of Neural Transmission, 114*(10), 1265–1278.

Nakamura, K., Sakai, K., & Hikosaka, O. (1998). Neuronal Activity in Medial Frontal Cortex During Learning of Sequential Procedures. *Journal of Neurophysiology, 80*(5), 2671-2687.

Neuper, C., Scherer, R., Reiner, M., & Pfurtscheller, G. (2005). Imagery of motor actions: Differential effects of kinesthetic and visual-motor mode of imagery in single-trial EEG. *Cognitive Brain Research, 25*(3), 668-677.

Nitsche, M. A., & Paulus, W. (2000). Excitability changes induced in the human motor cortex by weak transcranial direct current stimulation. *The Journal of Physiology, 527*(Pt 3), 633–639.

Oberman, L. M., Pineda, J. A., & Ramachandran, V. S. (2007). The human mirror neuron system: A link between action observation and social skills. *Social Cognitive and Affective Neuroscience, 2*(1), 62–66.

Papadelis, C., Kourtidou-Papadeli, C., Bamidis, P., & Albani, M. (2007). Effects of imagery training on cognitive performance and use of physiological measures as an assessment tool of mental effort. *Brain and Cognition, 64*(1), 74-85.

Parsons, L. M. (1987). Imagined spatial transformation of one's body. *Journal of Experimental Psychology: General, 116*(2), 172-191.

Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of Experimental Psychology: Human Perception and Performance, 20*(4), 709-730.

Parsons, L. M., Fox, P. T., Hunter Downs, J., Glass, T., Hirsch, T. B., Martin, C. C., . . . Lancaster, J. L. (1995). Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature, 375*, 54-58.

Pascual-Leone, A., Nguyet, D., Cohen, L. G., Brasil-Neto, J. P., Cammarota, A., & Hallett, M. (1995). Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *Journal of Neurophysiology, 74*(3), 1037-1045.

Passingham, R. E., Toni, I., & Rushworth, M. F. (2000). Specialization within the prefrontal cortex: The ventral prefrontal cortex and associative learning. *Experimental Brain Research, 133*(1), 103-113.

Payne, V. G., & Isaacs, D. L. (1987). *Human Motor Development: A Lifespan Approach.* Mountain View California: Mayfield Publishing Company.

Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Beraldi, P., Zuiani, C., . . . di Prampero, P. E. (1996). Primary Motor and Sensory Cortex Activation during Motor Performance and Motor Imagery: A Functional Magnetic Resonance Imaging Study. *Journal of Neuroscience, 16*(23), 7688-7698.

Quartarone, A., Morgante, F., Bagnato, S., Rizzo, V., Sant`angelo, A., Aiello, E., . . . Girlanda, P. (2004). Long lasting effects of transcranial direct current stimulation on motor imagery. *NeuroReport, 15*(8), 1287-1291.

Richter, W., Andersen, P. M., Georgopoulos, A. P., & Kim, S.-G. (1991). Sequential Activity in Human Motor Areas During a Delayed Cued Finger Movement Task Studied by Time-resolved FMRI. *NeuroReport, 8*, 1257–1261.

Roland, P. E., Larsen, B., Lassen, N. A., & Skinhoj, E. (1980). Supplementary motor area and other cortical areas in organization of voluntary movements in man. *Journal of Neurophysiology, 43*(1), 118-136.

Rosenbaum, D. (1980). Human movement initiation: Specification of arm, direction, and extent. *Journal of Experimental Psychology: General, 109*(4), 444-474.

Ruitenberg, M. F., De Kleine, E., Van der Lubbe, R. H., Verwey, W. B., & Abrahamse, E. L. (2011). Context-dependent motor skill and the role of practice. *Psychological Research, 76*(6), 812-820.

Sanders, C. W., Sadoski, M., Bramson, R., Wiprud, R., & Van Walsum, K. (2004). Comparing the effects of physical practice and mental imagery rehearsal on learning basic surgical skills by medical students. *American Journal of Obsterics and Gynecology, 191*(5), 1811-1814.

Schmidt, R. A. (1975). A Schema Theory of Discrete Motor Skill Learning. *Psychological Review, 82*(4), 225-260.

Schuster, C., Butler, J., Andrews, B., Kischka, U., & Ettlin, T. (2012). Comparison of embedded and added motor imagery training in patients after stroke: results of a randomised controlled pilot trial. *Trials, 13,* 11.

Schuster, C., Hilfiker, R., Amft, O., Scheidhauer, A., Andrews, B., Butler, J., … Ettlin, T. (2011). Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. *BMC Medicine, 9,* 75.

Shea, C. H., Kovacs, A. J., & Panzer, S. (2011). The Coding and Inter-Manual Transfer of Movement Sequences. *Frontiers in Psychology, 2,* 52.

Slotnick, S. D. (2004). Source localization of ERP generators. In T. C. Handy, *Event-Related Potentials: A Methods Handbook* (pp. 149-166). Cambridge: The MIT Press.

Sobierajewicz, J., Przekoracka-Krawczyk, Jaśkowski, W., Verwey, W. B., & van der Lubbe, R. (2017). The influence of motor imagery on the learning of a sequential motor skill. *Experimental Brain Research, 235*(1), 305-320.

Sobierajewicz, J., Szarkiewicz, S., Przekoracka-Krawczyk, A., Jaśkowski, W., & van der Lubbe, R. (2016). To what extent can motor imagery replace motor execution while learning a fine sequential motor skill? *Advances in Cognitive Psychology, 12*(4), 179-192.

Solodkin, A., Hlustik, P., Chen, E. E., & Small, S. L. (2004). Fine modulation in network Activation during motor execution and motor imagery. *Cerebral Cortex, 14*(11), 1246-1255.

Stecklow, M. V., Infantosi, A. F., & Cagy, M. (2010). EEG changes during sequences of visual and kinesthetic motor imagery. *Arquivos de Neuro-Psiquiatria, 68*(4), 556-561.

Stephan, K., & Franckowiak, R. (1996). Motor imagery - anatomical representation and electrophysiological characteristics. *Neurochemical Research, 21*(9), 1105-1116.

Stevens, J. (2005). Interference effects demonstrate distinct roles for visual and motor imagery during the mental representation of human action. *Cognition, 95*(3), 329-350.

Tangwiriyasakul, C., Mocioiu, V., van Putten, M. J., & Rutten, W. L. (2014). Classification of motor imagery performance in acute stroke. *Journal of Neural Engineering, 11*(3):036001.

Tanji, J. (2001). Sequential organization of multiple movements: Involvement of Cortical Motor Areas. *Annual Review of Neuroscience, 24*, 631-651.

Taube, W., Mouthon, M., Leukel, C., Hoogewoud, H.-M., Annoni, J.-M., & Keller, M. (2015). Brain activity during observation and motor imagery of different balance tasks: An fMRI study. *Cortex, 64*, 102-114.

Teplan, M. (2002). Fundamentals of EEG measurement. *Measurement Science Review, 2*, 1-11.

Thomson, T., Steffert, T., Ros, T., Leach, J., & Gruzelier, J. (2008). EEG applications for sport and performance. *Methods*, *45*(4), 279-288.

Tulving, E. (1972). Episodic and semantic memory. In E. Tulving, & W. Donaldson, *Organization of memory* (pp. 381-403). New York: Academic Press.

Van der Lubbe, R. H., Sobierajewicz, J., Jongsma, M. J., & Przekoracka-Krawczyk, A. (2017). To what extent does motor imagery resemble motor preparation? *Psychophysiology, 54.* 57th Annual Meeting of the Society for Psychophysiological Research 2017 - The Hofburg, Vienna, Austria.

Verwey, W. B. (2003). Effect of sequence length on the execution of familiar keying sequences: lasting segmentation and preparation? *Journal of Motor Behavior, 35*(4), 343-354.

Verwey, W. B., & Wright, D. L. (2004). Effector-independent and effector-dependent learning in the discrete sequence production task. *Psychological Research, 68*(1), 64-70.

Verwey, W. B., & Wright, D. L. (2014). Learning a keying sequence you never executed: Evidence for independent associative and motor chunk learning. *Acta Psychologica*, *151*, 24-31.

Verwey, W. B., Abrahamse, E. L., Ruitenberg, M. F., Jiménez, L., & de Kleine, E. (2011). Motor skill learning in the middle-aged: limited development of motor chunks and explicit sequence knowledge. *Psychological Research, 75*(5), 406-422.

Verwey, W. B., Groen, E. C., & Wright, D. L. (2016). The stuff that motor chunks are made of: Spatial instead of motor representations? *Experimental Brain Research, 234*(2), 353–366.

Vogt, S., Di Rienzo, F., Collet, C., Collins, A., & Guillot, A. (2013). Multiple roles of motor imagery during action observation. *Frontiers in Human Neuroscience, 7,* 807.

Warner, L., & McNeill, M. E. (2013). Mental imagery and its potential for physical therapy. *Physical Therapy, 68*(4), 516-521.

Wascher, E., & Wauschkuhn, B. (1996). The interaction of stimulus- and response-related processes measured by event-related lateralizations of the EEG. *Electroencephalography and Clinical Neurophysiology, 99*(2), 149-162.

Wriessnegger, S. C., Steyrl, D., Koschutnig, K., & Müller-Putz, G. R. (2014). Short time sports exercise boosts motor imagery patterns: implications of mental practice in rehabilitation programs. *Frontiers in Human Neuroscience, 8,* 469.

Wulf, G., Shea, C., & Lewthwaite, R. (2010). Motor skill learning and performance: a review of influential factors. *Medical Education, 44*(1), 75-84.

Xu, L., Zhang, H., Hui, M., Long, Z., Jin, Z., Liu, Y., & Yao, L. (2014). Motor execution and motor imagery: a comparison of functional connectivity patterns based on graph theory. *Neuroscience, 261,* 184-194.

Zang, Y., Jia, F., Weng, X., Enzhong, L., Cui, S., Wang, Y., . . . Ivry, R. (2003). Functional organization of the primary motor cortex characterized by event-related fMRI during movement preparation and execution. *Neuroscience Letters, 337*(2), 69-72.

Zapparoli, L., Invernizzi, P., Gandola, M., Berlingeri, M., De Santis, A., Zerbi, A., . . . Paulesu, E. (2014). Like the back of the (right) hand? A new fMRI look on the hand laterality task. *Experimental Brain Research, 232*(12), 3873-3897.

Zhang, H., Xu, L., Wang, S., Xie, B., Guo, J., Long, Z., & Yao, L. (2011). Behavioral improvements and brain functional alterations by motor imagery training. *Brain Research, 1407,* 38-46.

2. HOW EFFECTOR-SPECIFIC IS THE EFFECT OF LEARNING BY MOTOR EXECUTION AND MOTOR IMAGERY?[2]

Abstract

The aim of the present study was twofold. First, we wanted to examine how effector-specific the effect of sequence learning by motor execution is, and secondly, we wanted to compare this effect with learning by motor imagery. We employed a Go/NoGo discrete sequence production (DSP) task in which on each trial a spatial sequence of five stimuli was presented. After a Go signal the corresponding spatial response sequence had to be executed, while after a NoGo signal, the response sequence had to be mentally imagined. For the training phase, participants were divided into two groups. In the index finger group, participants had to respond (physically or mentally) with the left or right index finger, while in the hand group they had to respond with four fingers of the left or right hand. In a final test phase both execution modes were compared and all trials had to be executed. Response times and the percentage of correct responses were determined to establish learning effects. Results showed that sequence learning effects as assessed in the test phase were independent of the effector used during the training phase. Results revealed the presence of a-specific learning effects in the case of learning a required motor task with an index finger, but sequence-specific learning effects, both due to motor execution and to motor imagery, were not effector-specific.

Key words: motor imagery, motor execution, learning, execution mode, DSP task,

---

[2] Sobierajewicz, J., Przekoracka-Krawczyk, A., Jaśkowski, W., & van der Lubbe, R. (2017). How effector-specific is the effect of sequence learning by motor execution and motor imagery? *Experimental Brain Research, 235*(12), 3757-3769. doi: 10 1007/s00221-017-5096-z

2.1. Introduction

Fine motor skills involved in for example, writing, drawing, or playing a musical instrument demand the production of relatively small movements, which are learned with a particular effector system (e.g., using the fingers, hands, feet etc.), (Payne & Isaacs, 1987; Keele, Jennings, Jones, Caulton, & Cohen, 1995). It has been argued that motor sequences can be acquired either in an effector-dependent manner (learning effects are limited to the trained effector system) or in an effector-independent manner (learning effects can be generalized to other effector systems), (Keele et al., 1995; Kovacs, Muehlbauer, & and Shea, 2009; Shea, Kovacs, & Panzer, 2011). In the present study, we investigated how effector-specific the effect of learning a sequential fine motor skill is. We examined sequence learning effects of motor execution and compared them with sequence learning effects of motor imagery.

Different views have been forwarded with respect to effector-dependency of learned motor skills. For example, previous research showed that learning is effector-dependent, which implies that training of one group of muscles does not generalize to another group of muscles (Bapi, Doya, & Harner, 2000; Verwey & Wright, 2004; Osman, Bird, & Heyes, 2005; Verwey & Clegg, 2005). However, it has also been argued that motor skill learning is initially effector-independent and may become effector-dependent with extensive practice (Hikosaka, et al., 1999). Results of Keele et. al (1995) indeed suggest that motor skill learning can be effector-independent. Participants in a learning phase were asked to train a motor sequence with either three fingers (index-, middle-, and ring-finger) or only with an index finger. In a transfer phase, participants were asked to switch; half of the participants continued to use the same effector system as in the learning phase, while the other half changed to the untrained motor system. Results revealed a comparable reduction in response time for all keys in both groups which supports the idea that motor skill learning is rather effector-independent. Relevant to notice is that effects concerned all keys of the motor sequence. The first key of a motor sequence is generally thought to reflect the time to initiate the sequence, while the subsequent keys are more specific to execution (Abrahamse, Ruitenberg, de Kleine, & Verwey, 2013). Thus, learning effects transferred both with regard to initiation and execution of the relevant sequence.

Verwey and Wright (2004) examined sequence learning with one group of participants that trained with three fingers of one hand, and another group that trained with three fingers of two hands. In the subsequent test phase, participants of both groups executed familiar and unfamiliar sequences in the same manner as during practice and also with the hand configuration of the other group. Results for familiar sequences revealed slower execution for the unpracticed as compared with the practiced hand configuration, suggesting effector-specific learning. However, execution of familiar sequences with the unpracticed hand was still faster than execution of new (unfamiliar) sequences. These findings suggest that the learned sequence representation consist of both effector-independent and effector-dependent components.

The notion that motor skill learning transfers from an effector-independent stage to an effector-dependent stage may be due to the involvement of representations at two different levels. Initially, representations may develop at a cognitive level that for example contain spatio-temporal characteristics of the movement, while later representations develop at a motor level that are muscle-specific and concern more detailed characteristics of the movement (e.g., see (Verwey, Groen, & Wright, 2016)). This cognitive level seems related with the idea of a motor program (i.e., an abstract representation of a movement that organizes the performance of motor actions including their spatio-temporal aspects), (Schmidt, 1975). It has been proposed that the two types of representations (i.e., cognitive and motor) develop separately (Shea, Kovacs, & Panzer, 2011). Furthermore, these two representational levels have been related with different neural mechanisms (see Hikosaka, et al., 1999; Hikosaka, Nakamura, Sakai, & Nakahara, 2002), which will be further detailed in the discussion. The results obtained by Keele et. al (1995) may thus be understood as due to the development of representations at a cognitive level that can be easily transferred to an unpracticed effector system. On the other hand, the results from the study of Verwey and Wright (2004) support also the development of representations at a motor level but this requires more extensive practice.

In our earlier research, we were especially interested in the learning of a fine sequential motor skill by motor imagery (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017), which can be defined as the mental simulation of a movement without producing an overt action (Jeannerod, 2001). A question that emerged from our studies was whether learning by motor imagery involves a cognitive and/or a motor level. It is well known that motor skills can be acquired not only by repeating (i.e., physical practice) a particular movement, but also by motor imagery (Jackson, Lafleur, Malouin, & Richards, 2001; Allami, Paulignan, Brovelli, & Boussaoud, 2008; Doussoulin & Rehbein, 2011). It has additionally been argued that motor imagery relies on similar processes and obeys the same rules as motor execution (e.g., with regard to the timing and brain mechanisms underlying motor imagery and motor execution (Decety, Jeannerod, & Prablanc, 1989; Xu, et al., 2014; Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). However, the effect of motor imagery on sequence learning is not as strong as the effect of physical practice (Feltz & Landers, 1983; Hird, Landers, Thomas, & Horan, 1991; Gentili, Papaxanthis, & Pozzo, 2006; Gentili, Han, Schweighofer, & Papaxanthis, 2010; Schuster, et al., 2011; Debarnot, Abichou, Kalenzaga, Sperduti, & Piolino, 2015; Gentili & Papaxanthis, 2015; Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016), indicating that motor execution is more effective in acquisition of a motor skill. Although previous findings indicate that motor imagery improves the accuracy and may enhance the speed of a movement (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016), the relevance of the execution mode while learning a fine motor skill (i.e., small finger or hand movements like writing, tapping or drawing) with motor imagery was not yet examined.

A first issue to be addressed in the present study is whether the observations made by Keele et al. (1995), which pointed to the involvement of representations at a cognitive level, can be replicated in a slightly different paradigm that we used to examine the learning of a sequential motor skill by motor imagery. We employed a Go/NoGo DSP task wherein on each trial a spatial sequence of five stimuli was presented, which had to be next either executed or mentally simulated. A second issue to be addressed is whether the evidence for the involvement of representations at a cognitive level also applies to the learning of a motor skill with motor imagery. Two execution (and motor imagery) modes were employed. One group had to practice movement sequences physically (or mentally) by using the index fingers, while a second group had to practice by using four fingers of the left or right hand. Based on the ideas presented in the introduction, the following predictions can be made. If representations develop at a cognitive level then transfer from the practiced effector system to the unpracticed effector system is possible, thus, in that case sequence learning, either by execution or by motor imagery, is effector-independent. If representations develop at a motor level, then no transfer is possible. The possible transfer can be examined in a final test phase in which familiar executed, familiar imagined, and unfamiliar movement sequences have to be carried out, either in the same mode as during practice, or in a different mode.

2.2. Methods

2.2.1. Participants

Twenty-four participants (eight males, sixteen females) recruited from the Adam Mickiewicz University took part in our experiment. All participants were aged between 20 and 28 years (M_{age} = 23.6, SD 2.34). The inclusion criteria for participation were absence of any mental or neurological disorder. Informed consent was obtained from each participant prior to the start of the experiment. Participants were requested to complete Annett`s Handedness Inventory (Annett, 1970). Twenty-free of them were right-handed, and one of them was left-handed. All participants were naïve as to the purpose of the experiment. The study was approved by the local Ethics Committee of the Adam Mickiewicz University and was performed in accordance with the Declaration of Helsinki.

2.2.2. Stimuli and task

A trial consisted of the presentation of a sequence of five visual stimuli. An example of a stimulus sequence is presented in Figure 1. Stimuli were displayed on a CRT monitor with a refresh rate of 60 Hz. Each trial started with a beep of 300 Hz for 300 ms. A fixation cross (1.3°) was presented in the center of the screen with eight horizontally aligned squares (2.5°) – four on the left and four on the right side of the fixation cross. Each square was assigned to a button on the keyboard (*a, s, d, f* keys, and the *;, l, k, j* keys). The eight stimulus squares had a total visual angle of 26.5°. The fixation cross and the eight squares were drawn with a gray color line on a black background. After a time interval of 1000 ms one of the squares was filled yellow for 750 ms, a second square was filled, etc., until a fifth square was filled. The stimulus sequence always appeared on either the right or the left side of fixation. An informative cue (a cross) appeared after a preparation interval of 1500 ms relative to the offset of the last square. The cue was presented in one out of two possible colors. A green cross indicated that the cued response sequence had to be executed (a Go signal). A blue cross implied that the response sequence had to be mentally imagined (a NoGo signal). Participants should imagine executing the five spatially corresponding key presses in the same order as the stimulus sequence. They were also asked to execute or imagine executing the required sequence as fast and accurately as possible. All participants were requested to concentrate on the fixation cross during the presentation of the sequence and while carrying out the task.

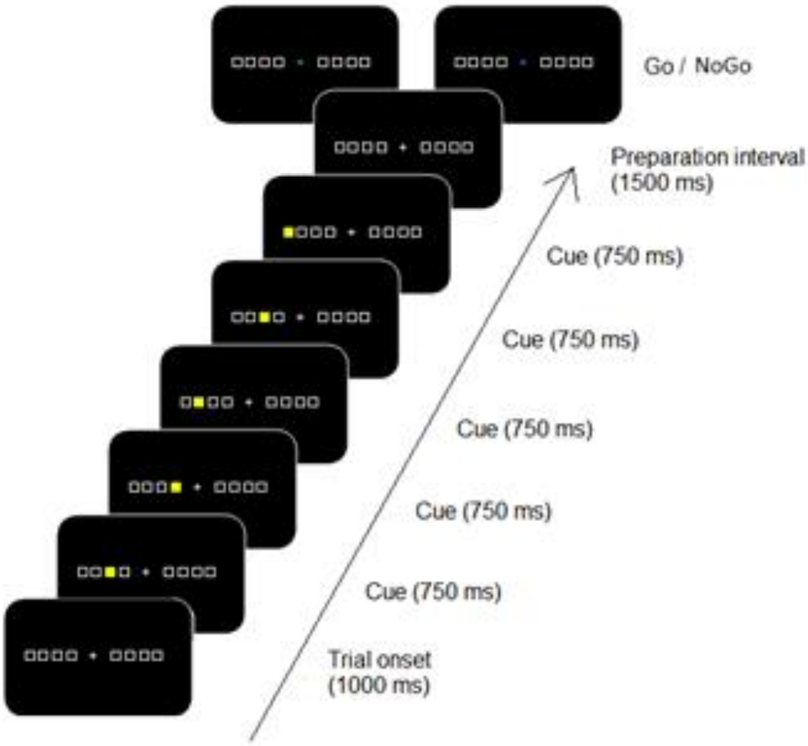

Figure 1. An overview of stimulus presentation in the Go/NoGo discrete sequence production (DSP) task. Two possible informative cues were presented: a green cross implied that the sequence had to be executed (Go signal) while a blue cross indicated that execution of the sequence had to be mentally imagined (NoGo signal).

2.2.3. Procedure

At the start of the experiment each participant received verbal instructions. Participants sat in a dimly lit room at a viewing distance of 70 cm from a screen. The experiment was conducted on two consecutive days (2 hours per day) to increase the number of trials. The measurement only in one day would last too long for participants and the effect could be distracted due to tiredness. On the first day, participants performed five training blocks. On the second day, two additional training blocks had to be carried out (40 sequences had to be executed and 40 sequences had to be imagined in each block, with the same number of repetitions for the right and for the left hand), and after a break two final test blocks had to be executed (40 sequences executed before; 40 sequences imagined before; 40 totally new sequences). To eliminate finger-specific effects for the hand condition and to ensure that all sequences had the same level of complexity, we employed different sequences, which are shown in the Appendix. We used six different structures (12432, 13423, 14213, 13241, 14312, and 21431) with four different versions of sequences per structure. We counterbalanced the sequences across participants and across fingers.

Participants were assigned to an index finger group (n=12) or to a hand group (n=12). In the index finger group, sequences had to be carried out in the training phase either physically or mentally by using the index finger of their left and right hand. In the hand group, participants had to execute or imagine sequences using four fingers (little finger, ring finger, middle finger and index finger) of their left and right hand. In the case of mental execution, all participants were instructed to use a first person perspective (i.e., to imagine the sensation of executing a sequence), i.e., they had to use kinesthetic motor imagery. To ensure that all participants understood the required task and the difference between visual vs. motor imagery, participants were given two examples (“imagine yourself walking on the street – you can see yourself walking”/ “imagine as if you are walking – you imagine your movements during walking”, respectively). In the test phase, six participants from the index finger group executed sequences in the first block using four fingers of the left or right hand, and in the second block they only used the index fingers; the other six participants received these blocks in a reversed order (see: Table 1). Similarly in the hand group, six participants executed the sequences in the first test block using four fingers of the left or right hand, and in the second block they only used the index fingers; the other six participants had these blocks in a reversed order. In the case of executing sequences with four fingers, all participants placed their little finger, ring finger, middle finger and index finger of their left and right hand respectively on the *a, s, d, f* keys, and the *;, l, k, j* keys.

Table 1. An overview of the execution mode for the index finger group and for the hand group in the training phase and the test phase. Four fingers implies executing the sequence with the little finger, ring finger, middle finger and index finger.

	The training phase	The test phase	
Group	Block 1-7	Block1	Block 2
Index finger group (n=12)	Index finger (n=12)	Index finger (n=6) Four fingers (n=6)	Four fingers (n=6) Index finger (n=6)
Hand group (n=12)	Four fingers (n=12)	Index finger (n=6) Four fingers (n=6)	Four fingers (n=6) Index finger (n=6)

Halfway each block and after each block a pause was provided during which the participant could relax. After completion of each block, participants were shown their mean reaction times and error percentages. Moreover, feedback about incorrect responses was given after the end of response only when a participant pressed the button before a Go/NoGo signal or in the case of a false response sequence.

Electroencephalographic (EEG) activity was also measured in this study, but we decided not to focus on these results (i.e., comparing EEG activity between groups during motor preparation in the training phase) as they seem beyond the scope of the current manuscript.

2.2.4. Behavioral parameters

Response time (RT) was defined as the time between onset of the Go signal and depression of the first key, and as the time between two consecutive key presses within a sequence (De Kleine & Van der Lubbe, 2011; Ruitenberg, De Kleine, Van der Lubbe, Verwey, & Abrahamse, 2011). To reduce the number of levels of the Key variable, we averaged RTs of keys 2 to 5, which results in two levels, one including the first key press, and the second including the averages of keys 2 to 5 (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016). In the training phase, mean RTs were statistically evaluated by a repeated measures analysis of variance (ANOVA) with Block (7), and Key (2) as within-subjects factors, and Group (2) as between-subjects factor. ANOVAs in the test phase were performed with Type of Sequence (3: familiar executed, familiar imagined, unfamiliar), and Key (2) as within-subjects factor, and Group (2) and Execution Mode (2) as between-subjects factors. This was done separately for the first and the second block as sequence-specific learning effects might no longer be detectable in the second test block due to learning the new sequences.

Analyses on PCs were carried out after performing an arcsine transformation to stabilize variances (Abrahamse & Verwey, 2008). A repeated measures ANOVA was run for the training phase with Group (2) as between-subjects factor, and Block (7) as within-subjects factor; and in the test phase for each block separately with Group (2), Execution Mode (2) as between-subjects factors, and Type of Sequence (3) as within-subjects factor.

2.2.5. EMG

Electromyographic activity (EMG) was measured to establish whether participants correctly executed the required task, i.e., in the case of the motor execution they should flex their muscles, while in the case of motor imagery they should not. EMG was measured bipolarly by attaching EMG electrodes on the musculus flexor digitorum superficalis and on the processus styloideus ulnae of the right and left hand. EMG from both hands was recorded with Vision Recorder (Brain Products – version 2.0.3) with a sampling rate of 1000 Hz. Offline, analyses were performed with Brain Vision Analyzer (version 2.0.4) software. The signal was low-pass filtered at 50 Hz (24 dB/oct) and high-pass filtered at 20 Hz (24 dB/oct). The threshold for a movement was set at 60-160 μV depending on the resting level of the individual participant Wavelet analyses were performed to determine the extent of motor activation of a required motor task. A complex Morlet wavelet was chosen (c=5) with the lower and upper boundaries for the extracted layer set at 20 and 50 Hz.

After logarithmic transformation, the results of the wavelet analysis were analyzed with the following factors: Group (2), Block (7), EMG-channel (right relevant hand, left relevant hand, 2), and Type of Sequence (2 – motor imagery/motor execution). We choose a time window from a Go/NoGo signal until 6000 ms, as this time window seems sufficient to execute or imagine the required type of sequence.

All statistical analyses were performed with SPSS (IBM Statistics SPSS 24). The level of significance was set at $p < 0.05$. Greenhouse–Geisser ε correction was applied whenever appropriate. We examined linear, quadratic and cubic contrasts in order to increase sensitivity for detecting gradual differences as a function of Block.

2.3. Results

2.3.1. The training phase

RT results for the training phase are presented in Figure 2. Results revealed faster RTs for the hand group than for the index finger group, $F(1,22) = 16.16$, $p = 0.001$, $\eta_p^2 = 0.42$. RTs changed as a function of Block, $F(6,132) = 30.98$, $\epsilon = 0.38$, $p < 0.001$, $\eta_p^2 = 0.59$. Contrast analyses revealed a linear trend, $F(1,22) = 75.28$, $p < 0.001$, and a quadratic trend, $F(1,22) = 8.12$, $p < 0.001$, suggesting that these effects reflect a general decrease in RT during practice, while this decrease seems to be stronger in the earliest blocks. A nearly significant interaction between Block and Group was observed, $p = 0.06$, indicating that RTs for the index finger group tended to decrease more across blocks than RTs for the hand group.

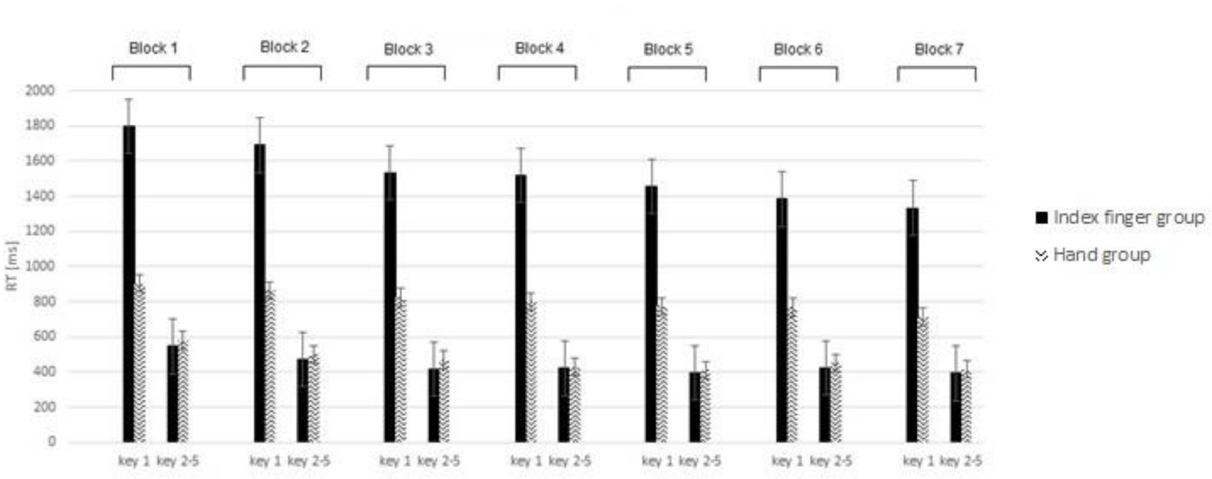

Figure 2. Mean response times (RTs) in milliseconds (ms) in the training phase as a function of Key. Error bars represent standard errors.

A main effect of Key was observed, $F(1,22) = 112.1$, $p < 0.001$, $\eta_p^2 = 0.84$, (mean RT for key 1 and the average of keys 2 to 5 in the index finger group, respectively 1531, 439 ms; in the hand group: 807, 466 ms, respectively). An interaction between Key and Group was observed, $F(1,22) = 30.78$, $p < 0.001$, $\eta_p^2 = 0.58$. Inspection of Figure 2 clearly shows that the first key press in the index group was executed slower than the first key press in the hand group. Separate *t*-tests confirmed this effect, $t(11) = 4.19$, $p = 0.002$. This observation may indicate that the time needed to initiate a sequence was longer for the index finger group than for the hand group. The average RTs of keys 2 to 5 was similar in both groups, $t(11) = 0.58$, $p = 0.57$. An interaction between Block and Key was observed, $F(6,132) = 4.79$, $\epsilon = 0.39$, $p = 0.009$, $\eta_p^2 = 0.18$. Separate tests revealed that RTs for the first key press changed as a function of Block, $F(6,132) = 15.46$, $\epsilon = 0.37$, $p < 0.001$, $\eta_p^2 = 0.41$. A significant interaction between Block and Group was observed, $p < 0.05$, indicating that RTs for the first key press for the index finger group decreased more across blocks than RTs for the hand group. RTs for the average of keys 2-5 also changed as a function of Block, $F(6,132) = 39.87$, $\epsilon = 0.5$, $p < 0.001$, $\eta_p^2 = 0.64$. No significant interaction between Block and Group was observed, $p = 0.51$, showing similar decrease of RTs in the case of both groups. We also observed an interaction between Block, Key and Group, $F(6,132) = 3.04$, $p = 0.05$, $\eta_p^2 = 0.12$, showing a stronger decrease of mean RT for the first key press for the index finger group as compared with the hand group with practice.

A repeated measures ANOVA was also performed on arcsin transformed error percentages as a function of Group (2) and Block (7). Results revealed no significant differences in accuracy between groups, $F(1,22) = 0.39$, $p = 0.54$, $\eta_p^2 = 0.02$. A main effect of Block was observed, $F(6,132) = 26.9$, $\epsilon = 0.57$, $p < 0.001$, $\eta_p^2 = 0.55$ (linear trend: $F(1,22) = 56.49$, $p < 0.001$; quadratic trend: $F(1,22) = 27.91$, $p < 0.001$), (Figure 3). These results indicate that the number of correct responses increased with practice and this effect was most prominent in the earlier blocks. No significant interaction between Block and Group was observed, $p = 0.19$. Thus, these results showed that the number of correct responses increased with practice in both groups.

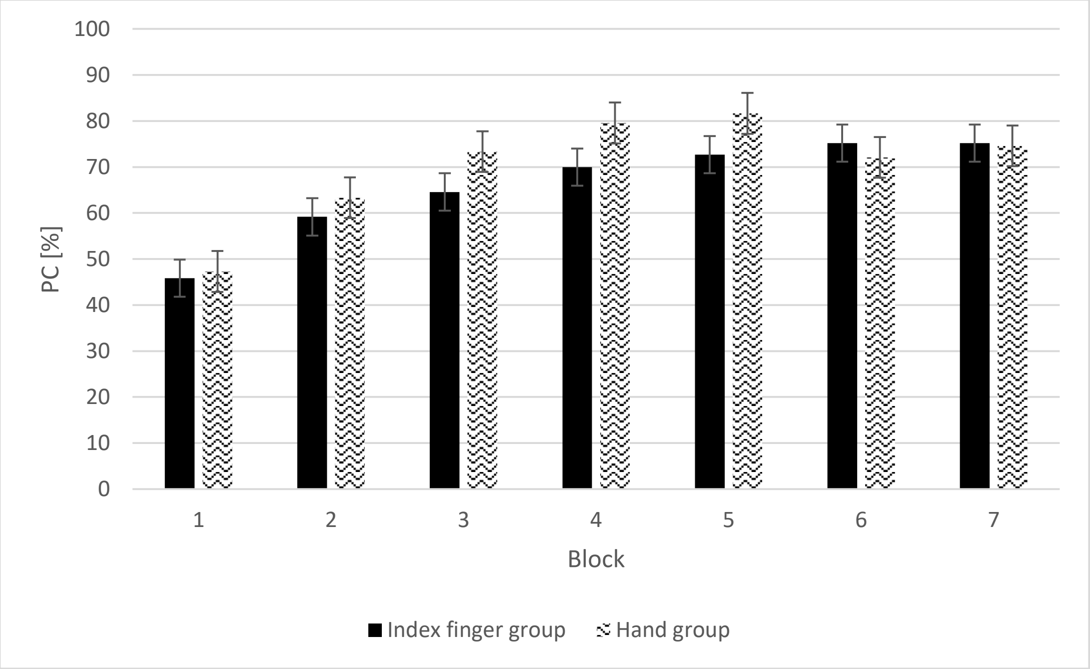

Figure 3. Percentage of correct response (PC) of the averages of to be executed sequences in the training phase for the index finger group (IG) and the hand group (HG). Error bars represent standard errors.

2.3.2. The test phase

For the test phase, analyses were performed for RTs for each block separately with the factors Group (2), Execution Mode (2, four fingers/index fingers), Type of Sequence (3), and Key (2). A repeated measures ANOVA was also performed on arcsin transformed error percentages as a function of Group (2), Execution Mode (2), and Type of Sequence (3) for each block of the test phase.

RT

The analysis for the first block revealed no significant difference in mean RT between groups, $F(1,20) = 0.91$, $p = 0.32$, $\eta_p^2 = 0.05$ (Figure 4). A significant difference was observed as a function of Execution Mode, $F(1,20) = 23.36$, $p < 0.001$, $\eta_p^2 = 0.54$, indicating that sequences were executed faster with four fingers than with the index finger (Figure 4). These results demonstrate that the use of different execution modes affect mean RTs, which we also observed in the training phase. No significant interaction between Group and Execution Mode was observed, $F(1,20) = 0.001$, $p = 0.98$, $\eta_p^2 < 0.001$. These results might indicate that motor execution in the test phase did not depend on the execution mode in the training phase (but see below). A main effect of Type of Sequence was observed, $F(2,40) = 4.2$, $\epsilon = 0.99$, $p = 0.02$, $\eta_p^2 = 0.17$. Separate *t*-tests revealed that unfamiliar sequences were executed slower than familiar executed sequences, $t(23) = 2.4$, $p < 0.03$, and also slower than familiar imagined sequences, $t(23) = 2.81$, $p = 0.01$. No difference in RT was observed between familiar executed and familiar imagined sequences, $p = 0.91$. These findings indicate that both motor execution and motor imagery in the training phase induced sequence-specific learning effects. No significant interaction between Type of Sequence and Group was observed, $F(2,40) = 1.36$, $p = 0.27$, $\eta_p^2 = 0.06$; and no significant interaction between Type of Sequence and Execution Mode was observed, $F(2,40) = 0.28$, $p = 0.76$, $\eta_p^2 = 0.01$. No significant interaction between Type of Sequence × Group × Execution Mode was observed, $F(2,40) = 0.07$, $p = 0.93$, $\eta_p^2 = 0.003$. The absence of interactions between Type of Sequence and the factor Group suggest that the observed sequence learning effects in the Test phase do not depend on the execution mode in the Training phase.

A main effect of Key was observed, $F(1,20) = 69.44$, $p < 0.001$, $\eta_p^2 = 0.78$, indicating that first key presses were slower than the average of key presses 2 to 5. No significant interaction between Key and Group was observed, $F(1,20) = 3.91$, $p = 0.06$, $\eta_p^2 = 0.16$, but a significant interaction was observed between Key and Execution Mode, $F(1,20) = 24.53$, $p < 0.001$, $\eta_p^2 = 0.55$. A significant interaction between Key × Group × Execution Mode was observed, $F(1,20) = 4.3$, $p = 0.05$, $\eta_p^2 = 0.18$. This observation suggests that motor execution in the test phase may depend on the execution mode in the training phase, either for the first key press, or for the average of key 2 to 5 (see below). Furthermore, a significant interaction between Type of Sequence and Key was observed, *F*(2,40) = 69.44, $p < 0.001$, $\eta_p^2 = 0.78$. No significant interaction between Type of Sequence × Key × Group was observed, *F*(2,40) = 1.13, $p = 0.33$, $\eta_p^2 = 0.05$; and no significant interaction between Type of Sequence × Key × Execution Mode was observed, *F*(2,40) = 1.19, $p = 0.31$, $\eta_p^2 = 0.05$. To clarify the aforementioned interactions, whether they concerned the first key or the average of keys 2-5, we performed separate analyses for each level of the factor Key with Type of Sequence (3), Group (2), and Execution Mode (2) as factors.

For the first key, a main effect of Type of Sequence was observed, *F*(2,40) = 3.54, $\epsilon = 0.93$, $p = 0.04$, $\eta_p^2 = 0.15$. Separate *t*-tests revealed that the first key press for familiar executed sequences was executed faster than the first key press for unfamiliar sequences, *t*(11) = 2.04, $p = 0.05$; the first key press for familiar imagined sequences was also executed faster than the first key press for unfamiliar sequences, *t*(11) = 2.83, $p = 0.009$. No group differences were observed for the first key, *F*(1,20) = 2.32, $p = 0.14$. A significant difference was observed as a function of Execution Mode, *F*(1,20) = 26.14, $p < 0.001$, indicating that the first key press was executed faster with four fingers than with the index finger (see above).

For the average of keys from 2 to 5, we observed a significant interaction between Group and Execution Mode, *F*(1,20) = 8.99, $p = 0.007$. Separate *t*-tests revealed no significant difference in pressing the keys with four fingers between the index finger group and the hand group, *t*(10) = 1.31, $p = 0.22$; in the case of executing a motor sequence only with the index fingers, participants in the index finger group pressed the keys from 2 to 5 faster relative to the hand group, *t*(10) = 3.0, $p = 0.01$. These results show a-specific learning effects of execution mode used in the training phase by participants from the index finger group.

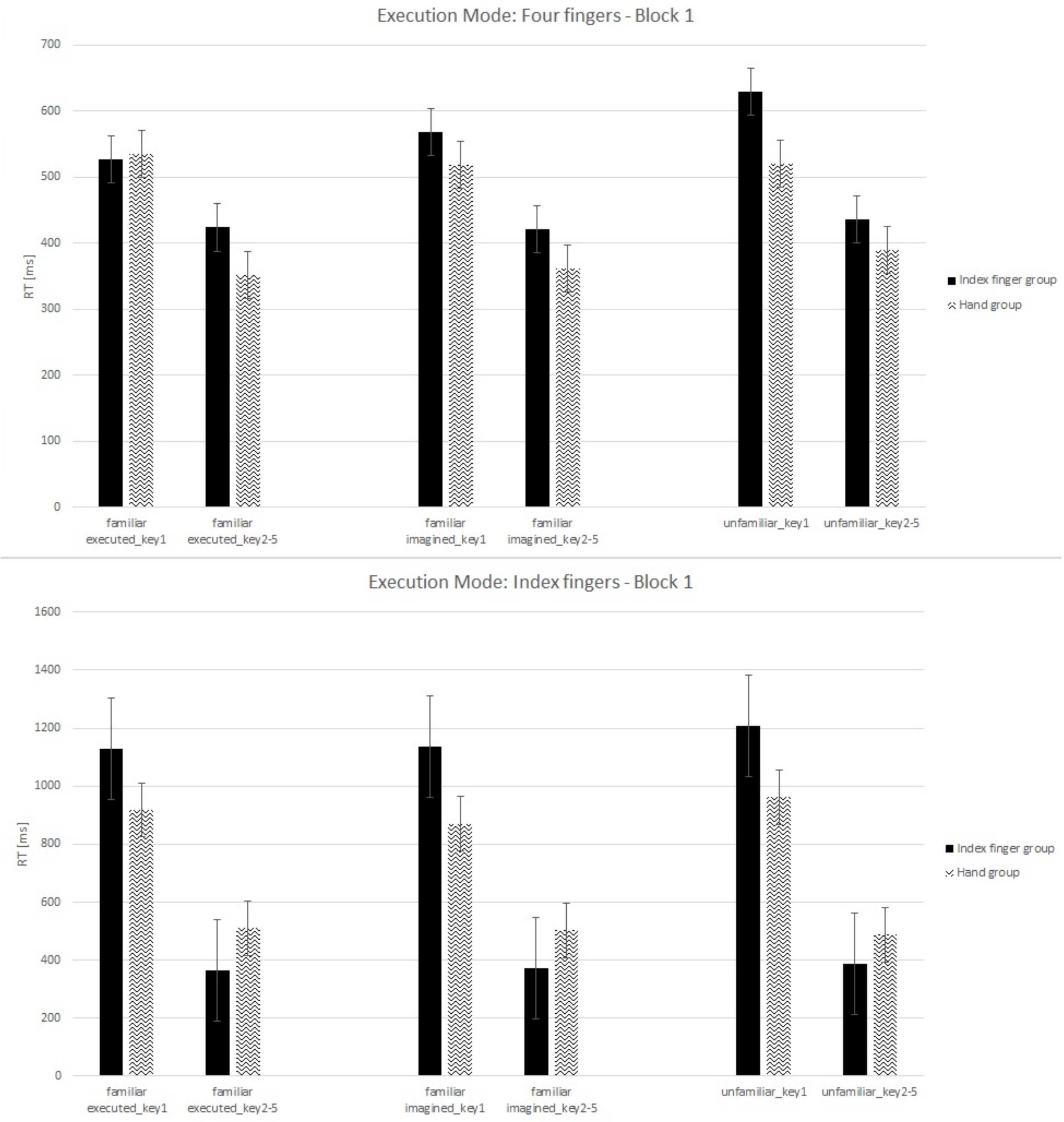

Figure 4. Response times (RTs) in milliseconds from the first block in the test phase for sequences, which were executed with four fingers and only with an index finger presented for each type of sequence. Different scales were used to emphasize the differences between groups. *Error bars* represent standard errors.

The RT analysis for the second block of the test phase revealed no effect of Group, $F(1,20) = 0.01$, $p = 0.92$, $\eta_p^2 = 0.001$. Furthermore, no significant interactions were observed between Group and Execution Mode, $F(1,20) = 0.006$, $p = 0.94$, $\eta_p^2 < 0.001$; between Type of Sequence and Group, $F(2,40) = 0.81$, $p = 0.43$, $\eta_p^2 = 0.04$; between Type of Sequence and Execution Mode, $F(2,40) = 0.64$, $p = 0.5$, $\eta_p^2 = 0.03$. No significant interaction between Type of Sequence × Group × Execution Mode was observed, $F(2,40) = 1.08$, $p = 0.34$, $\eta_p^2 = 0.05$. A main effect of Key was observed, $F(1,20) = 37.9$, $p < 0.001$, $\eta_p^2 = 0.66$, indicating that the first key press was slower than the average of key presses from 2 to 5. No significant interaction between Key and Group was observed, $F(1,20) = 0.2$, $p = 0.66$, $\eta_p^2 = 0.01$, but a significant interaction was observed between Key and Execution Mode, $F(1,20) = 5.31$, $p = 0.03$, $\eta_p^2 = 0.21$, which is detailed below. The interaction between Type of Sequence and Key was not significant, $F(2,40) = 1.29$, $p = 0.28$, $\eta_p^2 = 0.06$. No significant interactions were observed between Type of Sequence × Key × Group, $F(2,40) = 1.37$, $p = 0.26$, $\eta_p^2 = 0.06$; and between Type of Sequence × Key × Execution Mode, $F(2,40) = 1.25$, $p = 0.29$, $\eta_p^2 = 0.06$.

Separate analyses for each level of the factor Key revealed a significant difference of Execution Mode, $F(1,20) = 5.1$, $p < 0.04$, for the first key press, which showed again that the first key press was faster with four fingers than with the index finger. For the average of keys from 2 to 5, no significant differences were observed as a function of Group and Execution Mode, $p < 0.05$.

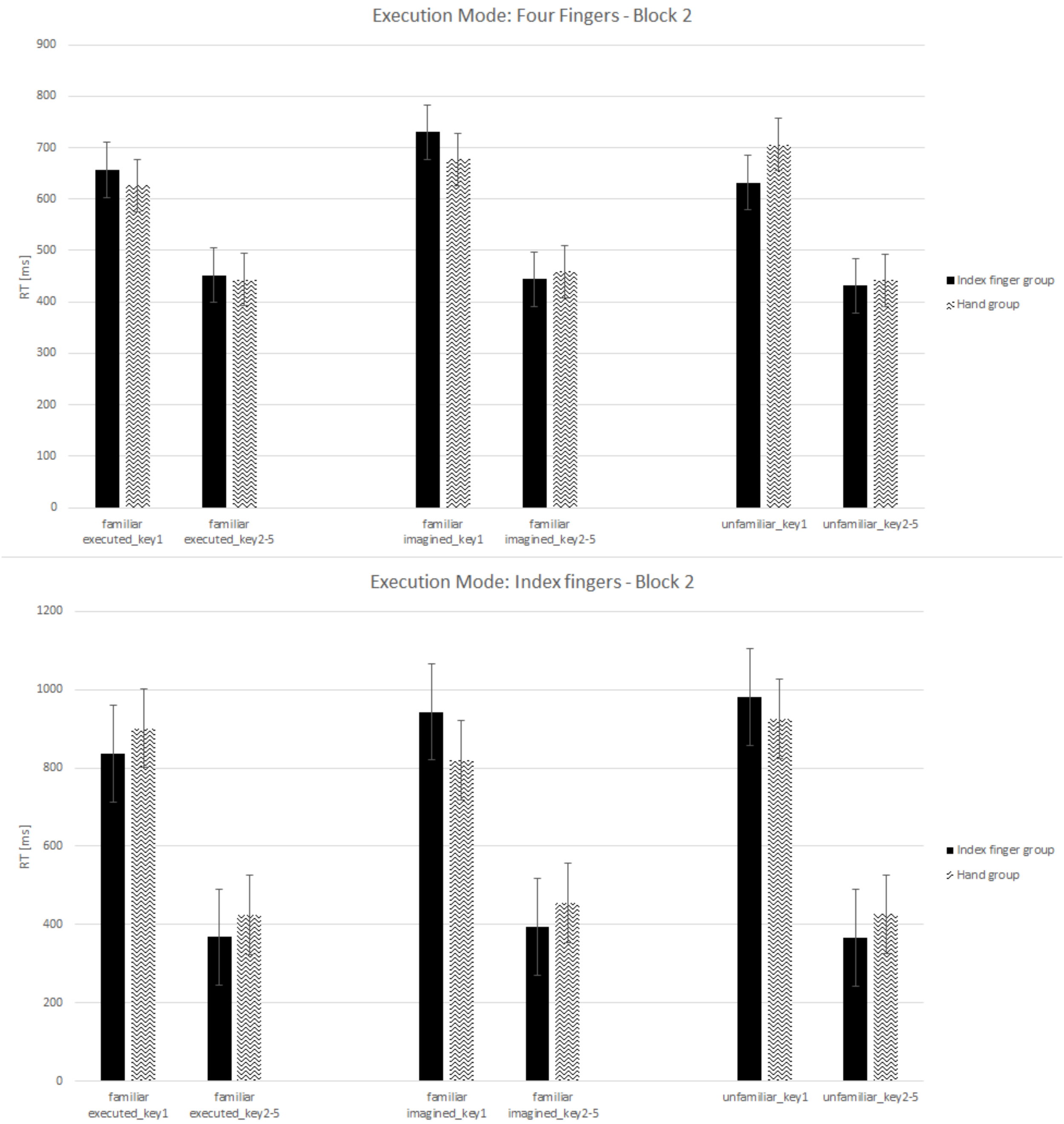

Figure 5. Response times (RTs) in milliseconds from the second block in the test phase for sequences, which were executed with four fingers and only with an index finger presented for each type of sequence. Different scales were used to emphasize the differences between groups. *Error bars* represent standard errors.

PC

A repeated measures ANOVA was performed on PC with the factors Group (2), Execution Mode (2), and Type of Sequence (3) for each block of the test phase. Results for the first block of the test phase revealed no significant difference in PC between groups, $F(1,20) = 0.09$, $p = 0.76$, $\eta_p^2 = 0.005$, and no significant difference as a function of Execution Mode, $F(1,20) = 2.6$, $p = 0.12$, $\eta_p^2 = 0.12$ (Figure 6). Furthermore, no significant interaction between Group and Execution Mode was observed, $F(1,20) = 0.32$, $p = 0.58$, $\eta_p^2 = 0.02$. These results indicate that accuracy of performance was not dependent on the execution mode in the training phase, which differed between the groups, not dependent on the execution mode in the test phase, and not dependent on whether the execution mode changed or initially stayed the same in test phase. A main effect of Type of Sequence was observed, $F(2,40) = 7.4$, $\epsilon = 0.97$, $p = 0.002$, $\eta_p^2 = 0.27$. Separate t-tests revealed that unfamiliar sequences were executed less accurately than familiar executed sequences, $t(23) = 3.69$, $p = 0.001$; and unfamiliar sequences were executed less accurately than familiar imagined sequences, $t(23) = 2.67$, $p = 0.01$; no difference between familiar executed and familiar imagined sequences was observed, $p = 0.34$. No significant interaction between Type of Sequence and Group was observed, $F(2,40) = 1.01$, $p = 0.37$, $\eta_p^2 = 0.05$; and no significant interaction between Type of Sequence and Execution Mode was observed, $F(2,40) = 1.11$, $p = 0.34$, $\eta_p^2 = 0.05$. The interaction between Type of Sequence × Group × Execution Mode was also not significant, $F(2,40) = 0.22$, $p = 0.8$, $\eta_p^2 = 0.01$.

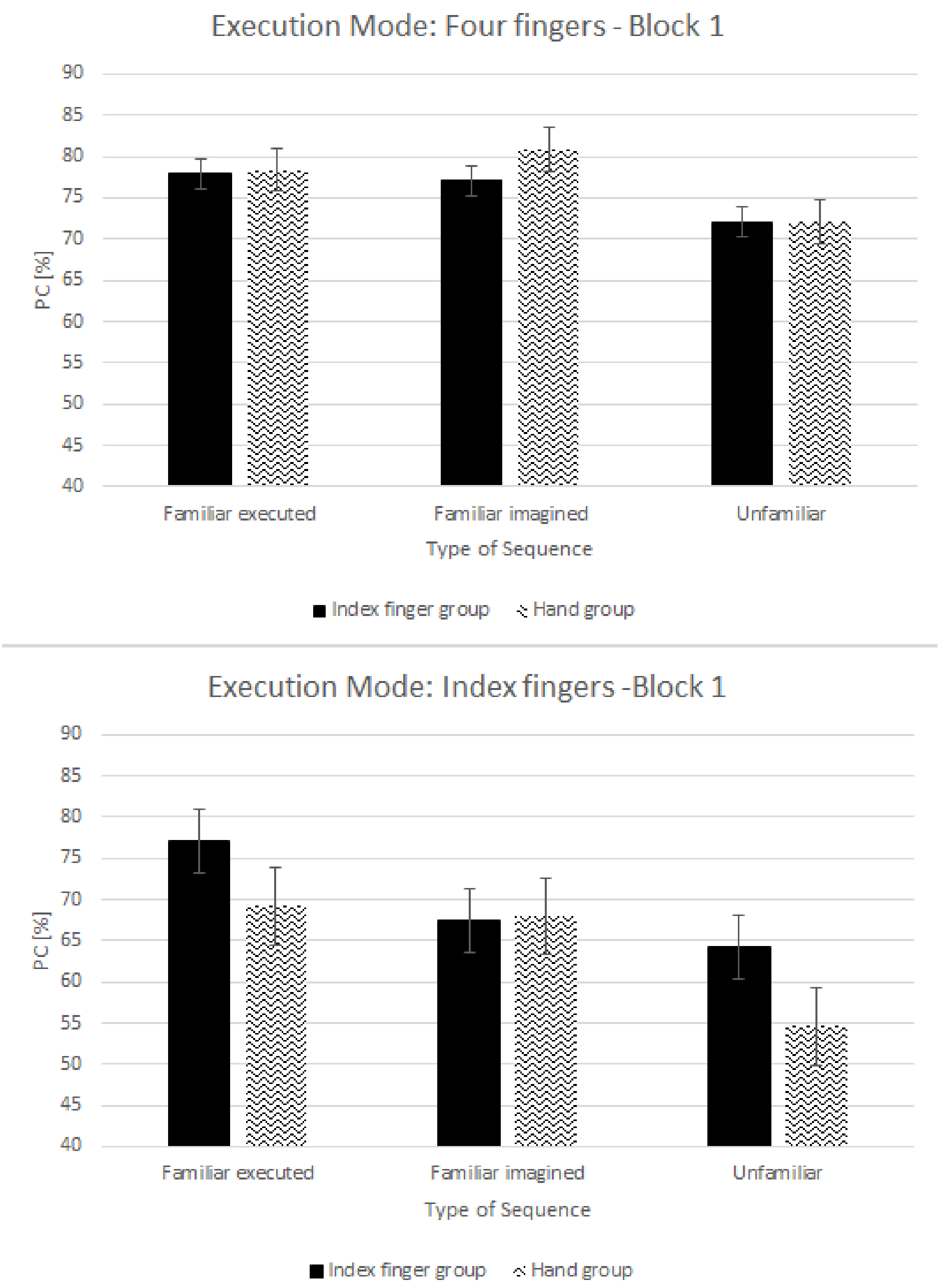

Figure 6. Percentage of correct responses (PC) from the first block in the test phase for sequences, which were executed with four fingers and with an index finger. *Error bars* represent standard errors.

Results for the second block of the test phase revealed no significant difference in PC between groups, $F(1,20) < 0.001$, $p = 0.99$, $\eta_p^2 < 0.001$, and no significant difference as a function of Execution Mode was observed, $F(1,20) < 0.001$, $p = 0.99$, $\eta_p^2 < 0.001$ (Fig.7). No significant interaction between Group and Execution Mode was observed, $F(1,20) = 0.39$, $p = 0.54$, $\eta_p^2 = 0.02$. These findings again indicate that accuracy of performance was not dependent on the execution mode in the training phase, and also not dependent on the execution mode in the test phase, and not dependent on the change of execution mode in this second block in the test phase. No main effect of Type of Sequence was observed, $F(2,40) = 0.8$, $\epsilon = 1.0$, $p = 0.46$, $\eta_p^2 = 0.04$. No significant interactions were observed between Type of Sequence and Group, $F(2,40) = 0.3$, $p = 0.74$, $\eta_p^2 = 0.02$; between Type of Sequence and Execution Mode, $F(2,40) = 0.32$, $p = 0.73$, $\eta_p^2 = 0.02$; and between Type of Sequence × Group × Execution Mode, $F(2,40) = 0.63$, $p = 0.54$, $\eta_p^2 = 0.03$.

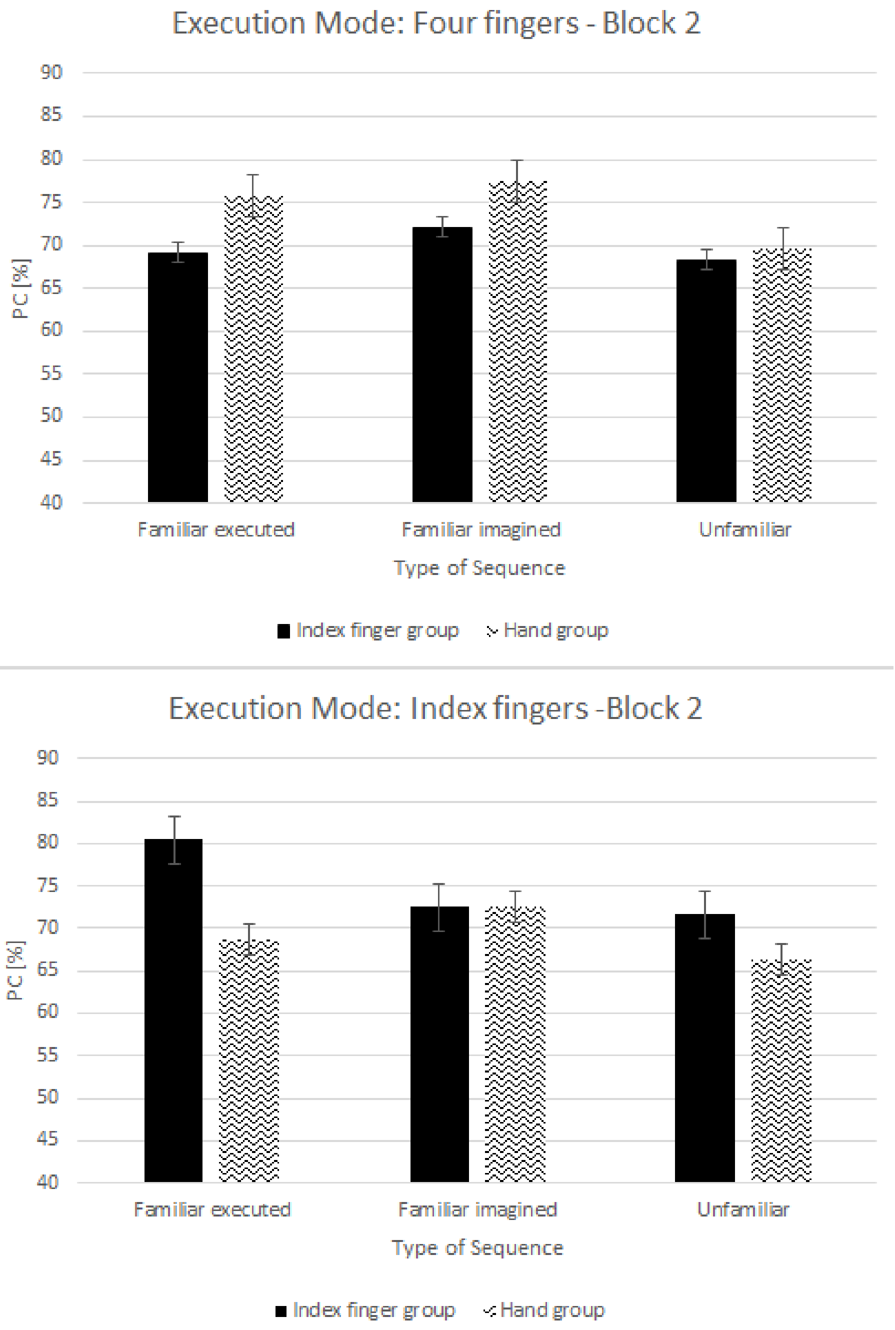

Figure 7. Percentage of correct responses (PC) from the second block in the test phase for sequences, which were executed with four fingers and only with an index finger. *Error bars* represent standard errors.

2.3.3. EMG

Muscular activity was examined in the training phase to check whether participants followed the instruction not to move their fingers in the case of motor imagery. In Figure 8 muscular activity is presented for relevant hand, separately for the average of trials that required motor execution and motor imagery for each group. No main effect of Group was observed, $p = 0.29$. No significant effect of Block was observed, $F(6,132) = 2.78$, $\epsilon = 0.39$, $p = 0.06$, $\eta_p^2 = 0.11$. A significant difference was observed as a function of Type of Sequence, $F(1,22) = 117.12$, $p < 0.001$, $\eta_p^2 = 0.84$. These results indicate that participants contracted their muscles according to the required motor task, i.e., during motor execution, and not during motor imagery. A significant interaction between Type of Sequence and Group was also observed, $F(1,22) = 10.44$, $p < 0.004$, $\eta_p^2 = 0.32$. Inspection of Figure 8 shows larger muscular activity in the index finger than in the four fingers group. No significant difference was observed as a function of EMG channel, $F(1,22) = 0.11$, $p = 0.74$, $\eta_p^2 = 0.005$; and no significant interaction between EMG channel and Group was observed, $F(1,22) = 0.94$, $p = 0.34$, $\eta_p^2 = 0.04$.

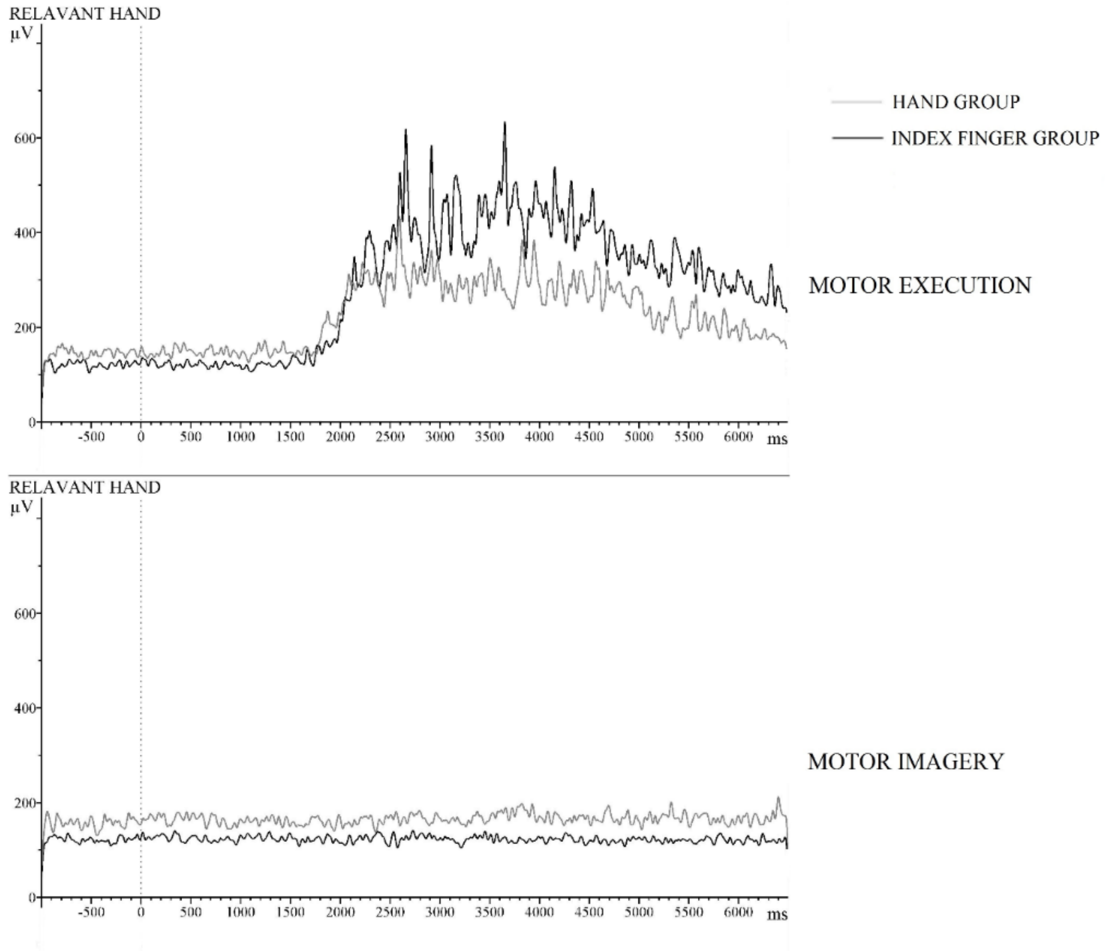

Figure 8. Outcome of the wavelet analysis performed on the raw EMG signal measured from the electrodes attached to the left and right forearms in the training phase. The grand averages are only presented for the relevant hands for the motor execution and motor imagery conditions from -1000 ms before the Go/NoGo signal (0 ms) to 6000 ms.

2.4. Discussion

In this study we questioned how effector-specific the effect of sequence learning by motor execution and motor imagery is by varying the execution mode during a training and a test phase. We wanted to establish whether during learning a sequential motor skill a representation at a motor level develops that is muscle-specific and therefore effector-dependent instead of a representation at a cognitive level that contains spatio-temporal characteristics and is effector-independent (see: Verwey, Groen, & Wright, 2016). Based on the study of Keele et al. (1995), it may be hypothesized that motor skill learning is rather effector-independent. On the other hand, several studies showed that the execution of motor sequences becomes increasingly effector-dependent with extensive practice (Hikosaka, et al., 1999; Bapi, Doya, & Harner, 2000; Verwey W. , 2001; Verwey & Wright, 2004). First, we adressed the question how effector-specific the effect of motor execution on sequence learning is. Secondly, we discussed whether sequence learning by motor imagery is effector-dependent or not.

First, we were interested how effector-specific the effect of sequence learning by motor execution is by varying the execution mode among participants. Behavioral results from the training phase showed a reduction in RT and an increase in PC. The reduction in RT mainly concerned the reduction of the initiation time (pressing the first key of a sequence). Learning effects obtained from the test phase revealed that only motor execution for keys from 2 to 5 in the first block of the test phase depended on the execution mode used in the training phase (i.e., participants who practiced with an index finger in the training phase, executed the sequences faster with an index finger in the test phase). These results indicate a-specific learning effects of execution mode used in the training phase by participants from the index finger group, but all other results (from the first, but also from the second block of the test phase) did not depend on group, which suggests that sequence-specific learning effects are effector-independent. Our results from the test phase seem to reflect the learning of a spatio-temporal sequence rather than the learning of a specific motor pattern in both groups. Thus, at this level learning a sequential skill seems not muscle-specific, which replicates several previous studies (Keele, Jennings, Jones, Caulton, & Cohen, 1995; Grafton, Hazeltine, & Ivry, 1998). Thus, the structure of a motor sequence has been reinforced more at a cognitive level (what is related with a motor program) than at a motor level (Frank, Land, Popp, & Schack, 2014; Verwey, Groen, & Wright, 2016). It has been proposed that with relatively limited practice spatial representations develop that are effector-independent, while the development of motor representations (being effector-dependent) is related with an extensive practice (Verwey, Groen, & Wright, 2016). For example, in the study of Verwey and Wright (2004), in which two components were developed (the effector-dependent and the effector-independent component), the number of sequences which were practiced was much larger than in our experiment (i.e., 1750 sequences in the first day of practice, whereas in our study the first day of practice consisted only of 400 sequences). The number of practiced sequences could play a relevant role in the development of the effector-dependent component.

Secondly, we examined how effector-specific the effect of motor imagery on motor learning is. Behavioral results from the test phase revealed that participants responded faster and more accurately while executing familiar imagined sequences relative to unfamiliar sequences, showing that motor imagery is beneficial during the acquisition of motor skills. Interestingly, no significant difference between the index finger group and the hand group was observed. These results indicate that learning by motor imagery is also effector-independent. Similarly to the motor learning with motor execution, the fact that motor imagery is effector-independent suggests the development of a spatio-temporal pattern rather than of the specific motor pattern. In other words, results from the test phase observed in the case of motor learning with motor imagery also revealed that the structure of motor sequence representation has been reinforced more at a cognitive level instead of motor level. The question remains open whether more practice with motor imagery could also result in the development of motor representation, which has been shown to be effector-dependent (Hikosaka, et al., 1999; Park & Shea, 2003; Verwey & Wright, 2004). Our results are in accordance with the study performed by Mizuguchi, Nakata and Kanosue (2014), showing that activation of brain regions during motor imagery is effector-independent. Similar brain activation has been found during motor imagery while imaging an extension and a flexion of right/left hand and right/left foot (Mizuguchi, Nakata, & Kanosue, 2014), i.e., the left supplementary motor area and inferior frontal gyrus/ventral premotor cortex. Future research needs to clarify whether comparable results can be obtained when learning a motor skill with motor execution and motor imagery with other effectors, i.e., the arms or legs.

In this study, we demonstrated that motor skill learning with motor execution and with motor imagery is effector-independent, indicating the development of spatial representation of a motor sequence. These results can be explained by several underlying neural mechanisms for motor skill learning (Hikosaka, Nakamura, Sakai, & Nakahara, 2002). Based on Hikosaka`s model (2002), two cortical systems are activated during learning a motor sequence (represented in two ways: spatial and motor), i.e., cortex-basal ganglia and cortex-cerebellum loop circuits. According to this model, spatial sequences are supported by parietal-prefrontal cortical loops (relying on attention and working memory), and these sequences are effector-independent. On the other hand, motor sequences are supported by premotor-motor cortical loops, and these sequences are effector-dependent. It has been postulated that processing of spatial sequence occurs earlier during acquisition of a motor skill than processing of motor sequence, which requires long-term practice, what is in line with previous findings (Hikosaka, et al., 1999; Bapi, Doya, & Harner, 2000; Verwey W. , 2001; Verwey & Wright, 2004). Our results suggest that this model may explain both motor skill learning with motor execution, and motor skill learning with motor imagery as we observed the learning of a spatio-temporal sequence rather than the learning of a specific motor pattern in both groups. As we mentioned above, more practice might be needed to induce effector-dependent learning, indicating the activation of premotor-motor cortical loops which is related with the development of motor sequence.

In the current study, better motor performance was observed for previously executed and imagined sequences as compared with unfamiliar sequences, indicating sequence-specific learning effects. These results replicate the learning effects that we found in our previous studies (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). In the case of learning a sequence of movements, it is important to differentiate sequence-specific learning which is based on sequence-specific representations at the central and motor processing level (Verwey, 2015) from sequence-a-specific learning which is more related with an improved ability to decode stimuli or familiarization with the task (e.g., keeping the fingers in a suitable posture), etc. (Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). In the current study, behavioral results revealed significant differences only in the first block of the test phase while executing familiar imagined, familiar executed, and unfamiliar sequences. These results are in line with our previous findings showing that both motor execution and motor imagery induce sequence-specific learning (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). The absence of significant differences in the second block of the test phase may be explained by the fact that unfamiliar sequences were learned by participants of both groups in the first block of the test phase.

In our analyses, we could also observe that using a different execution mode in the training phase has influence on particular processing phases of sequence skill. During the execution of a motor skill, three processing phases of sequence skill can be distinguished: an initiation phase, a concatenation phase, and an execution phase (Abrahamse, Ruitenberg, de Kleine, & Verwey, 2013). The first phase, an initiation, is related to the selection and preparation of the sequence. The key-presses following sequence initiation are typically much faster involving only execution processes. Our results from the training phase revealed that the time needed to initiate a sequence was, indeed, longer for the index finger group than for the hand group. These results for the first key press are in line with the notion that the first key press is typically much slower than the subsequent key presses (Verwey, 1999). The significant difference between groups in initiation might be explained by the fact that participant in the index group had to prepare moving their index finger to particular keys, what could slow down the first key press. Interestingly, our results from the training phase revealed that there was no significant difference between groups involving execution processes. Thus, our results show that the execution mode influenced the initiation phase, but not the execution phase during learning a required motor task.

Our findings showed that motor skill learning with motor execution and motor imagery is effector-independent. However, one might argue that in the present study the statistical power was too low. Null results are not easy to interpret. A potential limitation of this study arises from the fact that the number of participants was not enough to demonstrate effector-dependent effects. On the other hand, no trend effects were present, therefore we favor the interpretation that in our study, the sequential fine motor skill was acquired in an effector-independent manner.

In conclusion, our results demonstrate that learning a fine sequential motor skill by motor execution is effector-independent, which extends previous findings to the Go/NoGo DSP task. Importantly, we were also able to demonstrate that learning a motor skill with motor imagery is also effector-independent. In both cases of learning (i.e., either with motor execution or motor imagery), results suggest the development of spatio-temporal representations rather than muscle-specific representations.

References

Abrahamse, E. L., & Verwey, W. B. (2008). Context dependent learning in the serial RT task. *Psychological Research, 72*(4), 397-404.

Abrahamse, E. L., Ruitenberg, M. F. L., de Kleine, E., & Verwey, W. B. (2013). Control of automated behavior: insights from the discrete sequence production task. *Frontiers in Human Neuroscience, 7,* 82.

Allami, N., Paulignan, Y., Brovelli, A., & Boussaoud, D. (2008). Visuo-motor learning with combination of different rates of motor imagery and physical practice. *Experimental Brain Research, 184*(1), 105-113.

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61*(3), 303-321.

Bapi, R., Doya, K., & Harner, A. (2000). Evidence for effector independent and dependent representations and their differential time course of acquisition during motor sequence learning. *Experimental Brain Research, 132*(2), 149-162.

De Kleine, E., & Van der Lubbe, R. H. (2011). Decreased load on general motor preparation and visual-working memory while preparing familiar as compared to unfamiliar movement sequences. *Brain and Cognition*, *75*(2), 126-134.

Debarnot, U., Abichou, K., Kalenzaga, S., Sperduti, M., & Piolino, P. (2015). Variable motor imagery training induces sleep memory consolidation and transfer improvements. *Neurobiology of Learning and Memory, 119,* 85-92.

Decety, J., Jeannerod, M., & Prablanc, C. (1989). The timing of mentally represented actions. *Behavioural Brain Research*, *34*(1-2), 35-42.

Doussoulin, A., & Rehbein, L. (2011). Motor imagery as a tool for motor skill triaing in children. *Motricidade, 7*(3), 37-43.

Feltz, D. L., & Landers, D. M. (1983). The effects of mental practice on motor skill learning and performance: a meta-analysis. *Journal of Sport Psychology, 5*(1), 25-37.

Frank, C., Land, W. M., Popp, C., & Schack, T. (2014). Mental representation and mental practice: experimental investiagtion on the functional links between motor memory and motor imagery. *PLoS ONE, 9*(4):e95175.

Gentili, R., & Papaxanthis, C. (2015). Laterality effects in motor learning by mental practice in right-handers. *Neuroscience, 297*, 231-242.

Gentili, R., Han, C. E., Schweighofer, N., & Papaxanthis, C. (2010). Motor learning without doing: trial-by-trial improvement in motor performance during mental training. *Journal of Neurophysiology, 104*(2), 774-783.

Gentili, R., Papaxanthis, C., & Pozzo, T. (2006). Improvement and generalization of arm motor performance through motor imagery practice. *Neuroscience, 137*, 761-772.

Grafton, S. T., Hazeltine, E., & Ivry, R. B. (1998). Abstract and Effector-Specific Representations of Motor Sequences Identified with PET. *Journal of Neuroscience, 18*(22), 9420-9428.

Hikosaka, O., Nakahara, H., Rand, M., Sakai, K., Lu, X., Nakamura, K., . . . Doya, K. (1999). Parallel neural networks for learning sequential procedures. *Trends in Neuroscience, 22*(10), 464-471.

Hikosaka, O., Nakamura, K., Sakai, K., & Nakahara, H. (2002). Central mechanisms of motor skill learning. *Current Opinion in Neurobiology, 12*(2), 217–222.

Hird, J. S., Landers, D. M., Thomas, J. R., & Horan, J. J. (1991). Physical practice is superior to mental practice in enhancing cognitive and motor task performance. *Journal of sport & exercise psychology, 13*(3), 281-293.

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage, 14,* 103-109.

Keele, S. W., Jennings, P., Jones, S., Caulton, D., & Cohen, A. (1995). On the Modularity of Sequence Representation. *Journal of Motor Behavior, 27*(1), 17-30.

Kovacs, A. J., Muehlbauer, T., & and Shea, C. (2009). The Coding and Effector Transfer of Movement Sequences. *Journal of Experimental Psychology: Human Perception and Performance, 35*(2), 390–404.

Mizuguchi, N., Nakata, H., & Kanosue, K. (2014). Effector-independent brain activity during motor imagery of the upper and lower limbs: An fMRI study. *Neuroscience Letters, 581*, 69-74.

Osman, M., Bird, G., & Heyes, C. (2005). Action observation supports effector-dependent learning of finger movement sequences. *Experimental Brain Research, 165*(1), 19-27.

Park, J.-H., & Shea, C. H. (2003). Effect of Practice on Effector Independence. *Journal of Motor Behavior, 35*(1), 33-40.

Payne, V. G., & Isaacs, D. L. (1987). *Human Motor Development: A Lifespan Approach.* Mountain View California: Mayfield Publishing Company.

Ruitenberg, M. F. L., De Kleine, E., Van der Lubbe, R. H. J., Verwey, W. B., & Abrahamse, E. L. (2012). Context-dependent motor skill and the role of practice. *Psychological Research, 76*(6), 812–820.

Schmidt, R. A. (1975). A Schema Theory of Discrete Motor Skill Learning. *Psychological Review, 82*(4), 225-260.

Schuster, C., Hilfiker, R., Amft, O., Scheidhauer, A., Andrews, B., Butler, J., … Ettlin, T. (2011). Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. *BMC Medicine, 9*, 75.

Shea, C. H., Kovacs, A. J., & Panzer, S. (2011). The Coding and Inter-Manual Transfer of Movement Sequences. *Frontiers in Psychology, 2,* 52.

Sobierajewicz, J., Przekoracka-Krawczyk, Jaśkowski, W., Verwey, W. B., & van der Lubbe, R. (2017). The influence of motor imagery on the learning of a sequential motor skill. *Experimental Brain Research, 235*(1), 305-320.

Sobierajewicz, J., Szarkiewicz, S., Przekoracka-Krawczyk, A., Jaśkowski, W., & van der Lubbe, R. (2016). To what extent can motor imagery replace motor execution while learning a fine sequential motor skill? *Advances in Cognitive Psychology, 12*(4), 179-192.

Verwey, W. (1999). Evidence for a multistage model of practice in a sequential movement task. *Journal of Experimental Psychology. Human Perception and Performance, 25*(6), 1693-1708.

Verwey, W. (2001). Concatenating familiar movement sequences: the versatile cognitive processor. *Acta Psychologica, 106*, 69-95.

Verwey, W. B. (2015). Contributions from associative and explicit sequence knowledge to the execution of discrete keying sequences. *Acta Psychologica 157*, 122-130.

Verwey, W. B., & Clegg, B. A. (2005). Effector dependent sequence learning in the serial RT task. *Psychological Research, 69*(4), 242-251.

Verwey, W. B., & Wright, D. L. (2004). Effector-independent and effector-dependent learning in the discrete sequence production task. *Psychological Research, 68*(1), 64-70.

Verwey, W. B., Groen, E. C., & Wright, D. L. (2016). The stuff that motor chunks are made of: Spatial instead of motor representations? *Experimental Brain Research, 234*(2), 353–366.

Xu, L., Zhang, H., Hui, M., Long, Z., Jin, Z., Liu, Y., & Yao, L. (2014). Motor execution and motor imagery: a comparison of functional connectivity patterns basen on graph theory. *Neuroscience*, *261,* 184-194.

3. DO MUSICIANS LEARN A FINE HAND MOTOR SKILL DIFFERENTLY THAN NON-MUSICIANS?[3]

Abstract

Do professional musicians learn a fine sequential hand motor skill more efficiently than non-musicians? Is this also the case when they perform motor imagery, which implies that they only mentally simulate these movements? Musicians and non-musicians performed a Go/NoGo discrete sequence production (DSP) task, which allows to separate sequence-specific from a-specific learning effects. In this task five stimuli, to be memorized during a preparation interval, signaled a response sequence. In a practice phase, different response sequences had to be either executed, imagined, or inhibited, which was indicated by different response cues. In a test phase, responses were required to familiar (previously executed, imagined, or inhibited) and unfamiliar sequences. In both phases, response times and response accuracy were measured while the electroencephalogram (EEG) was only registered during the practice phase to compare activity between motor imagery, motor execution, and motor inhibition for both groups. Results in the practice phase revealed that musicians learned the response sequences faster and more accurately than non-musicians although no difference in initiation time was found. EEG analyses revealed similar lateralized activity during learning a motor skill for both groups. Our results from the test phase showed better sequence-a-specific learning effects (i.e., faster response times and increased accuracy) for musicians than for non-musicians. Moreover, we revealed that non-musicians benefit more from physical execution while learning a required motor sequence, whereas sequence-specific learning effects due to learning with motor imagery were very similar for musicians and non-musicians.

Key words: musicians, motor imagery, motor skill, motor execution, sequence learning, EEG, EMG, ERLs.

---

[3] Sobierajewicz, J., Naskręcki, R., Jaśkowski, W., & Van der Lubbe, R. H. J. (2018). Do musicians learn a fine sequential hand motor skill differently than non-musicians? *PLOS ONE, 13*(11): e0207449. doi: 10.1371/journal.pone.0207449

3.1. Introduction

Playing the piano is a highly complex motor task that requires a lot of practice. To play a piece of music one regularly has to coordinate a sequence of finger movements between two hands at different tempi. For example, for one measure, the left hand may need the simultaneous and subsequent key presses of two keys at a constant rhythm of three per measure, while the right hand requires six different single key presses at a constant rhythm within the same measure. The common way in which people learn to play a piece of music is by repeating it over and over again. However, it is also known that professional musicians use additional strategies like mental imagery (i.e., auditory and/or motor imagery) to improve their performance (Lotze M. , 2013). As musicians have to train fine motor skills significantly more often than novices, learning related motor skills may be easier for musicians than for non-musicians. The learning of a motor skill is thought to involve both a motor and a more cognitive level (Hikosaka, et al., 1999; Verwey W. , 2001; Verwey, Shea, & Wright, 2015), and recent research suggests that motor imagery may only be related to a cognitive level (Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2017). The potential benefit for musicians may thus be related to this cognitive and/or motor level, and one might propose that musicians additionally benefit from motor imagery. We hypothezised that this increased ability to perform motor imagery by musicians might also be visible in electrophysiological measures that reflect the involvement of relevant brain areas.

Learning to execute a motor skill can be examined with the so-called discrete sequence production (DSP) task, while the Go/NoGo variant of this task (De Kleine & Van der Lubbe, 2011) seems a perfect tool to study learning by motor imagery, and compare this with learning by motor execution (see (Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017)). The standard DSP task cannot be used to study motor imagery as in that task responses are required to trigger the next stimulus. In the Go/NoGo DSP task, a visually presented stimulus sequence has first to be memorized. Subsequently, after a Go signal the sequence should be either executed by pressing the relevant buttons, or the sequence has to be mentally imagined, while after a NoGo signal the action should be simply withheld (or inhibited). A major advantage of this task is the possibility to separate particular stages of brain activity during the acquisition of motor skills, i.e., encoding the stimuli, memorizing their sequence, preparing the responses, and finally executing the responses (either mentally or physically). During a practice phase different sequences of equal complexity are executed, imagined, and inhibited. Sequence-specific learning effects can subsequently be assessed by executing the previously executed, imagined and inhibited sequences in a test phase and comparing their performance with unfamiliar sequences. The difference between previously executed and unfamiliar sequences reflects the sequence learning effect of response execution, the difference between previously imagined and unfamiliar sequences reflects the sequence learning effect of motor imagery, and the difference between previously withheld and unfamiliar sequences reflects the sequence learning effect of motor inhibition. Sobierajewicz et al. (2017a) demonstrated with this paradigm that motor execution and motor imagery during the practice phase both induce sequence-specific learning effects. Furthermore, event-related lateralizations (ERLs) derived from electroencephalographic (EEG) recordings revealed increased contralateral negativity above motor areas during both motor execution and motor imagery trials, while no such effect was observed in a control condition (Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). The latter results suggest that relevant motor areas are activated during both motor execution and motor imagery, which corroborates with several earlier findings (Caldara, et al., 2004; Kranczioch, Mathews, Dean, & Sterr, 2009). In another study, it was examined whether learning effects of motor execution and motor imagery were muscle-specific or not (Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2017). This was done by varying the execution mode as sequences were either learned with four fingers or only with the index fingers of both hands. Results revealed that sequence-specific learning effects were not dependent on the execution mode during the practice phase, which suggests that these effects are not muscle-specific. These findings can be understood within the framework for sequential motor behavior as proposed by Verwey et al., (Verwey, Shea, & Wright, 2015).

Verwey et al. (2015) proposed that two different representational levels may be involved while learning to produce a sequence of movements. A cognitive level is thought to relate to spatio-temporal aspects of the movement sequence which already develops with limited practice. A second motoric level is thought to relate to the involved muscles or muscle groups (Verwey, Groen, & Wright, 2016), but representations at this level develop only after extended practice (Verwey & Wright, 2004). Thus, representations at a cognitive level develop faster (especially in the initial phase of the learning of a motor sequence) than motor or muscle-specific representations. The possible difference between musicians and non-musicians might in principle involve both types of representations. Thus, musicians might be better able to learn new spatio-temporal patterns which may show up in the benefits of learning by motor execution and motor imagery. Alternatively, musicians might already involve motor-specific representations at an earlier stage. In that case, the benefit would be most pronounced when learning by motor execution. Another possibility is that the potential benefit is related to a general increase in fine motor control that is not sequence-specific. In that case, the benefit for musicians would also be present for unfamiliar sequences.

Several researchers showed that differences in behavioral performance between musicians and non-musicians may be related to specific brain structures (Jäncke, Shah, & Peters, 2000; Krings, et al., 2000; Münte, Altenmüller, & Jäncke, 2002; Lotze, Scheler, Tan, Braun, & Birbaumer, 2003; Baumann, et al., 2007). Most of the studies investigating music performance or music improvisation focused on the role of frontal brain regions (Baumann, et al., 2007; Zatorre, Chen, & Penhune, 2007; Berkowitz & Ansari, 2008; Limb & Braun, 2008; Pinho, de Manzano, Fransson, Eriksson, & Ullén, 2014). Moreover, it has been revealed that the multiple-demand system (consisting of several areas in the prefrontal and parietal regions) is involved in many complex activities among musicians (Lu, et al., 2017). For example, it has been shown that activation of the multi-demand system is related with response selection, working memory, task novelty, and attentional control for goal-oriented behavior (Lu, et al., 2017; Duncan & Owen, 2000; Duncan J. , 2013; Crittenden & Duncan, 2014). Based on fMRI (functional magnetic resonance imaging) results, it has been proposed that highly trained individuals (as compared to novices) are characterized by a decrease in the overall volume of brain activation (e.g., the fronto-parietal network) while they display an increased activation of brain areas relevant for executing the task (e.g., the primary motor cortex), (Jäncke, Shah, & Peters, 2000; Debarnot, Sperduti, Di Rienzo, & Aymeric, 2014). In line with this proposal, an fMRI study by Lotze et al. (2003) revealed that professional musicians display more focused activation patterns during musical performance than amateurs. A recent EEG study of Zhao et al. (2017) additionally showed a reduction of the mismatch negativity (MMN) for musicians relative to non-musicians while passively listening to strong and weak tones. The latter results may indicate that musicians use less cognitive resources, which would be indicative of increased processing efficiency (Zhao, Lam, Sohi, & Kuhl, 2017). However, EEG results from another study of Bianco et al. (2017) suggested that attentional control, indexed with a prefrontal negativity and the P3 component, was enlarged for musicians (i.e., drummers) as compared with non-drummers while performing a visuo-motor discriminative response task (Bianco, Berchicci, Perri, Quinzi, & Di Russo, 2017). Bianco et al. (2017) explained their results by a long-term neural adaptation mechanism and increased visuo-spatial abilities for drummers (Bianco, Berchicci, Perri, Quinzi, & Di Russo, 2017). Based on the previous fMRI results (Jäncke, Shah, & Peters, 2000; Debarnot, Sperduti, Di Rienzo, & Aymeric, 2014) showing increased activation of motor areas, we hypothesized that electroencephalographic activity above cortical motor areas while executing a required motor sequence may also be more pronounced for professional pianists as opposed to non-musicians. A way to examine this possibility is to derive ERLs from the EEG. ERLs are highly specific for motor-related processes as activity that is unrelated to the relevant side is subtracted out (Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017; Kranczioch, Mathews, Dean, & Sterr, 2009; Galdo-Álvarez & Carrillo-de-la-Peña, 2004).

The previous section indicates that musicians may learn a motor skill more easily than non-musicians, which may be related to the extra involvement of motor areas. The question remains open whether this also applies to the learning of a motor skill with motor imagery, which implies that relevant movements are mentally simulated without any overt action (Jeannerod, 2001). Most of the prior studies that aimed to investigate motor learning with motor imagery showed that training with motor imagery can significantly promote the learning of a motor skill, however, in that case the training needs to be very intensive (Pascual-Leone, et al., 1995; Jackson, Lafleur, Malouin, Richards, & Doyon, 2003). For example, in the study of Pascual-Leone et al. (1995) participants practiced for two hours per day for a duration of five days, while in the study of Jackson et al. (2003) participants mentally practiced 1500 sequences in each of five training periods. Bernardi, De Buglio, Trimarchi, Chielli, and Bricolo (2013) questioned whether mental practice may optimize movement timing by employing expert pianists who performed difficult music sequences either with mental practice or with physical practice. Changes in performance were observed in movement velocity, timing and coordination. Improved performance was observed after mental practice, although better results were obtained after physical practice (Bernardi, De Buglio, Trimarchi, Chielli, & Bricolo, 2013). In the study of Brown and Palmer (2013) pianists' pitch accuracy was measured to examine how auditory and motor imagery abilities affect the learning of novel melodies and recall those melodies. Pianists learned melodies either by performing without sound (motor learning) or by listening without performing (auditory learning). Although results revealed that pitch accuracy was higher after auditory learning than after motor learning, both auditory and motor imagery skills improved pitch accuracy. The above-mentioned studies confirm the benefit of motor imagery on timing and accuracy during learning a motor skill. Given the fact that motor imagery is beneficial for motor skill learning, and it has been revealed that musicians are better in the acquisition of a motor skill than novices, it may be proposed that learning a sequential fine motor skill with motor imagery is more beneficial for musicians than for non-musicians.

In the current study, we first questioned whether learning a fine motor skill with motor execution is more effective for professional musicians than for non-musicians. The potential benefit for musicians may be related to the processing of a motor sequence at both a cognitive and a motor level due to long-term practice and expertise, while for non-musicians a motor sequence may only be reinforced at a cognitive level. We predicted that during the practice phase musicians would learn all motor sequences more efficiently than non-musicians. This would lead to better motor performance (faster and more accurately) in the test phase, indicating a-specific learning effects. Secondly, we hypothesized that due to the increased ability to perform motor imagery, musicians may benefit more from motor imagery than non-musicians while learning a motor skill (i.e., sequences that were learned with motor imagery may be executed faster and more accurately by musicians than by non-musicians, indicating sequence-specific learning effects). To improve our understanding of performance differences between musicians and non-musicians, we examined brain activity during motor execution, motor imagery, and motor inhibition for musicians and non-musicians in the practice phase (i.e., when executing, imaging, and inhibiting particular sequences) by comparing ERLs above cortical motor areas. We expected that the electrophysiological activity is more pronounced for professional pianists as opposed to non-musicians (Jäncke, Shah, & Peters, 2000; Lotze, Scheler, Tan, Braun, & Birbaumer, 2003).

3.2. Methods

3.2.1. Participants

A sample of 24 healthy volunteers (4 males, 20 females) aged between 21 and 29 (M_{age} = 24.5, SD 2.41) took part in the experiment. All of them reported to have no history of mental or neurological disorders. Musicians (either students of music or graduated musicians) (n = 12, M_{age} = 24.67, SD 1.56, 3 males, 9 females) were recruited mainly from the Ignacy Jan Paderewski Academy of Music in Poznań. The average reported time of daily practice with the piano amounted to 2-3 h (SD 0.71). Musical training started on average at the age of 10 years (SD 3.9). Non-musicians (n = 12, 1 male, 11, females) were recruited mainly from the Adam Mickiewicz University (M_{age} = 24.75, SD 2.9). They reported not having received any formal music education and never learned to play a musical instrument. All participants were requested to complete Annett`s Handedness Inventory (Annett, 1970). Ten of the musicians were assessed to be right-handed, and two of them were left-handed, while eleven of the non-musicians were assessed to be right-handed, and only one of them was left-handed. All participants gave their written consent before the start of the experiment. Prior ethical approval was granted by the local ethics committee at the Adam Mickiewicz University. The study was performed in accordance with the Declaration of Helsinki.

3.2.2. Stimuli and task

An overview of the stimulus sequence on a trial is presented in Fig 1. A sequence of five visual stimuli was displayed on a CRT monitor with a display frequency of 60 Hz. A trial started with a gray fixation cross (1.3°) presented in the center of the screen between eight horizontally aligned squares (2.5°), four on the left and four on the right side of the fixation cross. The squares were black with a gray border, which were presented on a black background. Each square was assigned to a button on the keyboard (a, s, d, f keys and the ;, l, k, j keys). The alignment of the eight stimulus squares had a total visual angle of 26.5°. Each trial started with a beep of 300 Hz for 300ms. After a time interval of 1000 ms one of the squares was filled yellow for 750 ms, a second square was filled, etc., until a fifth square was filled. The stimulus sequence was presented to either the right or the left side of the fixation cross. After a preparation interval of 1500 ms relative to the offset of the last stimulus, the Go/NoGo stimulus (a fixation cross) was presented in one of three possible colors in the practice phase. In the case of a green cross, the cued response sequence had to be executed (a Go signal). After a blue cross, the response sequence had to be mentally imagined (a Go signal) - participants should imagine to execute the five spatially corresponding key presses in the same order as the stimulus sequence. In the case of a red cross, the sequence had to be withheld. Thus, only after a Go signal, the volunteer had to reproduce the sequence by pressing or imagining to press corresponding buttons on the keyboard, while after a NoGo signal the action should simply be withheld. In the test phase, only a green cross was presented as all sequences (i.e., previously executed, imagined and withheld) had to be physically executed. All participants were requested to keep their eyes directed on the fixation cross during the presentation of the sequence, and during execution of the required task.

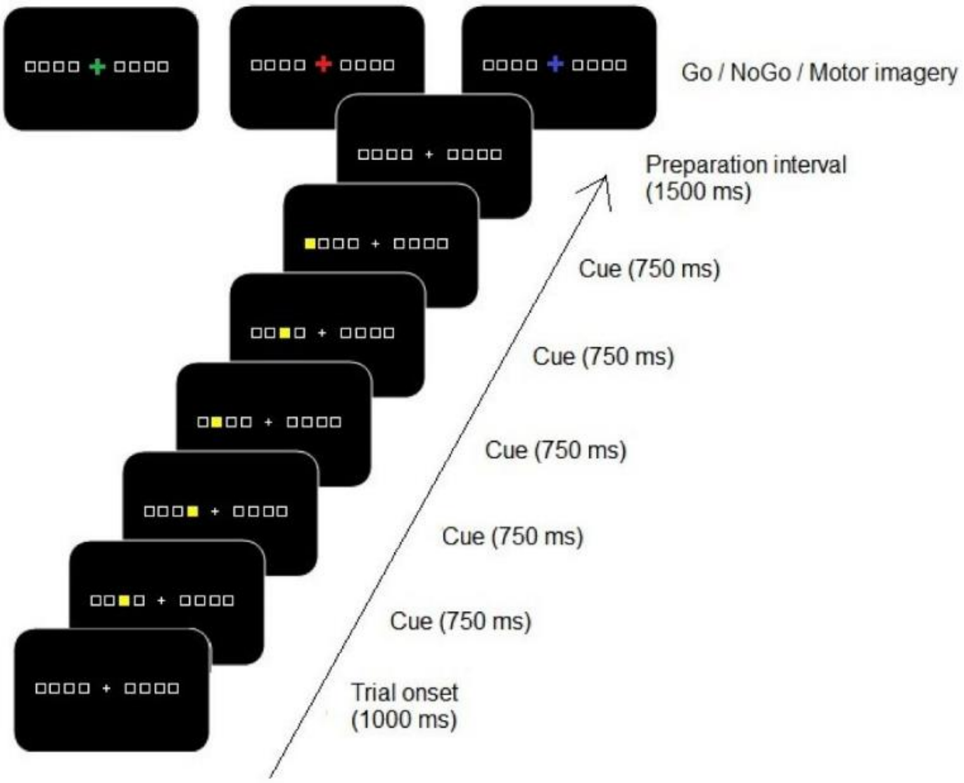

Fig 1. An overview of the sequence of events in the Go/NoGo DSP task. Three possible informative cues were presented after the preparation interval: a green cross implied that the sequence had to be executed (Go signal), a blue cross indicated that execution of the sequence had to be mentally imagined (Go signal), while a red cross indicated that the sequence had to be inhibited (NoGo signal). Participants were instructed to press or imagine pressing the required buttons only after a Go signal, while after a NoGo signal any reaction (also imagined) should be withheld.

3.2.3. Procedure

Participants were requested to sit relaxed and comfortably in a dimly lit room. At the start of the experiment, all participants placed their little finger, ring finger, middle finger, and index finger of the left hand on the *a, s, d, f* keys, and their little finger, ring finger, middle finger and index finger of the right hand on the*;, l, k, j* keys of a computer QWERTY keyboard. The distance from the computer screen was fixed at 70 cm for each individual. The experiment was conducted on a single day. At the start of the experiment each participant received instructions about the details of the experiment. Participants performed five training blocks (32 sequences had to be executed, 32 sequences had to be imagined, and 32 sequences had to be withheld in each block, the same number of repetitions for the right and for the left hand was used), and one final test block (32 sequences executed before; 32 sequences imagined before but now executed; 32 sequences withheld before but now executed, and 32 new sequences that had to be executed). In the Appendix the different sequences are shown which were used in order to eliminate finger-specific effects. We used six different structures (12432, 13423, 14213, 13241, 14312, and 21431) with four different versions of sequences per structure, which were counterbalanced across participants and across fingers.

In the practice phase, sequences had to be executed, imagined, or withheld. In the case of motor imagery, participants were instructed to use a first person perspective (i.e., to imagine the sensation of executing a sequence). To avoid the use of visual imagery, an example of visual and motor imagery was given to all participants ("imagine yourself walking on a street – you can see yourself walking"/ "imagine as if you are walking – you imagine your movements during walking", respectively). Moreover, participants were asked to imagine only a movement and not a sequence of numbers, symbols, or sounds.

Halfway each block and after each block, a pause was provided in which participants were informed on their mean reaction times and error percentages. Feedback about incorrect responses was given after executing a sequence but only when a participant pressed a button before the Go/NoGo signal or when a false button press was made. Participants were asked to execute or imagine the required sequence as fast and as accurately as possible.

3.2.4. Behavioral parameters

Response time (RT) was defined as the time between the onset of the Go signal and pressing the first key, and as the time between two consecutive key presses within a sequence (De Kleine & Van der Lubbe, 2011; Ruitenberg, De Kleine, Van der Lubbe, Verwey, & Abrahamse, 2011). For the practice phase, we tested mean RTs by performing an analysis of variance (ANOVA) with repeated measures with Group (2), Block (4), and

Key (5, the number of keys to be pressed within a sequence) as factors. For the test phase, an ANOVA with repeated measures was also applied with Group (2), Type of Sequence (4, familiar executed, familiar imagined, familiar inhibited, and unfamiliar), and Key (5) as factors. Error analyses were performed on arcsin transformed data to stabilize variances (Abrahamse & Verwey, 2008). A repeated measures analysis of variance (ANOVA) was performed both for the practice phase with Group (2), and Block (4) as factors, and for the test phase with Group (2), and Type of Sequence (4) as factors. In order to test the prediction that musicians are better in the acquisition of a motor skill (either with motor execution or motor imagery), one-tailed *t*-tests were used.

3.2.5. EEG parameters and data processing

EEG, EOG, EMG data, and markers signaling the onset of employed stimuli and the specific button presses were registered with Vision Recorder software (Brain Products – version 2.0.3). The EEG was recorded using an ActiCap (BrainProducts, GmbH) with 64 active channels, which were placed on standard locations according to the extended International 10-20 system (Oostenveld & Praamstra, 2001). A built-in average reference of the amplifier was used. Although a reference electrode standardization technique (REST) may be considered a very useful method in EEG recordings (Yao, 2001; Yao, Wang, Arendt-Nielsen, & C.N. Chen, 2007; Qin, Xu, & Yao, 2010; Tian & Yao, 2013), we used an average reference as for contralateral-ipsilateral difference potentials reference-related differences are subtracted out. Electrode impedances were kept below 5kΩ. To monitor ocular artifacts, the vertical and horizontal electrooculogram (vEOG and hEOG) was recorded using bipolar electrodes located above and below the right eye and on the left and right outer canthi, respectively.

Offline analyses were performed with Brain Vision Analyzer software (version 2.0.4). First, EEG data from the practice phase was low-pass filtered (30 Hz). Next, we selected the segments from -2500 ms to 4000 ms relative to the Go/NoGo signal. A baseline was set from -100 ms to 0 ms. We focused on the 1000 ms time interval after the Go/NoGo signal, as we wanted to contrast motor execution with motor imagery and motor inhibition. Trials with major artifacts were excluded from further analysis (maximum allowed voltage step: 100 µV/ms, minimum/maximum allowed amplitude: -/+150 µV, lowest allowed activity within 50 ms intervals: 0.1 µV). A semiautomatic Independent

Component Analysis (ICA) was used in order to remove residual activity due to horizontal or vertical eye movements from the EEG (averaged number of removed components: 3.5).

3.2.6. ERL measures

Contralateral-ipsilateral difference potentials (ERLs) were computed for the practice phase as we wanted to investigate EEG patterns for musicians and non-musicians while learning a motor skill. ERLs were derived from the ERPs, which were determined for each type of task and also per hand. ERLs are based on a double subtraction procedure performed on ERPs computed for left and right hand trials, which extracts activity that is specific to the relevant side: $\text{ERL} = ((\text{LH}(\text{contra-ipsi}) + \text{RH}(\text{contra-ipsi})))/2$.

ERLs were determined for all symmetrical electrode pairs, but on the basis of earlier results statistical analyses were restricted to two electrode pairs: C3/C4, CP3/CP4, (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). ERLs were analyzed in 40 ms intervals from 0 until 1000 ms after the Go/NoGo signal. Repeated measures ANOVAs were performed for two electrode pairs with the factors Group (2), Time Window (25), and Type of Sequence (3). With 25 time windows from 0 to 1000 ms, the critical *p* value for two successive time windows was estimated at 0.03 ($p_{\text{crit}} < \sqrt{(0.05/((\text{time windows} - 1) \times \text{electrodes}))} < 0.03$), (Van der Lubbe, Bundt, & Abrahamse, 2014). This procedure was applied to reduce the possibility of a Type I statistical error (Talsma, Wijers, Klaver, & Mulder, 2001).

3.2.7. EMG

In order to control whether participants flexed their muscles only in the case of motor execution, we measured EMG activity in the practice phase. It was measured bipolarly by attaching EMG electrodes on the musculus flexor digitorum superficalis and on the processus styloideus ulnae of the right and left hand.

To analyze EMG activity, a band-pass filter from 20 to 50 Hz was applied. Next, a wavelet analysis was performed to determine the extent of motor activation in the required motor task. The threshold for a movement was set at 80-120 μV depending on the resting level of the individual participant. A complex Morlet wavelet was chosen (c =

5) with the lower and upper boundaries for the extracted layer set at 20 and 50Hz. To perform the analyses, we choose the time window from the Go/NoGo signal until 5000 ms as it was time to execute or imagine the sequence. The EMG signal was analyzed with the following factors: Group (2), EMG-channel (right relevant hand, left relevant hand, 2), Block (4), and Type of Sequence (3, motor execution, motor imagery, and motor inhibition).

3.3. Results

All statistical analyses were performed with SPSS (IBM Statistics SPSS 22). $P < 0.05$ was chosen as the level of significance for the behavioral and EMG results. Greenhouse –Geisser ε correction was applied whenever appropriate.

3.3.1. Behavioral results

The practice phase

RT

Fig 2 gives an overview of mean RT results from the practice phase for both groups as a function of Key. The results revealed a trend to a significant difference in mean RTs between musicians and non-musicians (mean RTs for keys 1 to 5 for musicians were 802, 341, 352, 333, and 328 ms, respectively; mean RTs for keys 1 to 5 for non-musicians were 759, 478, 503, 497, and 424 ms, respectively), $F(1,22) = 3.99$, $p = .058$, $\eta_p^2 = .15$. RTs changed as a function of Block, $F(3,66) = 45.19$, $\epsilon = .67$, $p < .001$, $\eta_p^2 = .67$. Contrast analyses revealed a linear reduction in RT across blocks, $F(1,22) = 59.59$, $p < .001$, but also a quadratic trend, $F(1,22) = 13.53$, $p = .001$. These results indicate a general decrease in RT during learning, while the quadratic trend seems to indicate that this decrease was more pronounced in the initial learning phase. No interaction between Block and Group was observed, $p = .17$. However, trend analyses revealed a quadratic trend: $F(1,22) = 6.56$, $p = .018$, suggesting a stronger initial decrease of RTs for musicians than for non-musicians (see Fig 2). A main effect of Key was observed, $F(4,88) = 129.83$, $\epsilon = .37$, $p < .001$, $\eta_p^2 = .86$, and an interaction between Key and Group was observed, $F(4,88) = 8.20$, $p = .003$, $\eta_p^2 = .72$. No group differences were found for the first button press (*p* = .56), which reflects the initiation time, but the subsequent keys characterizing the response sequence were pressed faster by musicians than by non-musicians (*p* < .04). No significant interaction between Block and Key, *F*(12,26) = 0.38, ϵ = .26, *p* = .78, η_p^2 = .02, and no significant interaction between Block, Key and Group was observed, *F*(12,26) = .87, *p* = .46, η_p^2 = .04.

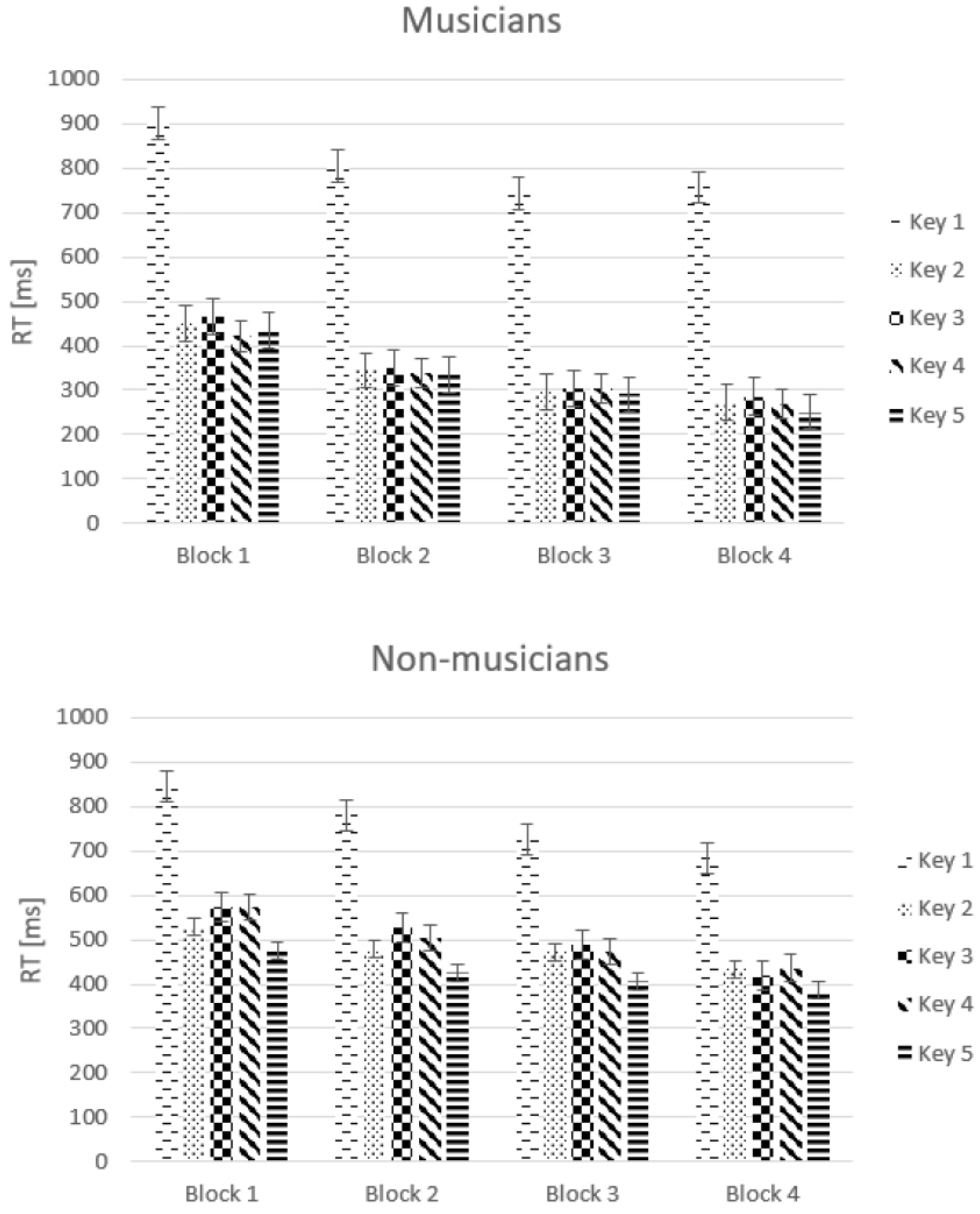

Fig 2**.** Mean response times (RTs) in milliseconds (ms) for each key press (Key 1-5) as a function of Block for both groups. *Error bars* represent standard errors.

PC

A repeated measures ANOVA was performed on arcsin transformed error percentages as a function of Group (2) and Block (4). A significant difference in accuracy was observed between musicians and non-musicians, $F(1,22) = 11.89$, $p = .002$, $\eta_p^2 = .35$. Musicians responded more accurately than non-musicians. A main effect of Block was observed, $F(3,66) = 23.24$, $\epsilon = .52$, $p < .001$, $\eta_p^2 = .51$ (linear trend: $F(1,22) = 29.51$, $p < .001$; quadratic trend: $F(1,22) = 13.0$, $p < .002$; a cubic trend: $F(1,22) = 10.1$, $p < .004$). Inspection of Fig 3 suggests that the number of correct responses increased with practice and this effect was most pronounced in the early stage of learning. No significant interaction between Block and Group was observed, $F(3,66) = 2.09$, $p = .15$. These results indicate that the effect of practice on the number of correct responses was similar for musicians than for non-musicians (Fig 3).

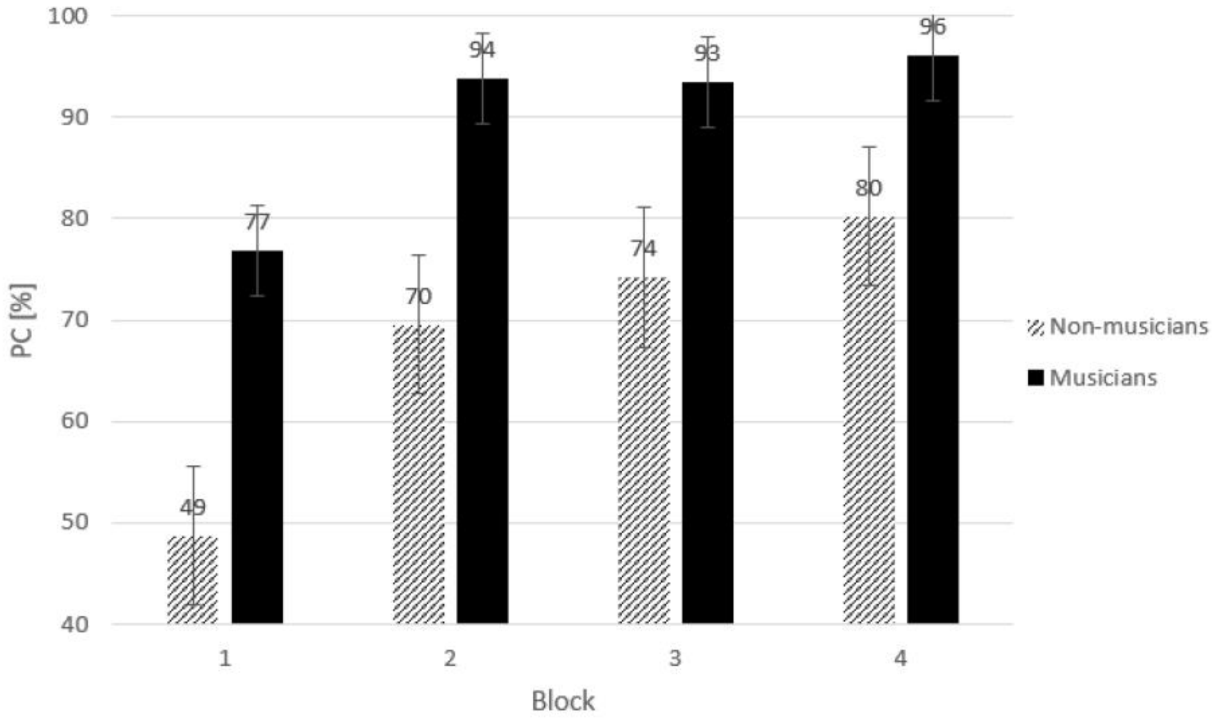

Fig 3. Correct response (PC) in percentages (%) of the total amount of to be executed sequences in the practice phase for each group. *Error bars* represent standard errors.

The test phase

RT

In the test phase, sequences that were executed before, imagined before, and withheld before now all had to be executed together with unfamiliar (not yet practiced) sequences to determine sequence-specific learning effects. Results showed significant differences in mean correct response time between the groups, $F(1,22) = 13.29$, $p = .001$, $\eta_p^2 = .38$. Musicians executed all the sequences faster than non-musicians. A significant difference as a function of Type of Sequence was observed, $F(3,66) = 7.58$, $\epsilon = .59$, $p = .002$, $\eta_p^2 = .26$. Separate *t*-tests (one-tailed) revealed that: unfamiliar sequences were executed slower than familiar executed sequences, $t(23) = 3.46$, $p = .001$; unfamiliar sequences were executed slower than familiar imagined sequences, $t(23) = 2.57$, $p < .01$; and unfamiliar sequences were executed slower than familiar withheld sequences, $t(23) = 1.75$, $p = .04$. Results also revealed that familiar executed sequences were executed faster than familiar withheld sequences, $t(23) = 1.7$, $p = .05$; and familiar withheld sequences were executed slower than familiar imagined sequences, $t(23) = 1.79$, $p = .04$. No significant interaction between Type of Sequence and Group was observed, $F(3,66) = 2.22$, $p = .13$, $\eta_p^2 = .09$. A main effect of Key, $F(4,88) = 60.33$, $\epsilon = .25$, $p < 0.001$, $\eta_p^2 = .73$, and an interaction between Key and Group was observed, $F(4,88) = 5.38$, $p = .02$, $\eta_p^2 = .2$, (a quadratic trend, $F(1,22) = 7.32$, $p < .001$). Results showed that the time to initiate the sequence was similar in both groups, but the time needed to execute the sequences (keys 2-5) was faster for musicians than for non-musicians. No significant interaction between Type of Sequence and Key was observed, $F(12,26) = 2.01$, $\epsilon = .43$, $p = .08$, $\eta_p^2 = .08$, (Fig 4).

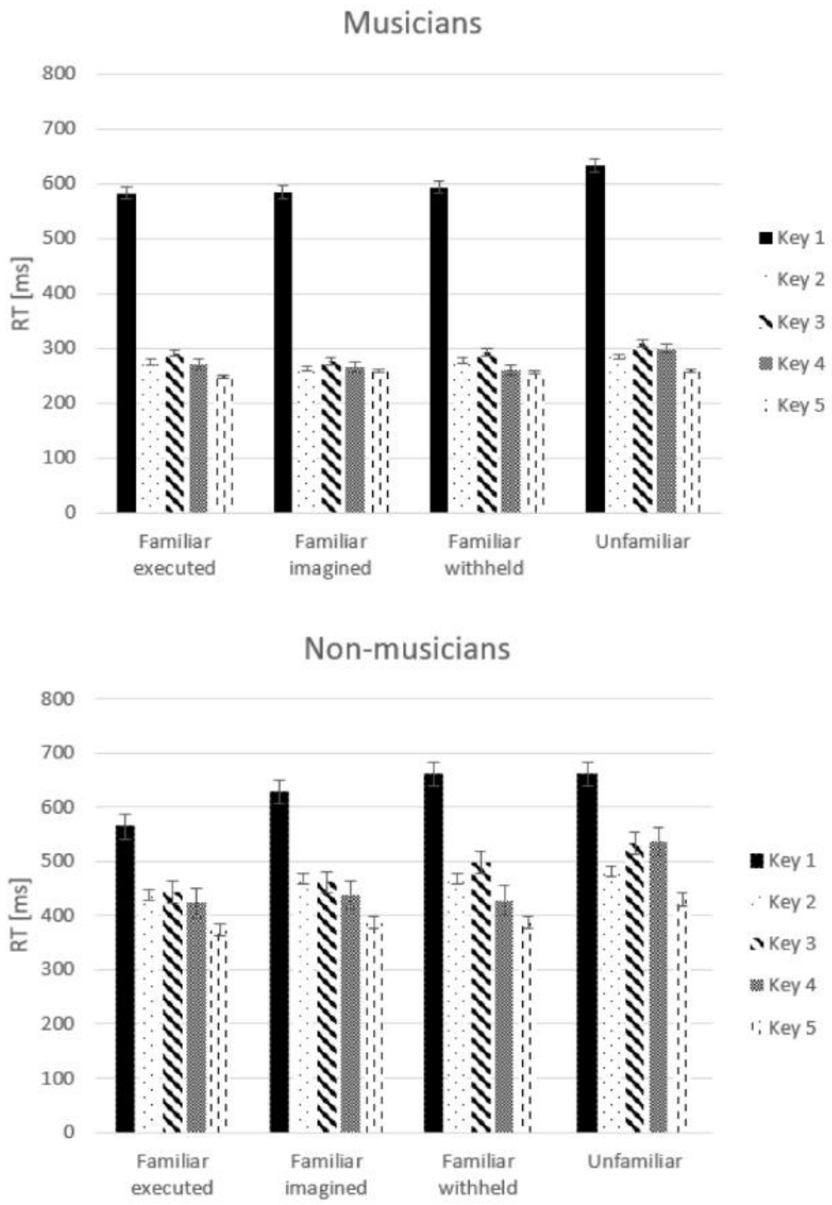

Fig 4. Mean response times (RTs) in milliseconds (ms) for each key presses (Key 1-5) as a function of Type of Sequence, for both groups separately. *Error bars* represent standard errors.

Although only a weak trend to an interaction between Type of Sequence and Group was observed, we tested our predictions directly to examine whether training with motor execution and motor imagery was more beneficial for musicians as compared with non-musicians. A separate ANOVA was performed with the factors: Type of Sequence (2, familiar executed/unfamiliar), Key (5), and Group (2). Furthermore, a separate ANOVA was performed with the factors: Type of Sequence (2, familiar imagined/unfamiliar), Key (5), and Group (2).

The results of training with motor execution again revealed faster execution of the sequences by musicians than by non-musicians, $F(1, 22) = 11.21$, $p = .003$, $\eta_p^2 = .34$. Furthermore, unfamiliar sequences were executed slower than familiar executed sequences, $F(1, 22) = 26.6$, $p < .001$, $\eta_p^2 = .55$. Most importantly, a significant interaction between Type of Sequence and Group was observed, $F(1, 22) = 8.21$,$p = .009$, $\eta_p{}^2 = .22$. Separate *t*-tests (one-tailed) were performed for each group. The results for musicians revealed that unfamiliar sequences were executed significantly slower than familiar executed sequences, $t(11) = 3.1$, $p = .005$; and for non-musicians the results also revealed that unfamiliar sequences were executed significantly slower than familiar executed sequences, $t(11) = 2.92$, $p = .01$. Inspection of Fig 5 shows a large difference in mean RTs between unfamiliar and familiar executed sequences for non-musicians (62 ms), while this difference was clearly much smaller for musicians (19 ms), which explains the observed interaction.

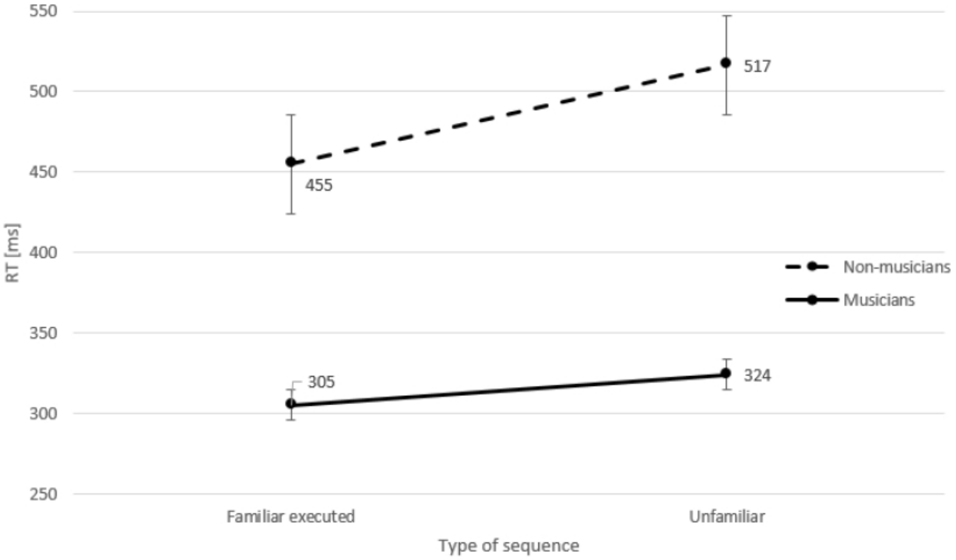

Fig 5. Mean response times (RTs) in milliseconds (ms) for familiar executed and unfamiliar sequences, for both groups separately. *Error bars* represent standard errors.

PC

In the test phase, a similar repeated measures ANOVA was performed on arcsin transformed error percentages as a function of Group (2), and Type of Sequence (4). A significant difference in accuracy was observed between groups, $F(1,22) = 20.06$, $p < .001$, $\eta_p^2 = .48$. These findings show that musicians made less errors than non-musicians.

A main effect of Type of Sequence was observed, $F(3,66) = 10.69$, $\epsilon = .57$, $p < .001$, $\eta_p^2 = .33$.Separate *t*-tests revealed that the number of correct responses was significantly smaller for unfamiliar than for familiar executed sequences, $t(23) = 3.89$, $p = .001$, for unfamiliar sequences as compared to familiar imagined sequences, $t(23) = 3.79$, $p = .001$, and for unfamiliar sequences as compared to familiar withheld sequences, $t(23) = 3.0$, $p = .006$. No other significant differences in PC between sequences were observed, $p > 0.8$. No significant interaction between Type of Sequence and Group was observed, $p = .12$.

Similar as for RTs, to examine directly whether training with motor execution and motor imagery was more beneficial for musicians compared with non-musicians, first a separate ANOVA was performed with the factors: Type of Sequence (2, familiar executed/unfamiliar), and Group (2). Secondly, a separate ANOVA was performed with the factors: Type of Sequence (2, familiar imagined/unfamiliar), and Group (2).

The analysis for familiar executed and unfamiliar sequences revealed that musicians were more accurate than non-musicians, $F(1,22) = 16.26$, $p = .001$, $\eta_p^2 = .43$. A significant difference was observed as a function of Type of Sequence, $F(1,22) = 19.06$, $p < .001$, $\eta_p^2 = .46$, indicating that participants made more errors for unfamiliar sequences than for familiar executed sequences. No significant interaction between Type of Sequence and Group was observed, $F(1, 22) = 3.5$, $p = .08$, $\eta_p^2 = .14$.

The analysis for familiar imagined and unfamiliar sequences also revealed that musicians were more accurate than non-musicians, $F(1,22) = 17.87$, $p < .001$, $\eta_p^2 = .45$. A significant difference was observed as a function of Type of Sequence, $F(1,22) = 17.73$, $p < .001$, $\eta_p^2 = .45$, indicating that participants made more errors for unfamiliar sequences than for familiar imagined sequences. No significant interaction between Type of Sequence and Group was observed, $F(1, 22) = 2.72$, $p = .11$, $\eta_p^2 = .11$.

Although no interaction between Type of Sequence and Group was observed, to examine whether musicians benefit more from motor execution and motor imagery than non-musicians during learning a motor skill, separate *t*-tests were performed for each group. In both groups, the number of correct responses was significantly smaller in the case of unfamiliar sequences as compared with familiar executed, familiar imagined, and familiar withhold sequences, $t(11) > 2.48$, $p < .03$. Inspection of Fig 6 clearly reveals that the highest number of errors was observed for unfamiliar sequences.

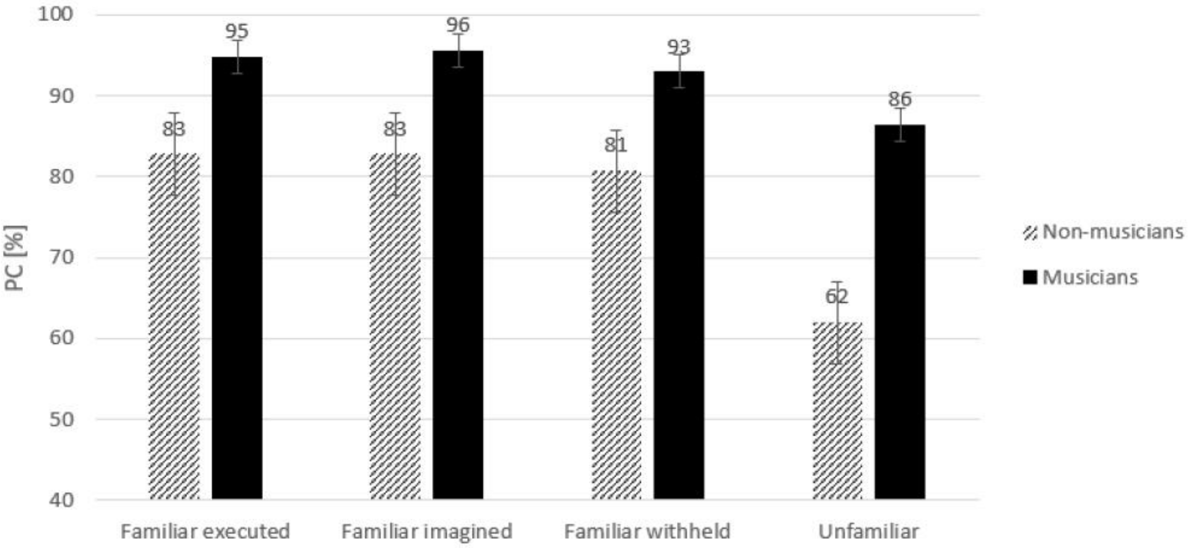

Fig 6. Percentage of correct responses (PC) in percentages (%) in the test phase for each type of sequence. *Error bars* represent standard errors.

3.3.2. EMG

In the practice phase, EMG was measured to control whether participants did not flex their muscles in the case of motor imagery and motor inhibition as only during motor execution EMG activity should be observed. Fig 7 shows the averaged EMG signal for both groups while carrying out the required motor task (execution, imagery, or inhibition). No significant differences were observed between groups, $F(1,22) = .05$, $p = 0.83$, $\eta_p^2 = .002$. Results revealed a trend to a significant interaction between EMG-channel and Group, $F(1,22) = 3.98$, $p = .06$, $\eta_p^2 = .15$, These results suggest that muscular activity tended to be larger for the executing (relevant) hand for musicians than non-musicians. A main effect of Block was observed, $F(3,66) = 6.09$, $\epsilon = .72$, $p = .004$, $\eta_p^2 = .22$, (a linear trend: $F(1,22) = 9.07$, $p = .006$; a quadratic trend: $F(1,22) = 5.7$, $p = .026$). A significant difference was observed as a function of Type of Sequence, $F(2,44) = 115.03$, $\epsilon = .55$, $p < .001$, $\eta_p^2 = .84$. An inspection of Fig 7 shows higher muscular activity in the motor execution condition than in the motor imagery and motor inhibition conditions.

We were especially interested whether muscular activity differed between motor imagery and motor inhibition to determine whether participants possibly flexed their muscles in the case of motor imagery. Results revealed no significant difference as function of Type of Sequence, $p = .11$. Although participants did not move their fingers, some EMG activity seems present during motor imagery and motor inhibition.

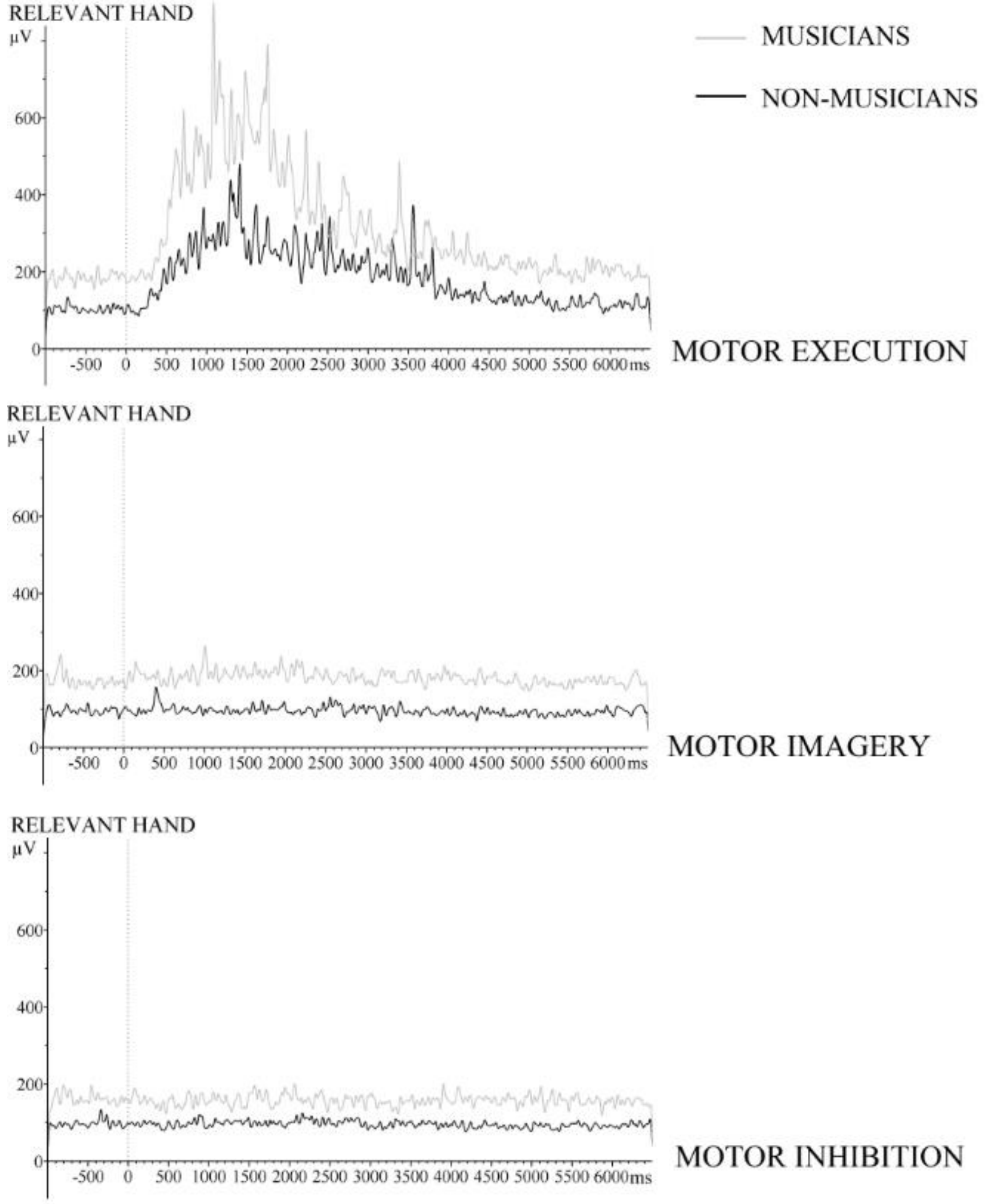

Fig 7. Outcome of the wavelet analysis performed on the raw EMG signal measured from electrodes attached to the *left* and the *right* forearm. The grand averages are only presented for the relevant hands for the motor execution, motor imagery, and motor inhibition from -1000 ms before the Go/NoGo signal (0 ms) to 6500 ms.

3.3.3. ERL results

Behavioral results from the practice phase revealed that the average time needed to execute the sequence was shorter for musicians than non-musicians, and sequences were additionally executed more accurately by musicians than by non-musicians. We questioned to what extent differences in behavioral performance between musicians and non-musicians are related to differences in ERLs, which were determined for each type of task (i.e., motor execution, motor imagery, and motor inhibition).

Topographical maps for activity during the practice phase, from the onset of the Go/NoGo signal until 1000 ms are displayed in Fig 8 for each condition. ANOVAs were performed with the factors Group (2), and Type of Sequence (3), for each of two electrode pairs (C3/4, and CP3/CP4) that were selected on the basis of earlier results (Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, The influence of motor imagery on the learning of a sequential motor skill, 2017).

C3/C4 electrode pair

Separate analyses for lateralized activity (for two consecutive time windows) revealed a significant deviation from zero for motor execution starting from 280 ms to 1000 ms at C3/C4, being most pronounced from 680 ms to 720 ms, $t(23) = -7.51$, $p < 0.001$. For motor imagery, lateralized activity was observed starting from 480 ms to 880 ms at C3/C4, being most pronounced from 760 ms to 800 ms, $t(23) = -3.48$, $p = .002$. This increased negativity on the contralateral site as compared to the ipsilateral site in the case of motor execution and motor imagery is thought to reflect motor-related activity. For motor inhibition, a significant deviation from zero was only observed from 880 ms to 1000 ms, being most pronounced from 960 ms to 1000 ms, $t(23) = 3.17$, $p = 0.004$, however this activity concerned increased contralateral positivity.

No significant difference was observed between groups from the Go/NoGo signal (0ms) to 1000 ms, $p > .2$.The analysis with the factor of Type of Sequence revealed that ERLs differed from 240 ms to 1000 ms, being most pronounced from 800 to 840 ms, $F(2,44) = 42.59$, $\epsilon = .9$, $p < .001$, $\eta_p{}^2 = .66$. Separate *t*-tests revealed that from 240 ms to 320 ms lateralized activity was significantly different only between motor execution and motor inhibition, $t(23) > -3.19$, $p < .01$. From 320 ms to 560 ms, more negativity on contralateral than on ipsilateral electrodes was observed in favor of motor execution compared with motor inhibition, $t(23) > -6.72$, $p < .001$; the analysis also revealed a significant difference between motor execution and motor imagery, revealing more negativity in the case of motor execution, $t(23) > -5.5$, $p < .003$. From 560 ms to 1000 ms, lateralized activity differed between all types of sequences. We observed a significant difference between motor execution and motor inhibition, $t(23) > -10.79$, $p < .001$, being most pronounced from 800 ms to 840 ms, $t(23) = -10.79$, $p < .001$. A significant difference was also observed between motor execution and motor imagery, $t(23) > -4.4$, $p < .02$, being most pronounced from 640 ms to 680 ms, $t(23) > -4.4$, $p < .001$. We also observed that motor inhibition differed from motor imagery, $t(23) > 2.43$, $p < .02$, being most pronounced from 800 ms to 840 ms, $t(23) = 5.39$, $p < .001$.These results demonstrated increased contralateral negativity for motor execution and motor imagery compared with motor inhibition. No significant interaction between Type of Sequence and Group was observed from 0 ms to 1000 ms, $p > .07$.

CP3/CP4 electrode pair

Separate analyses for lateralized activity at CP3/CP4 revealed a significant deviation from zero for motor execution starting from 280 ms to 1000 ms, being most pronounced from 480 ms to 520 ms, $t(23) = -5.89$, $p < .001$. For motor imagery, lateralized activity was observed starting from 160 ms to 240 ms, being most pronounced from 160 ms to 200 ms, $t(23) = 2.9$, $p = .008$. Similarly as at C3/C4 electrode pair, this increased negativity on the contralateral site as compared to the ipsilateral site is thought to reflect motor-related activity. For motor inhibition, no significant deviation from zero was observed at CP3/CP4.

No significant difference was observed between groups from 0 ms to 1000 ms, $p > 0.1$. The analysis with the factor of Type of Sequence revealed that ERLs differed from 280 ms to 1000 ms, being most pronounced from 680 to 720 ms, $F(2, 44) = 14.75$, $\epsilon = .9$, $p < .001$, $\eta_p{}^2 = .4$. Separate *t*-tests revealed that from 280 ms to 680 ms lateralized activity was significantly different only between motor execution and motor inhibition, $t(23) > -4.0$, $p < .001$; and between motor execution and motor imagery, $t(23) > -4.4$, $p < .001$, showing more negativity in favor of motor execution. From 680 ms to 1000 ms, lateralized activity differed between all types of sequences. A significant difference was observed between motor execution and motor inhibition, $t(23) > -4.89$, $p < .002$, being most pronounced from 880 ms to 920 ms, $t(23) = -4.89$, $p < .001$. A significant difference was observed between motor execution and motor imagery, $t(23) > -3.21$, $p < .03$, being most pronounced from 640 ms to 680 ms, $t(23) > -4.4$, $p < .001$. We also observed that motor inhibition differed from motor imagery, $t(23) > 2.43$, $p < .02$, being most pronounced from 800 ms to 840 ms, $t(23) = 5.39$, $p < .001$.These results also demonstrated more increased contralateral negativity for motor execution and motor imagery as compared with motor inhibition. No significant interaction between Type of Sequence and Group was observed from 0 ms to 1000 ms, $p > .44$.

In conclusion, the results of our EEG analyses revealed similar lateralized activity for both groups while learning a motor skill, showing stronger contralateral activation of motor areas in the case of motor execution and motor imagery as compared with motor inhibition. The results revealed a polarity reversal in the case of motor inhibition above primary motor areas in both groups, which suggests a deactivation of motor areas.

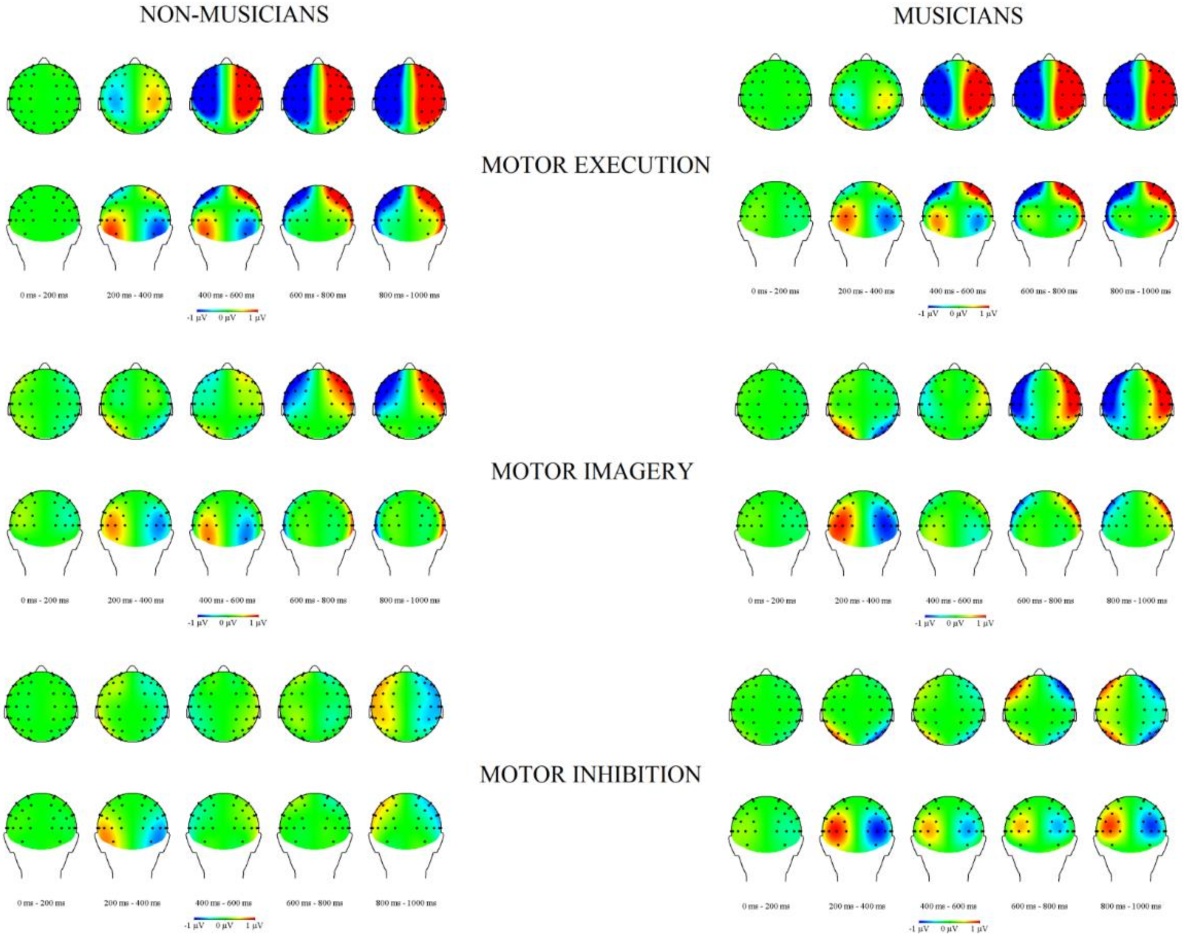

Fig 8. Topography of event related lateralizations (ERLs) for musicians and non-musicians for the three conditions (motor execution, motor imagery and motor inhibition) in the practice phase from the Go/NoGo signal (0 ms) to 1000 ms after the Go/NoGo signal. The left side of the brain displays the contra-ipsilateral difference. Negativity on the left hemisphere implies that activity was more negative on contralateral than on ipsilateral electrodes, which is visible for motor execution and motor imagery, while the opposite pattern seems to be present for motor inhibition.

3.4. Discussion

This work aimed to investigate whether learning a fine sequential hand motor skill with motor execution and motor imagery is more efficient for musicians than for non-musicians. The experiment was divided into a practice phase (sequences had to be physically executed, imagined or inhibited), and a test phase in which all sequences had to be executed. Moreover, unfamiliar (i.e., unpracticed) sequences were added to the test phase to determine sequence-specific learning effects. As a consequence, we could establish whether motor learning is in general more efficient for musicians (a-specific learning effects), and whether sequence-specific learning effects might be influenced by increased expertise. Moreover, we were also interested whether this increased expertise of musicians may be reflected in electrophysiological changes in brain activation above cortical motor areas while imagining, inhibiting, and executing a required movement. First, we focused on learning a sequential motor skill with motor execution and possible group differences. Secondly, we examined the learning effects of motor imagery and possible group differences. Finally, we answered the question of whether increased motor expertise is reflected in electrophysiological changes in brain activation while executing, imaging, and inhibiting a fine motor skill between groups.

Considering the fact that musicians have to train fine motor skills significantly more often than novices, we hypothesized that learning a sequential motor skill with motor execution will differ between musicians and non-musicians. Behavioral results from the practice phase revealed a trend to an overall difference in mean RTs between musicians and non-musicians. Although the time required to initiate a sequence was similar for both groups, the averaged time needed to execute the rest of the sequence was shorter for musicians compared with non-musicians, suggesting that motor learning was more efficient for musicians. Moreover, sequences were executed more accurately by musicians. In both groups the number of correct responses increased with practice, and this effect was most pronounced in the early stage of learning, in line with our previous findings (Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017; Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016). In conclusion, the results from the practice phase revealed that musicians learned response sequences more easily than non-musicians as their responses were faster and more accurate. Better motor performance in the practice phase for musicians may be related with the presence of enhanced visual cognition and improved sensorimotor integration, in line with previous studies (Brochard, Dufour,, & Després, 2004; Rodrigues, Loureiro, & & Caramelli, 2014; Gaser & Schlaug, 2003; Groussard, et al., 2010; Herdener, et al., 2010; Huang, et al., 2010). Moreover, several of those studies also pointed out that musicians are characterized by a greater efficiency of mnemonic processes (Gaser & Schlaug, 2003; Groussard, et al., 2010; Herdener, et al., 2010; Huang, et al., 2010), which leads to better performance for musicians.

The better performance of musicians was evident in the test phase. Musicians executed all sequences (i.e., familiar executed, familiar imagined, familiar inhibited, and unfamiliar) faster and more accurately than non-musicians, indicating better sequence-a-specific learning effects for musicians. Moreover, by comparing unfamiliar sequences with familiar executed, familiar imagined, and familiar inhibited sequences in the test phase, we could also assess the influence of increased expertise on sequence-specific learning effects. Our results revealed that the difference in mean RTs between familiar executed sequences and unfamiliar sequences was actually greater for non-musicians than for musicians, which indicates sequence-specific learning was greater for non-musicians than for musicians. These results suggest that physical execution while learning the required motor sequence was more beneficial for non-musicians relative to musicians. In other words, a-specific learning effects for musicians were greater than sequence-specific learning effects.

Based on the notion that professional musicians regularly use motor imagery to improve their motor performance, we also questioned whether learning a motor skill with motor imagery is more beneficial for musicians than non-musicians. Similarly as for motor execution, motor imagery also induced sequence-specific learning effects, but these effects were independent of the increased expertise (regarding RTs and accuracy). These results suggest a comparable reinforcement of the structure of the motor sequence at a cognitive level for both non-musicians and musicians in the case of motor imagery. A possible reason why learning with motor imagery was beneficial for both groups is the lack of proprioceptive feedback during motor imagery in both groups. Proprioceptive feedback allows to regulate the proper pattern of muscle activation during movement which can be crucial to execute a required sequence movement accurate (see (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016)). In contrast to the learning with motor execution, which was shown to be dependent on increased expertise, our results suggest that learning with motor imagery is more related with the development of the spatio-temporal aspects of a movement (constituting a motor program of a movement (Verwey, Shea, & Wright, 2015)) being independent of increased expertise.

As we demonstrated, musicians learned a motor skill more easily than non-musicians. In order to better understand how a motor skill was acquired by these two groups, we also examined whether increased motor expertise is reflected in electrophysiological changes in brain activation while executing, imaging, and inhibiting a fine motor skill. This was examined in the practice phase. We wanted to establish whether activation above motor areas (which are involved in motor execution and motor imagery) differs between musicians and non-musicians while learning a motor skill. In both groups, we observed increased negative lateralized activity above motor areas in the case of motor execution and motor imagery. In contrast to the findings of Baumann et al. (2007), we did not reveal a significant difference between the groups. Their study showed that sensorimotor regions in the human brain are more involved while imagining the motor movements associated with music performance for musicians than non-musicians (Baumann, et al., 2007). Interestingly, previous research also indicated the increased activation of specific brain areas involved in the execution of the task (e.g., the primary motor cortex, the primary somatosensory cortex, the supplementary motor area), (Lotze, Scheler, Tan, Braun, & Birbaumer, 2003; Debarnot, Sperduti, Di Rienzo, & Aymeric, 2014). The difference between our results and the aforementioned studies (Lotze, Scheler, Tan, Braun, & Birbaumer, 2003; Debarnot, Sperduti, Di Rienzo, & Aymeric, 2014; Baumann, et al., 2007) could be due to different measurement methods (i.e., EEG and functional magnetic resonance imaging, respectively). Moreover, the computation of ERPs and ERLs implies that activity that is not strongly time-locked to a relevant event will be canceled out (e.g., see (Van der Lubbe, Szumska, & Fajkowska)). The employment of time-frequency analyses on the EEG such as wavelet analyses might reveal group differences that are not visible in ERPs. This is something that may need to be explored in a follow-up paper.

Our results also allowed to advance our understanding of acquiring a motor sequence. By measuring EEG we could establish how a motor sequence is acquired with motor execution, motor imagery and motor inhibition, and thereby we could verify previous findings (Caldara, et al., 2004; Kranczioch, Mathews, Dean, & Sterr, 2009; Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). The negativity above contralateral motor areas was related with motor activation during motor execution and motor imagery. Furthermore, ERLs revealed a polarity reversal in the case of motor inhibition, showing positivity on the contralateral hemisphere. These findings are in line with our previous study (Sobierajewicz, Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017), which focused on the resemblance between motor execution and motor imagery relative to motor inhibition. Our ERLs results from the current study confirm the similar activation of brain motor areas during motor imagery and motor execution; whereas the activity during motor inhibition indicates a deactivation of motor areas.

Although the main purpose of this study concerned possible group differences in the acquisition of a fine motor skill, we could also determine sequence-specific learning effects for all participants as unfamiliar sequences were included next to the familiar imagined, familiar executed and familiar withheld sequences in both groups. The results from both groups revealed that unfamiliar sequences were executed slower than familiar executed, familiar imagined sequences, and familiar inhibited sequences indicating indeed sequence-specific learning effects. Moreover, the highest number of errors was observed for unfamiliar sequences, which were not practiced before for both groups. Interestingly, we observed that familiar inhibited sequences were executed more accurately than unfamiliar sequences. This can be related with the fact that inhibited sequences required motor preparation in the practice phase, even when they were not physically or mentally practiced. This result is in accordance with our previous study (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016), showing that motor preparation may be already sufficient for learning a fine motor skill. In our previous study, we employed two groups of participants, who were instructed to imagine the movement sequence (a motor imagery group) or to inhibit the movement sequence after a NoGo signal (a control group). Behavioral results showed that both groups improved their RT and accuracy regardless of the different instruction. Even though participants did not receive an explicit instruction to imagine the movement, they may have imagined the movement during the preparation intervals. As a consequence they could also mentally practice the sequences. In the current study, we also revealed that familiar inhibited sequences were executed slower than familiar imagined sequences, which suggest that learning by motor imagery has a stronger effect than just learning by motor preparation and then motor inhibition.

The purpose of the present study was to evaluate whether learning a fine sequential hand motor skill with motor execution and motor imagery is more efficient for musicians than for non-musicians. Although the research has reached its aims, the potential limitations of this study should be considered. First, it can be argued that the results may be partly due to fact that participants could mentally execute the sequences in a different way as they were requested (i.e., to use motor imagery). We cannot exclude the fact that they imagined a sequence of sounds (Lotze M. , 2013; Keller, 2012) even if they were instructed to imagine the execution of a required sequence. However, our EEG results clearly showed activation above motor areas; therefore, we favor the conclusion that participants indeed used motor imagery. A second limitation concerns possible sex differences, which could influence our results. Testing mainly females makes the generalization of the finding difficult (Miles, Miranda, & Ullman, 2016). It should also be noticed that the group of musicians in our study consisted only of pianists, which could have driven the obtained results. The required task in our experiment resembles the specific sensorimotor representation of a piano keyboard. Thus, it may be the case that different types of musicians (e.g., guitar players, violin players, drummers) would produce different results. In the future, more effort may also be put into clarifying the specific effects of motor imagery training among professional musicians, e.g., by measuring the functional changes protracted by increased expertise.

In conclusion, our results indicated that learning a fine motor skill only depends on increased expertise in the case of learning with motor execution. We showed that learning a fine motor skill with motor execution was more efficient for non-musicians relative to musicians. In the case of learning with motor imagery, we revealed its independence of increased expertise, as we observed similar sequence-specific learning effects in both groups. Nevertheless, we established that motor learning was in general more efficient for musicians (indicating a-specific learning effects) compared with non-musicians. These results support the notion that learning a motor skill is easier for musicians than for non-musicians. A comparison of electrophysiological activation during learning a fine motor skill between professional musicians and non-musicians revealed similar lateralized activity in both groups. In other words, we demonstrated that music experience did not influence electrophysiological brain activation above motor brain areas during learning a fine motor skill.

References

Abrahamse, E. L., & Verwey, W. B. (2008). Context dependent learning in the serial RT task. *Psychological Research, 72*, 397-404.

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61*, 303-321.

Baumann, S., Koeneke, S., Schmidt, C. F., Meyer, M., Lutz, K., & Jancke, L. (2007). A network for audio–motor coordination in skilled pianists and non-musicians. *Brain Research, 1161*, 65-78.

Berkowitz, A. L., & Ansari, D. (2008). Generation of novel motor sequences: The neural correlates of musical improvisation. *NeuroImage, 41*, 535-543.

Bernardi, N. F., De Buglio, M., Trimarchi, P. D., Chielli, A., & Bricolo, E. (2013). Mental practice promotes motor anticipation: evidence from skilled music performance. *Frontiers in Human Neuroscience, 7*, 1-14.

Bianco, V., Berchicci, M., Perri, R., Quinzi, F., & Di Russo, F. (2017). Exercise-related cognitive effects on sensory-motor control in athletes and drummers compared to non-athletes and other musicians. *Neuroscience, 360*, 39–47.

Brochard, R., D. A., & Després, O. (2004). Effect of musical expertise on visuospatial abilities: evidence from reaction times and mental imagery. *Brain Cognition, 54*, 103–109.

Caldara, R., Deiber, M.-P., Andrey, C., Michel, C. M., Thut, G., & Hauert, C.-A. (2004). Actual and mental motor preparation and execution: a spatiotemporal ERP study. *Experimental Brain Research, 159*, 389-399.

Crittenden, B. M., & Duncan, J. (2014). Task Difficulty Manipulation Reveals Multiple Demand Activity but no Frontal Lobe Hierarchy. *Cerebral Cortex, 24*, 532–540.

De Kleine, E., & Van der Lubbe, R. H. (2011). Decreased load on general motor preparation and visual-working memory while preparing familiar as compared to unfamiliar movement sequences. *Brain and Cognition, 75*, 126-134.

Debarnot, U., Sperduti, M., Di Rienzo, F., & Aymeric, G. (2014). Experts bodies,experts minds:How physical and mental training shape the brain. *Frontiers in Human Neuroscience, 8*, 1-17.

Duncan, J. (2013). The Structure of Cognition: Attentional Episodes in Mind and Brain. *Neuron, 80*, 35–50.

Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences, 23,* 475-483.

Galdo-Álvarez, S., & Carrillo-de-la-Peña, M. T. (2004). ERP evidence of MI activation without motor response execution. *MOTOR SYSTEMS, 15,* 2067-2070.

Gaser, C., & Schlaug, G. (2003). Brain Structures Differ between Musicians and Non-Musicians. *Journal of Neuroscience, 23,* 9240-9245.

Groussard, M., La Joie, R., Rauchs, G., Landeau, B., Chételat, G., Viader, F., & … Platel, H. (2010). When music and long-term memory interact: effects of musical expertise on functional and structural plasticity in the hippocampus. *PLoS ONE, 5*.

Herdener, M., Esposito, F., di Salle, F., Boller, C., Hilti, C. C., Habermeyer, B., & … Cattapan-Ludewig, K. (2010). Musical Training Induces Functional Plasticity in Human Hippocampus. *The Journal of Neuroscience, 30,* 1377–1384.

Hikosaka, O., Nakahara, H., Rand, M., Sakai, K., Lu, X., Nakamura, K., & al., e. (1999). Parallel neural networks for learning sequential procedures. *Trends in Neuroscience, 22,* 464-471.

Huang, Z., Zhang, J., Yang, Z., Dong, G., Wu, J., Chan, A., & al., e. (2010). Verbal memory retrieval engages visual cortex in musicians. *Neuroscience, 168,* 179-189.

Jackson, P., Lafleur, M., Malouin, F., Richards, C., & Doyon, J. (2003). Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. *NeuroImage, 20,* 1171-1180.

Jäncke, L., Shah, N., & Peters, M. (2000). Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Cognitive Brain Research, 10,* 177-183.

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage, 14,* 103-109.

Keller, P. E. (2012). Mental imagery in music performance: underlying mechanisms and potential benefits. *Annals of the New York Academy of Sciences, 1252,* 206-213.

Kranczioch, C., Mathews, S., Dean, P. J., & Sterr, A. (2009). On the equivalence of executed and imagined movements: evidence from lateralized motor and nonmotor potentials. *Human Brain Mapping, 30,* 3275-3286.

Krings, T., Töpper, R., Foltys, H., Erberich, S., Sparing, R., Willmes, K., & al., e. (2000). Cortical activation patterns during complex motor tasks in piano players and control subjects. A functional magnetic resonance imaging study. *Neuroscience Letters 278,* 189-193.

Limb, C., & Braun, A. (2008). Neural Substrates of Spontaneous Musical Performance: An fMRI Study of Jazz Improvisation . *PLOS ONE, 3*.

Lotze, M. (2013). Kinesthetic imagery of musical performance. *Frontiers in Human Neuroscience, 7*, 1-9.

Lotze, M., Scheler, G., Tan, H.-R., Braun, C., & Birbaumer, N. (2003). The musician`s brain functional imaging of amateurs and professionals during performance and imagery. *Neuroimage, 20*, 1817-1829.

Lu, J., Yang, H., He, H., Jeon, S., Hou, C., Evans, A. C., & al., e. (2017). The Multiple-Demand System in the Novelty of Musical Improvisation: Evidence from an MRI Study on Composers. *Frontiers in Neuroscience, 11*.

Miles, S. A., Miranda, R. A., & Ullman, M. T. (2016). Sex Differences in Music: A Female Advantage at Recognizing Familiar Melodies. *Frontiers in Psychology, 7*.

Münte, T. F., Altenmüller, E., & Jäncke, L. (2002). The musician`s brain as a model of neuroplasticity. *Nature reviews. Neuroscience., 3*, 473-478.

Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology, 112*, 713-719.

Pascual-Leone, A., Nguyet, D., Cohen, L. G., Brasil-Neto, J. P., Cammarota, A., & Hallett, M. (1995). Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *Journal od Neurophysiology, 74*, 1037-1045.

Pinho, A. L., de Manzano, Ö., Fransson, P., Eriksson, H., & Ullén, F. (2014). Connecting to Create: Expertise in Musical Improvisation Is Associated with Increased Functional Connectivity between Premotor and Prefrontal Areas. *Journal of Neuroscience, 34* , 6156-6163.

Qin, Y., Xu, P., & Yao, D. (2010). A comparative study of different references for EEG default mode network: The use of the infinity reference. *Clinical neurophysiology: official journal of the International Federation of Clinical Neurophysiology, 121*, 1981-1991.

Rodrigues, A. C., Loureiro, M., & & Caramelli, P. (2014). Visual memory in musicians and non-musicians. *Frontiers in Human Neuroscience, 8*.

Ruitenberg, M. F., De Kleine, E., Van der Lubbe, R. H., Verwey, W. B., & Abrahamse, E. L. (2011). Context-dependent motor skill and the role of practice. *Psychological Research, 76*, 812-820.

Sobierajewicz, J., Przekoracka-Krawczyk, A., Jaśkowski, W., & van der Lubbe, R. H. (2017). How effector-specific is the effect of learning by motor execution and motor imagery? *Experimental Brain Research, 35,* 3757-3769.

Sobierajewicz, J., Przekoracka-Krawczyk, A., Jaśkowski, W., Verwey, W. B., & van der Lubbe, R. (2017). The influence of motor imagery on the learning of a sequential motor skill. *Experimemental Brain Research, 235,* 305-320.

Sobierajewicz, J., Szarkiewicz, S., Przekoracka-Krawczyk, A., Jaśkowski, W., & van der Lubbe, R. (2016). To what extent can motor imagery replace motor execution while learning a fine motor skill? *Advances in Coginitive Psychology, 12,* 170-183.

Talsma, D., Wijers, A. A., Klaver, P., & Mulder, G. (2001). Working memory processes show different degrees of lateralization: Evidence from event-related potentials. *Psychophysiology, 38,* 425-439.

Tian, Y., & Yao, D. (2013). Why do we need to use a zero reference? Reference influences on the ERPs of audiovisual effects. *Psychophysiology, 50,* 1282-1290.

Van der Lubbe, R. H., Bundt, C., & Abrahamse, E. L. (2014). Internal and external spatial attention examined with lateralized EEG power spectra. *Brain Research, 1583,* 179-192.

Van der Lubbe, R. H., Szumska, I., & Fajkowska, M. (n.d.). Two Sides of the Same Coin: ERP and Wavelet Analyses of Visual Potentials Evoked and Induced by Task-Relevant Faces. *Advances in Cognitive Psychology, 12,* 154–168.

Verwey, W. (2001). Concatenating familiar movement sequences: the versatile cognitive processor. *Acta Psychologica, 106,* 69-95.

Verwey, W. B., & Wright, D. L. (2004). Effector-independent and effector-dependent learning in the discrete sequence production task. *Psychological Research, 68,* 64-70.

Verwey, W. B., Groen, E. C., & Wright, D. L. (2016). The stuff that motor chunks are made of: Spatial instead of motor representations? *Experimental Brain Research, 234,* 353–366.

Verwey, W., Shea, C., & Wright, D. (2015). A cognitive framework for explaining serial processing and sequence execution strategies. *Psychonomic bulletin & review, 22,* 54-77.

Yao, D. (2001). A method to standardize a reference of scalp EEG recordings to a point at infinity. *Physiological Measurement, 22,* 693-711.

Yao, D., Wang, L., Arendt-Nielsen, L., & C.N. Chen, A. (2007). The effect of reference choices on the spatio-temporal analysis of brain evoked potentials: The use of infinite reference. *Computers in Biology and Medicine 37*, 1529-1538.

Zatorre, R., Chen, J. L., & Penhune, V. B. (2007). When the brain plays music: auditory-motor interactions in music perception and production. *Nature reviews Neuroscience, 8*, 547-558.

Zhao, T. C., Lam, H. G., Sohi, H., & Kuhl, P. K. (2017). Neural processing of musical meter in musicians and non-musicians. *Neuropsychologia 106* , 289-297.

Supporting Information

S1 File. Additional results on RT in the test phase.

The results of training with motor execution revealed a faster execution of the sequences by musicians than by non-musicians, $F(1, 22) = 11.21$, $p = .003$, $\eta_p^2 = .34$. Furthermore, unfamiliar sequences were executed slower than familiar executed sequences, $F(1, 22) = 26.6$, $p < .001$, $\eta_p^2 = .55$. Most importantly, a significant interaction between Type of Sequence and Group was observed, $F(1, 22) = 8.21$,$p = .009$, $\eta_p^2 = .22$. Separate *t*-tests (one-tailed) were performed for each group (detailed results are presented in Table 1). The results for musicians revealed that unfamiliar sequences were executed significantly slower than familiar executed sequences, $t(11) = 3.1$, $p = .005$; and for non-musicians the results also revealed that unfamiliar sequences were executed significantly slower than familiar executed sequences, $t(11) = 2.92$, $p = .01$. Inspection of Fig 5 shows a large difference in mean RTs between unfamiliar and familiar executed sequences for non-musicians (62 ms), while this difference was clearly much smaller for musicians (19 ms), which explains the observed interaction. Again a main effect of Key was observed, $F(4, 88) = 48.79$, $\epsilon = .05$, $p < 0.001$, $\eta_p^2 = .69$, and an interaction between Key and Group was observed, $F(4, 88) = 6.26$, $p = .01$, $\eta_p^2 = .22$, (a linear trend: $F(1, 22) = 5.82$, $p < .03$; a quadratic trend: $F(1, 22) = 7.94$, $p = .01$). No significant interaction between Type of Sequence and Key was observed, $F(4, 88) = 2.35$, $\epsilon = .73$, $p = .08$, $\eta_p^2 = .1$.

Table 1. Results of *t*-tests on RT for each group comparing different types of sequence (i.e., familiar imagined, familiar executed, familiar withheld, and unfamiliar). * $p < 0.05$ (one-tailed test).

	Musicians		Non-musicians	
Type of sequence	*t*(11)	*p*	*t*(11)	*p*
Unfamiliar – familiar executed	3.1	**0.005***	2.92	**0.005***
Unfamiliar – familiar withheld	1.55	0.08	1.48	0.09
Unfamiliar – familiar imagined	3.99	**0.001***	2.0	**0.04***
Familiar imagined – familiar executed	0.51	0.31	0.89	0.2
Familiar withheld – familiar executed	1.95	**0.04***	1.17	0.14
Familiar withheld – familiar imagined	1.59	0.07	1.08	0.15

Results for the comparison of familiar imagined and unfamiliar sequences again revealed faster responses for musicians than for non-musicians, $F(1,22) = 13.35$, $p = .001$, $\eta_p^2 = .38$. Unfamiliar sequences were executed slower than familiar imagined sequences, $F(1, 22) = 9.45$, $p = .006$, $\eta_p^2 = .3$.No significant interaction between Type of Sequence and Group was observed, $F(1, 22) = .91$, $p = .35$, $\eta_p^2 = .04$. These results show that training with motor imagery was not more beneficial for musicians compared with non-musicians. Again, a main effect of Key, $F(4,88) = 47.9$, $\epsilon = .39$, $p < 0.001$, $\eta_p^2 = .69$, and an interaction between Key and Group was observed, $F(4,88) = 4.74$, $p = .02$, $\eta_p^2 = .18$, (a quadratic trend, $F(1,22) = 6.85$, $p < .02$). No significant interaction between Type of Sequence and Key was observed, $F(4, 88) = 1.96$, $\epsilon = .82$, $p = .12$, $\eta_p^2 = .08$.

S2 File. Additional results on PC in the test phase.

Separate *t*-tests were performed for each group - results are presented in Table 2 - to examine whether musicians benefit more from motor execution and motor imagery than non-musicians during learning a motor skill, In both groups, the number of correct responses was significantly smaller in the case of unfamiliar sequences as compared with familiar executed, familiar imagined, and familiar withhold sequences, $t(11) > 2.48$, $p < .03$.

Table 2. *t*-test results of PC for each group comparing different types of sequence (i.e., familiar imagined, familiar executed, familiar withheld, and unfamiliar). * $p < 0.05$

	Musicians		Non-musicians	
Type of sequence	*t*(11)	*p*	*t*(11)	*p*
Unfamiliar – familiar executed	3.18	**0.009***	3.39	**0.006***
Unfamiliar – familiar imagined	4.16	**0.002***	3.08	**0.01***
Unfamiliar – familiar withheld	2.48	**0.03***	2.56	**0.03***
Familiar imagined – familiar executed	0.36	0.73	0.00	1.0
Familiar withheld – familiar executed	0.75	0.47	0.45	0.66
Familiar withheld – familiar imagined	1.02	0.33	0.71	0.49

4. DOES TRANSCRANIAL DIRECT CURRENT STIMULATION AFFECT THE LEARNING OF A FINE SEQUENTIAL HAND MOTOR SKILL WITH MOTOR IMAGERY? [4]

Abstract

Learning a fine sequential hand motor skill, like playing the piano or learning to type, improves not only due to physical practice, but also due to motor imagery. Previous studies revealed that transcranial direct current stimulation (tDCS) and motor imagery independently affect motor learning. In the present study, we investigated whether tDCS combined with motor imagery above the primary motor cortex influences sequence-specific learning. Four groups of participants were involved: an anodal, cathodal, sham stimulation, and a control group (without stimulation). A modified discrete sequence production (DSP) task was employed: the Go/NoGo DSP task. After a sequence of spatial cues, a response sequence had to be either executed, imagined, or withheld. This task allows to estimate both non-specific learning and sequence-specific learning effects by comparing the execution of unfamiliar sequences, familiar imagined, familiar withheld, and familiar executed sequences in a test phase. Results showed that the effects of anodal tDCS were already developing during the practice phase, while no effects of tDCS on sequence-specific learning were visible during the test phase. Results clearly showed that motor imagery itself influences sequence learning, but we also revealed that tDCS does not increase the influence of motor imagery on sequence learning.

Key words: motor imagery, motor learning, transcranial direct current stimulation (tDCS), Go/NoGo DSP task.

---

[4] Sobierajewicz, J., A., Jaśkowski, W., & Van der Lubbe, R. H. J. (2017). Does transcranial direct current stimulation affect the learning of a fine sequential hand motor skill with motor imagery? *Journal of Motor Behavior, 21*:1-15. doi:10.1080/00222895.2018.1513395

4.1. Introduction

Transcranial direct current stimulation (tDCS) is a noninvasive technique that aims to modulate cortical excitability by delivering a weak constant current between two electrodes placed over the scalp. It has been shown that anodal stimulation of the motor cortex enhances cortical excitability, while excitability diminishes in the case of cathodal stimulation (Nitsche & Paulus, 2000; Quartarone, et al., 2004). The common explanation of these effects is that cathodal stimulation induces hyperpolarization of neurons, while anodal stimulation results in depolarization (Nitsche & Paulus, 2000), leading to a decrease or an increase of cerebral excitability, respectively (Bindman, Lippold, & Redfearn, 1964; Purpura & McMurtry, 1965). These cortical changes in excitability due to tDCS can be explained by phenomena like long-term potentiation (LTP) and long-term depression (LTD), (Malenka & Nicoll, 1999). Apart from the type of stimulation (anodal or cathodal), the effects of tDCS depend on the intensity of the stimulation, the precise location of the electrodes, and stimulation duration (Nitsche & Paulus, 2001; Nitsche, et al., 2003; Kaminski, et al., 2013).

It has been shown in previous studies that tDCS may have positive effects on motor skill learning (Antal, Nitsche, Kruse, Hoffmann, & Paulus, 2004; Ciechanski & Kirton, 2016; Buch, et al., 2017). Interestingly, several studies also revealed that motor skills may improve due to motor imagery (defined as the mental simulation of a movement without its actual execution (Jeannerod, 2001)). For example, it has been shown that training with motor imagery has positive effects on motor performance in athletes, musicians and healthy subjects (Driskell, Copper, & Moran, 1994; Pascual-Leone, et al., 1995; Jackson, Lafleur, Malouin, & Richards, 2001; Gentili, Papaxanthis, & Pozzo, 2006; Debarnot, Clerget, & Olivier, 2011). Moreover, it has been revealed that motor imagery improves motor strength (Lebon, Collet, & Guillot, 2010), movement velocity (Pascual-Leone, et al., 1995), and motor recovery (Cho, Kim, & Lee, 2013; Maillet, et al., 2013). However, an important distinction that needs to be made when considering improved performance is whether the effect can be considered as a non-specific learning effect, which may simply be due to increased task familiarity, or as a sequence-specific learning effect, which relates to learning to carry out a specific sequence of actions (Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003; Verwey & Wright, 2014). In our study we focused on both non-specific and sequence-specific learning effects due to tDCS. Thus, the question may be raised whether tDCS affects sequence-specific learning. Additionally, the combined use of tDCS and motor imagery might boost sequence-specific learning.

Foerster, Rocha, Wiesiolek, Chagas, Machado, Silva, Fregni, and Monte-Silva (2013) examined whether tDCS combined with motor imagery enhances motor performance by using a handwriting test. Their results revealed that anodal tDCS combined with motor imagery significantly reduced the time needed in the handwriting task as compared with sham stimulation. In line with Nitsche and Paulus (2000), Foerster et al. (2013) explained their findings in terms of increased cortical excitability induced by anodal tDCS and mental practice. However, no effect of training with motor imagery was observed, therefore the reduction of handwriting time could also be solely due to anodal tDCS. As the effect of tDCS alone was not examined, this possibility cannot be excluded. The results of Foerster et al. (2013) are partially consistent with the results of a recent study of Saimpont, Mercier, Malouin, Guillot, Collet, Doyon, and Jackson (2016). In that study, it was examined whether anodal tDCS strengthened the effect of motor imagery while learning a finger tapping sequence. Results revealed that anodal tDCS together with motor imagery training significantly increased the number of correct sequences compared with sham stimulation or tDCS alone. Motor imagery training and tDCS alone also significantly improved motor performance (Saimpont, et al., 2016), but the combination of tDCS and motor imagery induced stronger learning effects than each method alone. Saimpont et al. (2016) explained these findings by the reinforcement of synaptic strength within the primary motor cortex. Importantly, both above-mentioned studies focused on rather general non-specific learning effects instead of sequence-specific learning effects (see: (Sobierajewicz J. , Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017)). Thus, the question remains whether the combination of tDCS and motor imagery also enhances sequence-specific learning of a fine motor skill.

Sequence learning refers to acquiring the skill to produce a sequence of actions as fast and accurately as possible (Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003; Verwey & Wright, 2014). Non-specific learning effects, reflected in improved performance may occur due to multiple factors like increased familiarity with the task procedure or an improved ability to decode stimuli. To establish whether sequence learning effects are not non-specific, control (unfamiliar) sequences should be added to a final test phase. Thus, during practice participants execute particular sequences (either physically or mentally), and in the test phase motor performance of these familiar sequences is compared with unfamiliar sequences. Application of this method revealed that motor execution and motor imagery both induce sequence-specific learning effects (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz J. , Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017).

The aim of the current study was twofold. We were interested in establishing whether learning effects of tDCS can be considered as non-specific and/or sequence-specific. Furthermore, we wanted to know whether these effects increase when tDCS is combined with motor imagery. First of all, we expected that tDCS improves motor performance, which can be examined by comparing results between groups of participants that receive anodal or cathodal tDCS or not. In contrast with the above-mentioned studies in which anodal and sham stimulation were compared (Foerster, et al., 2013; Saimpont, et al., 2016), we examined the influence of anodal and cathodal stimulation, and next to sham stimulation we also included a control group. We expected to observe better performance in the anodal tDCS group, and in the case of cathodal stimulation we expected that the effects of learning would be diminished; while similar results were expected for the sham stimulation and the control group as these groups did not receive any stimulation. Furthermore, by including a control group the possibility of a placebo effect can be ruled out. Secondly, by employing the Go/NoGo discrete sequence production task (see: (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz J. , Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017)) we can examine the influence of tDCS on sequence-specific learning by comparing performance for familiar sequences (trained in the practice phase) with unfamiliar (untrained) sequences in the final test phase, and examine this difference between groups. Importantly, as we observed that motor imagery induces sequence-specific learning effects (Sobierajewicz et al., 2016, 2017), we also wanted to verify if this effect increases due to the application of tDCS. By comparing the results between familiar imagined and unfamiliar sequences in the test phase and comparing this difference between groups, we might demonstrate that tDCS boosts the effect of motor imagery on sequence-specific learning.

4.2. Methods

4.2.1. Participants

Forty-eight volunteers took part in the experiment (34 female, 14 male). All participants reported to have no history of mental and neurological disorders, no family history of epilepsy, cardiac pacemaker or metallic implants. Participants were aged between 20 and 34 years (M_{age} = 24.5, SD 3.7). Prior to the experiment they were asked to sign an informed consent and to complete Annett`s Handedness Inventory (Annett, 1970). Participants were randomly assigned to one of four groups (12 participants in each group): 1) *anodal* – six female, six male, all right-handed, M_{age} = 25.08, SD 3.32; 2) *cathodal* – seven female, five male, 11 right-handed, one left-handed M_{age} = 25, SD 4.47; 3) *sham* – ten female, two male, 11 right-handed, one left-handed M_{age} = 23.08, SD 2.87; 4) *control* – eleven female, one male, 11 of them were right-handed, and one of them was left-handed M_{age} = 24.92, SD 4.03. Participants (except for the control group) were informed about the possibility that they would feel a slight tingling sensation during stimulation. The current study was approved by the local ethics committee of the Adam Mickiewicz University and was performed in accordance with the Declaration of Helsinki.

4.2.2. Stimuli and task

At the start of the experiment, all participants placed their little finger, ring finger, middle finger, and index finger of the non-dominant hand on the *a, s, d, f* keys of a computer QWERTY keyboard. A trial started with a default picture with four horizontally arranged squares presented in the center of the screen. The squares were black with a gray border and were presented on a black background. An overview of the sequence of stimuli is displayed in Figure 1. The four squares spatially corresponded with four response keys (e.g., the left most square corresponded with the *"*a*"* key, and the right most square corresponded with the "f" key). Each trial started with a beep of 300 Hz for 300 ms. After 1000 ms five squares, one after another, turned yellow, each for 750 ms (Figure 1). After a preparation interval of 1500 ms relative to stimulus offset, a response cue was presented by changing the color of the borders. In the practice phase, the sequence had to be executed after a green border (Go signal), the sequence had to be mentally imagined after a blue border (Go signal), and after a red border nothing had to be done (NoGo signal), so the action should be inhibited. In the case of a Go signal, participants should either press or imagine pressing the corresponding keys in the same order as in the stimulus sequence. The sequence applied for each condition (i.e., motor execution, motor imagery, and motor inhibition) was unique and was repeated throughout the practice phase. In the test phase, only a green border was presented, because all sequences had to be physically executed. The employed sequences per condition were the same as in the practice phase, but now all sequences had to be physically executed. Participants were instructed to respond as fast and accurately as possible after presentation of the Go/NoGo signal.

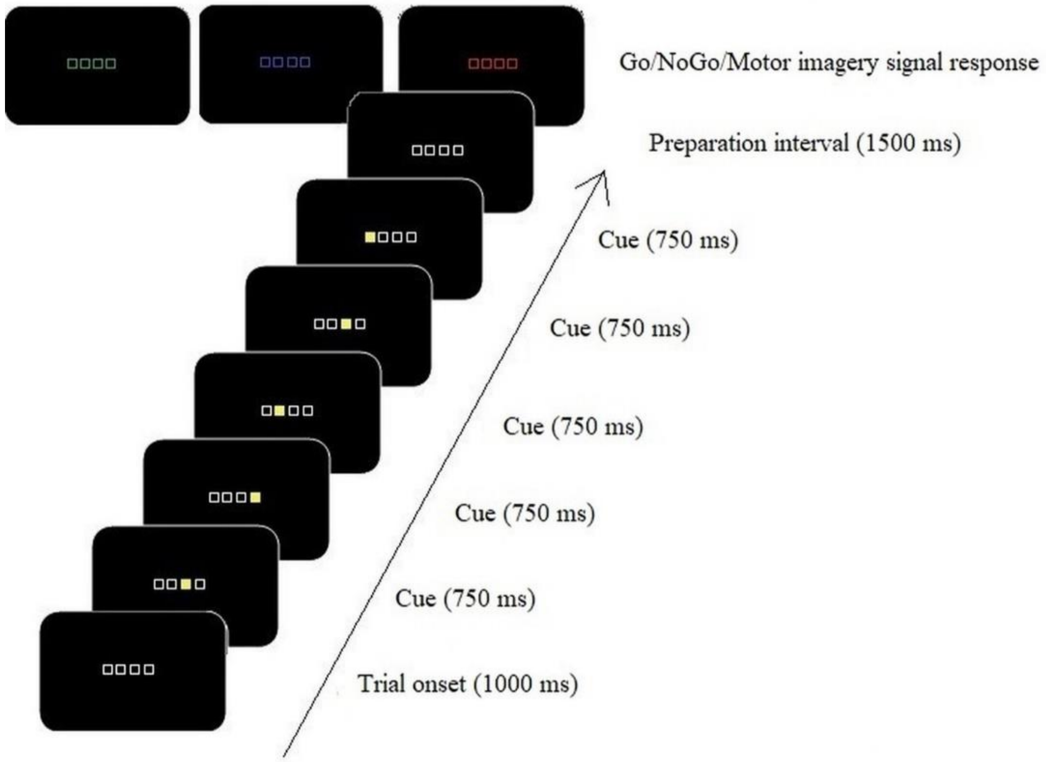

Figure 1. An overview of sequence presentation in the Go/NoGo discrete sequence production (DSP) task. In the practice phase, a Go/NoGo/Motor imagery signal was indicated by three possible informative cues at the end of the stimulus sequence: a green border implied that the sequence had to be executed (Go signal), a blue border indicated that execution of the sequence had to be mentally imagined (Go signal) while a red border indicated that the sequence had to be inhibited.

4.2.3. Procedure

At the start of the experiment, participants received oral instructions about the experiment. They were asked to sit comfortably on a chair at a desk in a dimly lit room. The monitor was placed right in front of them at a distance of 70 cm. Participants were instructed not to move their fingers or contract their muscles during motor imagery and the control condition (i.e., motor inhibition). If participants incorrectly pressed a button during motor execution, information about this error was given. Feedback about incorrect responses (“incorrect response” was displayed) was also given when participants pressed the button before the Go/NoGo signal or when a false button press was made only in the motor execution trials (both in the practice and the test phase). Halfway each block and after each block, participants could relax during a pause. During these pauses, participants were informed about their mean response times (RTs) and percentage of correct responses (PC).

Participants were randomly assigned to one of four groups, i.e., the anodal, cathodal, sham, and control group - 12 participants in each group. Every participant received the same instruction: either to execute a sequence, to imagine a sequence or to do nothing (withhold a response). In the case of motor imagery, participants were instructed to simulate a movement from a first-person perspective, i.e., to imagine the execution of a sequence. They were asked to *feel* a movement. To be certain that participants understood the required task as motor imagery instead of visual imagery, they were given examples for each type of imagery: “imagine as if you are walking – you imagine your movements during walking” (for motor imagery) and “imagine yourself walking on the street – you can see yourself walking” (for visual imagery), (Sobierajewicz J. , Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). Participants were also told to imagine only the sensation of executing a sequence instead of memorizing numbers, symbols or sounds.

The experiment was divided into a practice phase (40 minutes) and a test phase (30 minutes). The time between the end of the practice phase and the start of the test phase lasted approximately five minutes. During the practice phase, participants performed two blocks consisting of 96 sequences which had to be executed (32 sequences), imagined (32 sequences), or inhibited (32 sequences). The test phase consisted of one block with 128 sequences which now all had to be executed, including sequences from the practice phase: 32 familiar imagined before, 32 familiar executed before, 32 familiar inhibited before, and 32 unfamiliar new sequences. The different type of sequences were randomized within blocks.

In our experiment, six different structures of movement sequences were created with four response variants (12432, 13423, 14213, 13241, 14312, and 21431). The sequences which were used in the experiment are shown in the Appendix. This procedure enables to eliminate finger-specific effects and to maintain the same level of complexity for all participants. The presented sequences were counterbalanced across participants and fingers.

4.2.4. tDCS

The electrical stimulation was carried out with a battery driven stimulator (BrainSTIM, Italy). tDCS was delivered during the practice phase through two saline-soaked sponge electrodes with a surface area of 35 cm^2. In the case of anodal stimulation, the active electrode was placed over the primary motor cortex contralateral to the non-dominant hand according to the international 10-20 system of electrode placement (C3/4), (Saimpont, et al., 2016; Foerster, et al., 2013; Cuypers, et al., 2013). The reference electrode was located ipsilaterally relative to the non-dominant hand over the supraorbital region (Fp1/Fp2). The electrode positions were exchanged in the cathodal stimulation condition (Figure 2). Thus, regardless of the type of stimulation (anodal, cathodal or sham), for right-handed participants the electrodes were placed on the left supraorbital area and right primary motor area, and for left-handed participants on the right supraorbital area and left primary motor area.

The practice phase lasted 40 minutes, and tDCS started in parallel with the practice phase. The constant direct current ramped up for 30 s until it reached an intensity of 2 mA. It was kept constant for 15 minutes, before ramping down over 30 s to 0 mA. During sham stimulation, the electrode montage was identical to the anodal stimulation. The current also increased over the first 30 s to ramp down in 30 s and was turned off without informing the participant. Sham stimulation is aimed to elicit the same sensation of current onset as in real stimulation (i.e., anodal or cathodal) but should not result in depolarization or hyperpolarization. Apart from the control group, all participants were informed that they could receive either real (anodal/cathodal) or sham stimulation, but they were informed that these three conditions would feel the same (e.g., tingling, itching). We did not test whether participants were able to distinguish between real or sham stimulation.

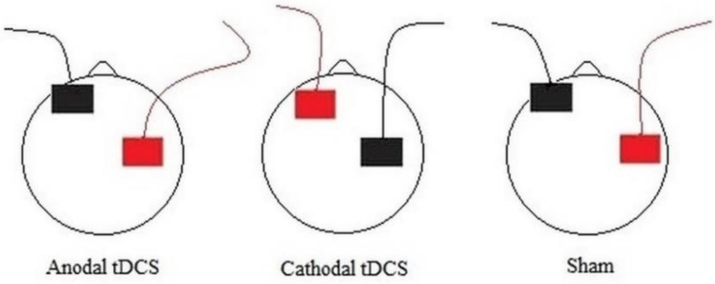

Figure 2. Example of the electrode montage for anodal tDCS (the active electrode was placed over the primary motor cortex contralateral to the non-dominant hand while the reference electrode was located ipsilaterally to the non-dominant hand over the supraorbital region), cathodal tDCS (the electrode positions were exchanged relative to anodal tDCS), and for sham stimulation for a right-handed participant. For the tDCS conditions red represents the anode and black represents the cathode.

4.2.5. EMG

The electromyographic (EMG) activity was recorded during the practice phase to control whether a movement occurred only on those trials that required physical execution (Miyaguchi, et al., 2013; Saimpont, et al., 2016). EMG was measured bipolarly by attaching the electrodes on the musculus flexor digitorum superficalis (which enables to record finger movements) and on the processus styloideus ulnae of the non-dominant hand.

EMG was recorded with Vision Recorder (Brain Products – version 2.0.3). Offline, analyses were performed with Brain Vision Analyzer (version 2.0.4) software. The EMG signal was low-pass filtered at 50 Hz (24 dB/oct) and high-pass filtered at 20 Hz (24 dB/oct). The threshold for a movement was set at 40-90 µV depending on the resting level of the individual participant. A Complex Morlet wavelet was chosen (c=5) to extract the relevant muscle activity, with the lower and upper boundaries for the extracted layer set at 20 and 50 Hz, respectively (Carillo-de-la-Peña, Galdo-Álvarez, & Lastra-Barreira, 2008).

The execution period included 6000 ms starting from the Go/NoGo signal during which the sequence was executed, imagined or inhibited. After a logarithmic transformation, separate repeated measures ANOVAs were carried out with Task (3), (motor execution, motor imagery, motor inhibition trials) and Group (4) as factors, to determine whether participants selectively contracted their muscles only during motor execution in the practice phase.

4.2.6. Response parameters

Response time (RT) was defined as the time interval between the onset of the Go signal and the depression of the first key, and subsequently as the time between two consecutive key presses within a sequence (Ruitenberg, De Kleine, Van der Lubbe, Verwey, & Abrahamse, 2011; De Kleine & Van der Lubbe, 2011). Only RTs from correct responses were analyzed. A trial was considered incorrect when the button was pressed before the Go/NoGo signal or when a false button (in the wrong order) was pressed. The Percentage Correct (PC) for each block indicated the number of fully correct responses in all Go trials. We divided each practice block into four parts (i.e., subblocks) to examine more precisely the effect on RT and PC during the practice phase between groups. Mean RTs in each practice block were evaluated statistically by an analysis of variance (ANOVA) with repeated measures with Subblock (4), and Key (5) as within-subject factors, and Group (4), (anodal, cathodal, sham, and control group) as between-subjects factor. The test phase involved a repeated measures ANOVA with the factors Type of Sequence (4), (familiar executed, familiar imagined, familiar inhibited and unfamiliar sequences), Key (5), and Group (4). To perform more detailed analyses for keys (to differentiate the initiation time and the execution time), we decided to reduce the number of levels of the variable Key from five to two (including the first key press and the average of keys 2 to 5), (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz J. , Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017).

Error analyses were performed on arcsin transformed error proportions to stabilize variances. For the practice phase, repeated measures ANOVAs were performed for each practice block with Subblock (4) as within-subjects factor, and Group (4; anodal, cathodal, sham, and control group) as between-subjects factor. The test phase involved a repeated measures ANOVA with the factors Type of Sequence (4; familiar executed, familiar imagined, familiar inhibited and unfamiliar sequences), and Group (4) as between-subjects factor.

All statistical analyses were performed with STATISTICA 12®. The threshold for significant effects was fixed at $p < .05$. Greenhouse-Geisser epsilon correction was applied to the analyses whenever appropriate. Post-hoc tests involved Tukey`s HSD test. To increase sensitivity for detecting gradual differences as a function of Subblock, we examined linear, quadratic, and cubic contrasts.

4.3. Results

4.3.1. The practice phase

RT

Figure 3 gives an overview of mean RTs results from the two blocks of the practice phase for each group as a function of Key. The analysis performed for the first block revealed no difference in mean RTs between groups, $F(3, 44) = 1.3$, $p = .29$, $\eta_p^2 = .08$. RTs changed as a function of Subblock $F(3, 132) = 22.49$, $\epsilon = .76$, $p < .001$, $\eta_p^2 = .34$, (linear trend: $F(1, 44) = 36.09$, $p < .001$; quadratic trend: $F(1, 44) = 8.16$, $p = .007$), indicating a general decrease in RT for all groups during the first block of learning a motor skill. No interaction between Subblock and Group was observed, $p = .19$, suggesting that the decrease of RT was similar in all groups. A main effect of Key was observed, $F(1, 44) = 208.46$, $p < .001$, $\eta_p^2 = .83$. Inspection of Figure 3 shows that RT in the first block for the first key was longer than for the subsequent keys. No interaction between Key and Group was observed, $p = .4$. No significant interaction between Subblock and Key was observed, $p = .48$. Importantly, a significant interaction between Subblock, Key, and Group was observed, $F(9, 132) = 3.68$, $p = .001$, $\eta_p^2 = .2$ (linear × linear trend: $F(3, 44) = 7.03$, $p = .001$). To clarify this interaction, separate ANOVAs for each key were performed with Subblock (4) and Group (4) as factors. The analysis for the first key press revealed no significant difference between groups, $F(3, 44) = .76$, $p = .53$, $\eta_p^2 = .05$. The time required for the first key press changed as a function of Subblock, $F(3, 132) = 11.25$, $\epsilon = .8$, $p < .001$, $\eta_p^2 = .2$, (linear trend: $F(1, 44) = 21.13$, $p < .001$), indicating a general decrease of RT in all groups during the first block of learning a motor skill. A significant interaction between Subblock and Group was observed, $p = .02$. Separate analyses per Group revealed that RTs changed as a function of Subblock in the control group: $F(3, 33) = 11.86$, $\epsilon = .52$, $p < .001$, $\eta_p{}^2 = .52$, and in the anodal group: $F(3, 33) = 10.96$, $\epsilon = .67$, $p < .001$, $\eta_p{}^2 = .5$. The analysis performed for the average of keys 2 to 5 revealed no significant difference in RTs between groups, $F(3, 44) = 1.95$, $p = .14$, $\eta_p{}^2 = .12$. The time needed to execute the rest of the sequence changed as a function of Subblock, $F(3, 132) = 27.43$, $\epsilon = .62$, $p < .001$, $\eta_p{}^2 = .38$, (linear trend: $F(1, 44) = 36.6$, $p < .001$; quadratic trend: $F(1, 44) = 16.77$, $p < .001$), also indicating a general decrease of RT in all groups during the first block of learning a motor skill. No significant interaction between Subblock and Group was observed, $p = .13$.

The analysis performed for the second block of the practice phase also revealed no significant difference in mean RTs between groups, $F(3, 44) = 2.03$, $p = .12$, $\eta_p{}^2 = .12$. RTs changed as a function of Subblock, $F(3, 132) = 3.46$, $\epsilon = .7$, $p = .03$, $\eta_p{}^2 = .07$, (linear trend: $F(1, 44) = 9.54$, $p = .003$), indicating a decrease in RT in all groups in the second practice block. No interaction between Subblock and Group was observed, $p = .31$. A main effect of Key was observed, $F(1, 44) = 243.61$, $p < .001$, $\eta_p{}^2 = .85$. No interaction between Key and Group was observed, $p = .63$. No significant interaction between Subblock and Key was observed, $p = .78$; and no significant interaction between Subblock, Key and Group was observed, $p = .3$.

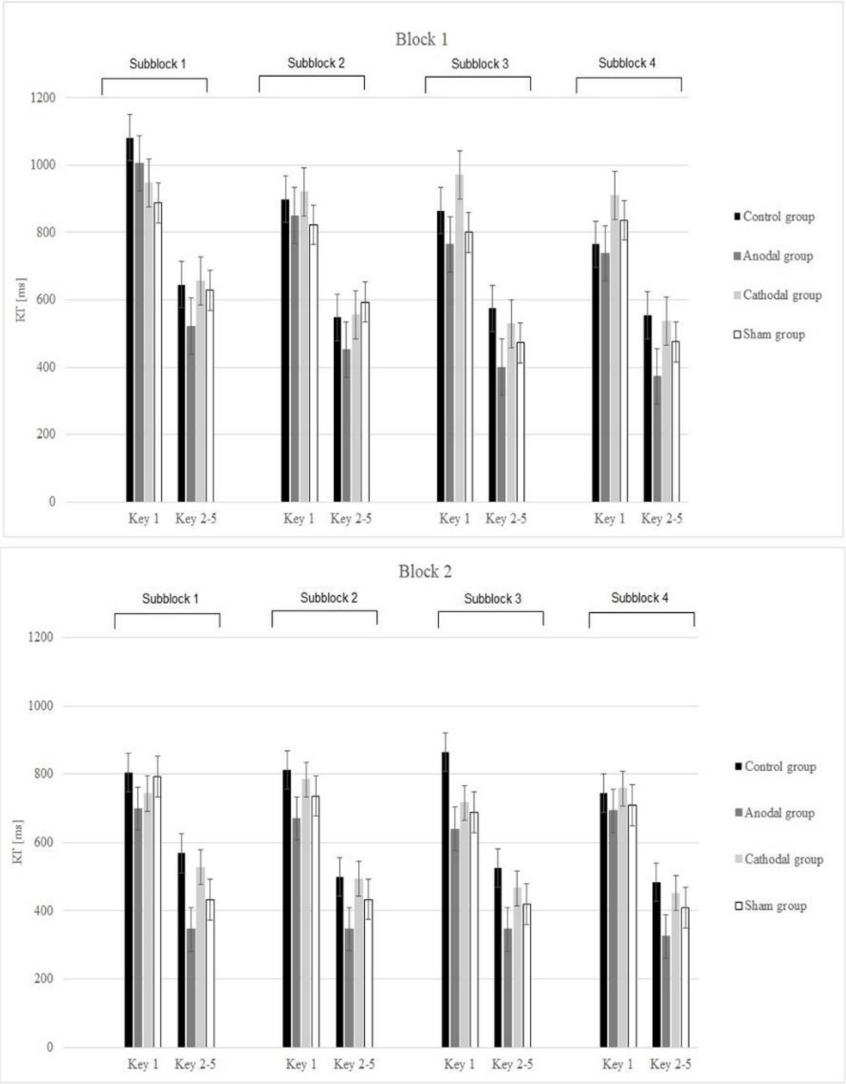

Figure 3. Response times (RTs) in milliseconds (ms) from two separate blocks of practice phase for all groups as a function of Key. *Error bars* represent standard errors.

PC

A repeated measures ANOVA was performed on arcsin transformed error percentages as a function of Group (4) and Subblock (4) for each block of the practice phase. In the first practice block, no significant difference in accuracy was observed between the groups, $F(3, 44) = 2.06$, $p = .12$, $\eta_p^2 = .12$ (Figure 4). A main effect of Subblock was observed, $F(3, 132) = 17.99$, $\epsilon = .89$, $p < .001$, $\eta_p^2 = .29$, (linear trend: $F(1, 44) = 49.55$, $p < .001$), indicating that response accuracy increased with practice. No significant interaction between Subblock and Group was observed, $p = .18$. In the second practice block, a significant difference in accuracy between groups was observed, $F(3, 44) = 5.87$, $p = .002$, $\eta_p^2 = .29$. Post hoc tests only revealed that participants in the anodal group responded more accurately than participants in the control group, $p = .001$. A main effect of Subblock was observed, $F(3, 132) = 12.11$, $\epsilon = .72$, $p < .001$, $\eta_p^2 = .22$, (linear trend: $F(1, 44) = 31.59$, $p < .001$; quadratic trend: $F(1, 44) = 4.68$, $p < .001$). No significant interaction between Subblock and Group was observed, $p = .11$.

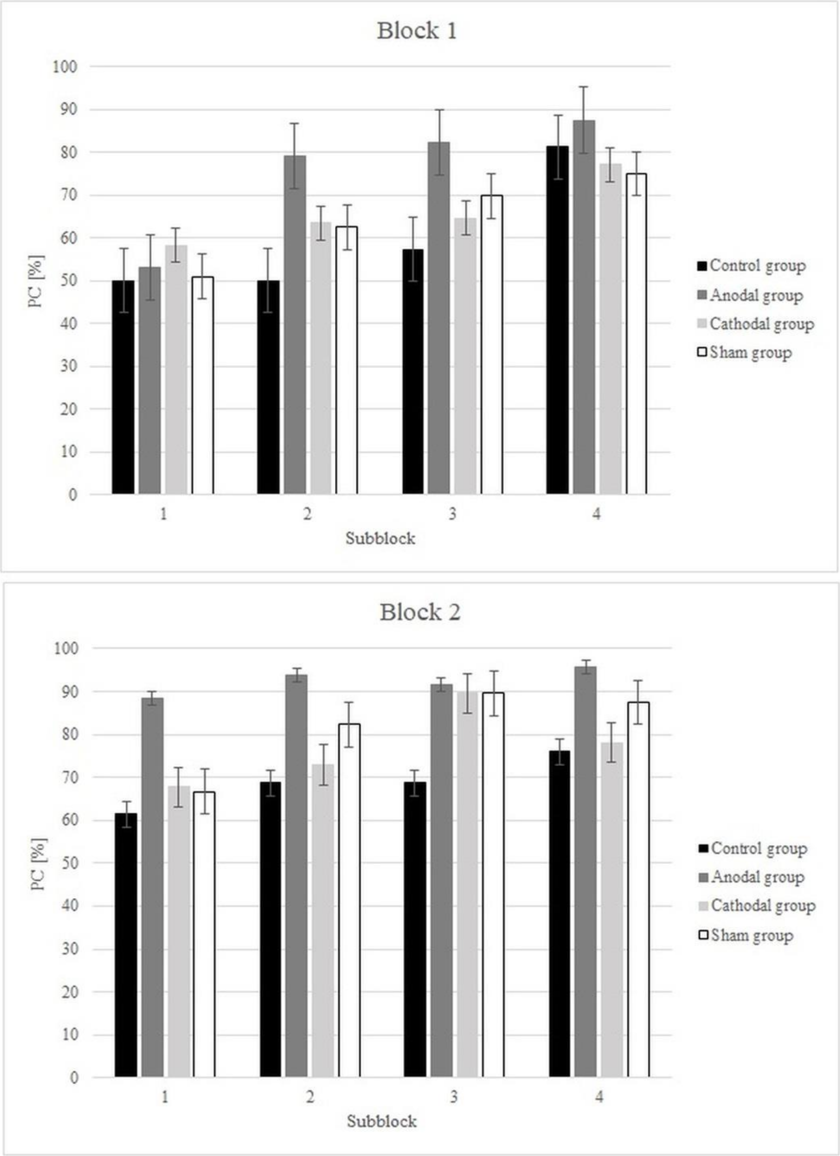

Figure 4. Percentage of correct response (PC) for each Block of the practice phase as a function of Subblock. *Error bars* represent standard errors.

4.3.2. The test phase

RT

In the test phase, the sequences that were executed, imagined, or inhibited in the practice phase now all had to be executed. Results showed significant differences in mean correct response time between the groups, $F(3, 44) = 3.24$, $p = .03$, $\eta_p^2 = .18$ (Figure 5). Post-hoc tests revealed that participants in the anodal group executed sequences faster than participants in the control group, $p < .02$. No other significant differences between groups were observed, $p > .24$. A significant difference as a function of Type of Sequence was observed, $F(3, 132) = 22.87$, $\epsilon = .83$, $p < .001$, $\eta_p^2 = .34$. Post-hoc test revealed that familiar executed sequences were executed faster than unfamiliar sequences, $p < .001$, and familiar imagined sequences were also executed faster than unfamiliar sequences, $p < .001$. No significant difference was observed between unfamiliar and familiar inhibited sequences, $p = .2$; and no significant difference was observed between familiar imagined sequences and familiar inhibited sequences, $p = .08$. Post-hoc tests also revealed that familiar executed sequences were carried out faster than familiar imagined sequences, $p < .001$, and familiar inhibited sequences, $p < .001$.

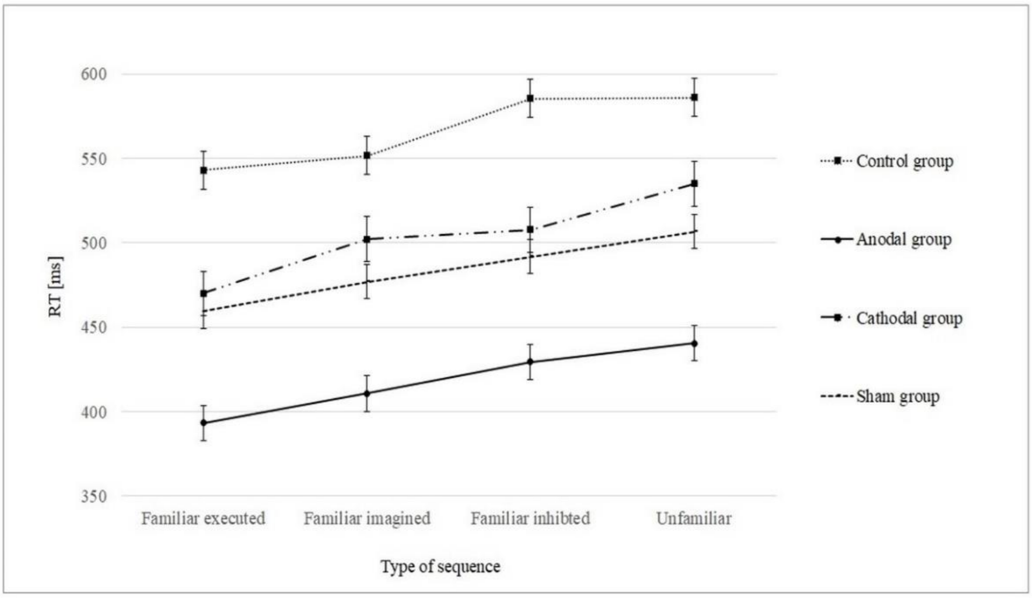

Figure 5. Mean response times (RTs) in milliseconds (ms) in the test phase for all groups as a function of Type of Sequence. *Error bars* represent standard errors.

No significant interaction between Type of Sequence and Group was observed, $p = .68$. A main effect of Key was observed, $F(4, 176) = 129.53$, $\epsilon = .5$, $p < .001$, $\eta_p^2 = .75$, but no interaction between Key and Group was observed, $p = .74$. An interaction between Type of Sequence and Key was observed, $F(12, 528) = 2.8$, $\epsilon = .59$, $p < .001$, $\eta_p^2 = .06$. Separate t-tests for the first key revealed that the time to initiate a sequence was faster for familiar executed sequences as compared with familiar imagined, $t(47) = 2.77$, $p = .008$; familiar inhibited, $t(47) = 4.99$, $p < .001$; and unfamiliar sequences, $t(47) = 4.14$, $p < .001$. The first key press was also faster for familiar imagined sequences than for familiar inhibited sequences, $t(47) = 3.13$, $p = .003$; and unfamiliar sequences, $t(47) = 2.76$, $p = .008$. No significant difference in initiation was observed between familiar inhibited and unfamiliar sequences, $t(47) = .36$, $p = .07$. For the average of 2-5 keys, results revealed faster execution for familiar executed sequences as compared with familiar imagined, $t(47) = 3.7$, $p = .001$; familiar inhibited, $t(47) = 5.02$, $p < .001$; and unfamiliar sequences, $t(47) = 5.25$, $p < .001$. No significant difference in execution was observed between familiar imagined and familiar inhibited sequences, $t(47) = 1.03$, $p = .03$. Results revealed slower execution in the case of unfamiliar sequences relative to the familiar imagined, $t(47) = 3.19$, $p < .003$; and familiar inhibited sequences, $t(47) = 2.14$, $p < .04$.

PC

In the test phase, a similar repeated measures ANOVA was performed on arcsin transformed PCs as a function of Group (4), and Type of Sequence (4). A significant difference in accuracy was observed between groups, $F(3, 44) = 3.49$, $p = .02$, $\eta_p^2 = .19$ (Figure 6). Post hoc tests revealed that the anodal group made less errors than the control group, $p = .02$. No other significant differences were observed between groups, $p > .05$. A main effect of Type of Sequence was observed, $F(3, 132) = 9.17$, $\epsilon = .7$, $p < .001$, $\eta_p^2 = .17$. Post hoc tests only revealed that unfamiliar sequences were executed less accurately than familiar executed, familiar imagined, and familiar inhibited sequences, $p < .001$. Inspection of Figure 6 clearly shows that the lowest number of correct responses were observed in all groups in the case of unfamiliar sequences (not practiced before). No significant interaction between Type of Sequence and Group was observed, $p = .98$.

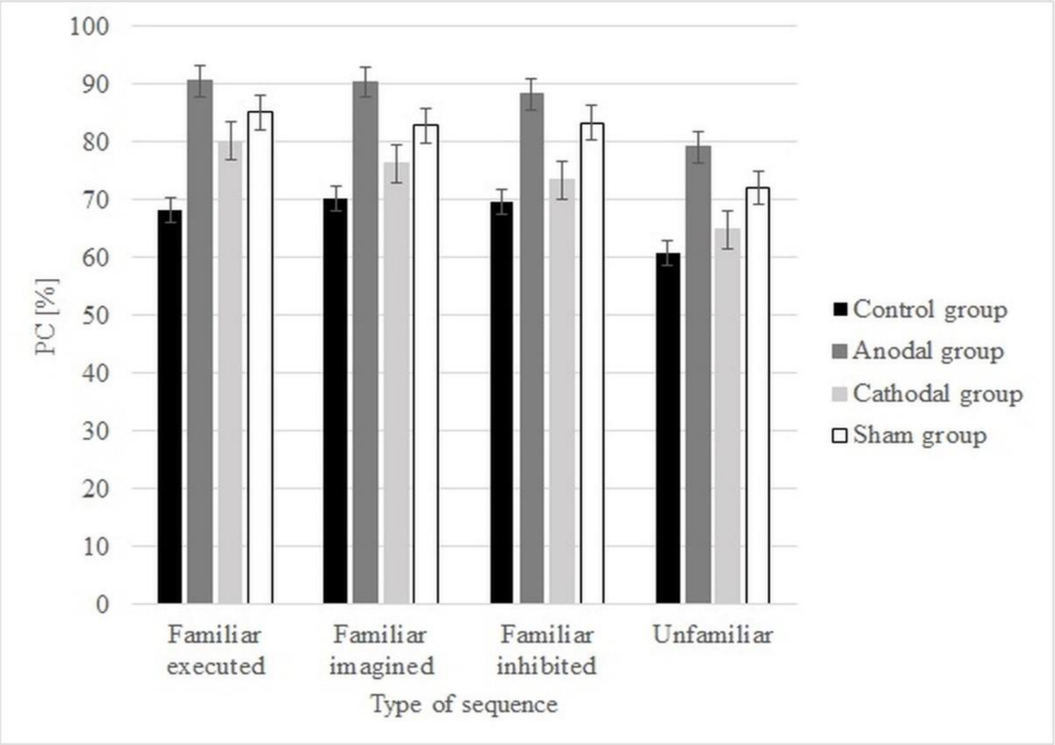

Figure 6. Percentage of correct response (PC) in percentages (%) in the test phase for each group as a function of Type of Sequence. *Error bars* represent standard errors.

4.3.3. EMG

Figure 7 shows the EMG signal related to the non-dominant hand while performing the required motor task in the practice phase (i.e., during motor execution, motor imagery, and motor inhibition). First, we compared EMG as a function of Task; secondly, we focused on the comparison of motor imagery and motor inhibition to establish whether participant really did not flex their muscles during motor imagery. Figure 7 shows that in all groups the EMG signal was larger for executed sequences than for imagined and inhibited sequences. The EMG signal did not differ between groups, $F(3, 42) = 1.12$, $p = .35$. A significant difference was observed as a function of Task, $F(2, 84) = 123.25$, $\epsilon = .56$, $p < .001$, $\eta_p^2 = .75$. Separate *t*-tests revealed that the EMG signal during motor execution was larger than during motor imagery, $t(47) = 7.6$, $p < .001$; the EMG signal was also larger in the case of motor execution as compared with motor inhibition, $t(47) = 7.8$, $p < .001$. We were especially interested whether there was a significant difference between motor imagery and motor inhibition. The reason is because in the case of motor imagery participants were asked only to imagine performing a motor sequence, as a consequence they could unintentionally induce some muscles tension. Results revealed no difference in EMG activity during motor imagery and motor inhibition, *t*(45) = 1.75, *p* = .09. In conclusion, the results of our EMG analyses revealed that participants in all groups moved their fingers mainly in the case of motor execution and they did not flex their muscles during motor imagery and motor inhibition.

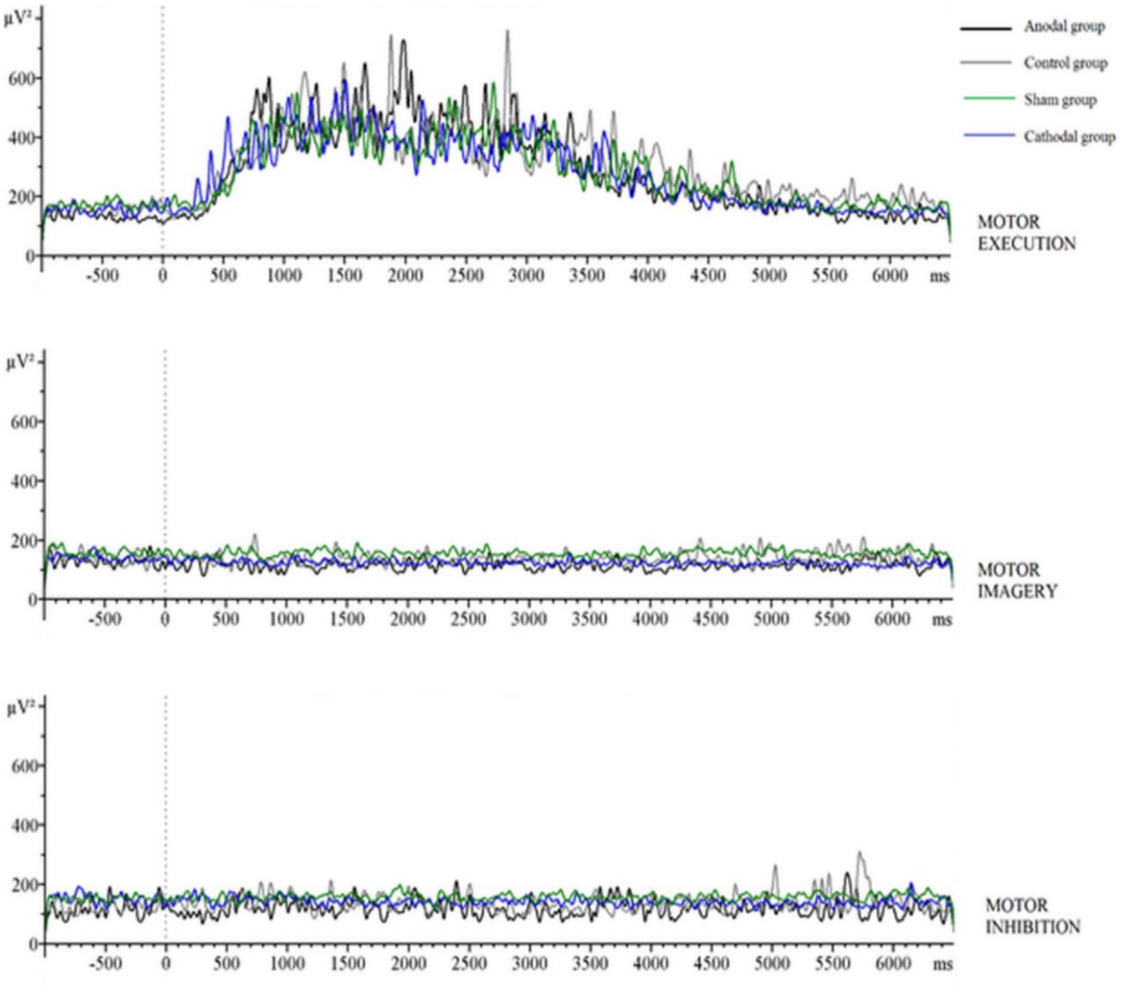

Figure 7. Outcome of the wavelet analysis performed on the raw EMG signal measured from the electrodes attached to the non-dominant hand in the practice phase. The grand averages are presented for all groups, for motor execution, motor imagery and motor inhibition -1000 ms before the Go/NoGo signal (0 ms) to 6000 ms.

4.4. Discussion

In the present study, we wanted to establish the influence of tDCS on learning a fine sequential hand motor skill by examining both non-specific learning effects and sequence-specific learning effects. Furthermore, we wanted to investigate whether learning by motor imagery combined with tDCS might increase sequence-specific learning effects. In order to examine this, we stimulated the primary motor cortex of the non-dominant hand to be used in the Go/NoGo DSP task, which allows to estimate both non-specific and sequence-specific learning effects. As an extension relative to previous studies (Cuypers, et al., 2013; Foerster, et al., 2013; Saimpont, et al., 2016), we involved four groups of participants: an anodal, cathodal, sham stimulation group, and a control group (without stimulation). First, we will concentrate on non-specific learning effects of tDCS by comparing learning effects between groups. Secondly, we will focus on sequence-specific learning effects of tDCS on motor learning by comparing familiar sequences with unfamiliar sequences between groups. Finally, we will answer the question whether learning a fine motor skill with motor imagery is boosted by tDCS.

First, we questioned to what extent tDCS affects the learning of a fine motor skill. In the final test phase a significant difference in mean RTs was observed only between the anodal group and the control group, i.e., participants in the anodal group executed sequences significantly faster than the control group. Comparable effects were observed for accuracy, i.e., results showed that participants in the anodal group made less errors relative to the control group. Besides the fact that all groups were faster and more accurate with practice (indicating non-specific learning effects), we revealed that tDCS increased motor performance only when comparing the results of the anodal group with the control group. In other words, our results showed that anodal tDCS affects non-specific learning effects, in line with previous studies (Cuypers, et al., 2013; Ciechanski & Kirton, 2016). These results are also consistent with findings reported by Antal et al. (2004). They observed improved motor performance on a visuo-motor task after anodal, but not after cathodal stimulation, although this was only observed in the initial learning phase. Antal et al. (2004) explained these findings by the improvement of perceptual-motor performance, which can be related with improved visual perception or cognitive processing (see: (Antal, Nitsche, Kruse, Hoffmann, & Paulus, 2004). In our study, more long-lasting effects of anodal stimulation were observed, as group differences were already visible in the practice phase, and remained present in the test phase, which may be due to different task procedure. Nevertheless, our results also indicate that anodal stimulation affects non-specific learning effects which can be explained by the increased familiarity with the task procedure instead of learning of a particular motor sequence (Sobierajewicz J. , Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). Our results are also consistent with the findings of earlier studies that showed increased learning effects with anodal tDCS (Nitsche, et al., 2003; Reis, et al., 2009; Stagg, et al., 2011), but only when anodal tDCS was applied *during* the required motor task. Stagg et al. (2011) demonstrated that the effects of tDCS are time-dependent, i.e. anodal tDCS applied during the task increased motor learning while either anodal or cathodal tDCS applied *before* the motor task diminished learning (as compared with sham stimulation). Based on results of Stagg et al. (2011) it may be hypothesized that application of tDCS before the practice phase in our experiment could have led to diminished learning. Thus, the moment of applying tDCS seems to have a crucial role in learning effects of brain stimulation, this seems also quite relevant for neurorehabilitation practices that aim to help patients with for example stroke to recover their motor functions.

In the current study, we also included a control group, which may allow to examine whether tDCS effects are possibly due to a placebo effect. Similar results for the sham stimulation and the control group would indicate that a placebo effect for sham stimulation is unlikely. Although no difference between sham stimulation and the control group was observed, we also did not observe any difference in motor performance (i.e., motor execution of a sequence) between sham stimulation, anodal stimulation, and cathodal stimulation. Our results revealed that anodal stimulation leads to a significant improvement of motor performance but only when compared with the control group. In contrast to previous studies (Kang & Paik, 2011; Cuypers, et al., 2013; Kidgell, Goodwill, Frazer, & Daly, 2013), we did not observe a significant difference between the anodal group and the sham group. These results indicate that we cannot exclude the possibility that participants improved performance because they were stimulated (either real or sham stimulation) which may reflect a placebo effect (Aslaksen, Vasylenko, & Fagerlund, 2014). For example, it might be the case that as participants were stimulated they became more motivated to carry out the task. In order to examine the potential benefit of tDCS due to a modulation of local excitability, one could use EEG and/or transcranial magnetic stimulation (TMS). For example, anodal tDCS above the primary motor cortex is thought to increase cortical excitability which can be observed by an increase in the hand motor evoked potential (MEP), while cathodal stimulation leads to a decrease in MEP amplitude (Nuzum, Hendy, Russell, & Teo, 2016). Another method to measure the effects of tDCS is EEG, which allows to observe the influence on spectral power and event-related desynchronization (ERD) due to tDCS (Mondini, Mangia, & Cappello, 2018). The examination of MEP or ERD can be useful to determine the efficacy of tDCS above the primary motor cortex.

Our second aim of this study refer to the influence of tDCS on sequence-specific learning, which was examined by comparing familiar sequences with unfamiliar sequences between groups. Results confirmed our previous findings that familiar sequences were executed more efficiently than unfamiliar sequences (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016; Sobierajewicz J. , Przekoracka-Krawczyk, Jaśkowski, Verwey, & van der Lubbe, 2017). However, we did not observe any influence of tDCS on sequence-specific learning effects as similar effects were observed in all groups (i.e., anodal group, cathodal group, sham group, and control group). It can be argued that the number of participants was not enough to demonstrate the effects of stimulation on sequence-learning. Thus, a potential limitation of this study may arise from the fact that the statistical power was too low. Nevertheless, our results showed the influence of tDCS on non-specific learning effects. Therefore, we think that tDCS has an influence on non-specific learning but not on sequence-specific learning.

The third aim of this study was to examine and better understand the effects of the combination of motor imagery with tDCS. We were interested whether learning a fine motor skill with motor imagery may further increase due to tDCS. Although results showed that anodal tDCS improved motor performance, we revealed that it does not increase the influence of motor imagery on sequence learning, neither in terms of speed nor accuracy. As mentioned-above, we observed that motor imagery itself influenced sequence-specific learning, but this effect was present in all groups. These results indicate that tDCS did not reinforce the effect of motor imagery on learning a sequential motor skill. For a comparison with studies of Saimpont et al. (2016) and Foerster et al. (2013), only non-specific learning effects will be discussed as sequence-specific learning effects were not examined in these studies. In contrast to the study of Saimpont et al. (2016), our results did not reveal that tDCS combined with motor imagery improved the accuracy of motor responses. In their study, the improvement of accuracy has been observed after anodal stimulation combined with motor imagery relative to motor imagery combined with sham stimulation and tDCS alone. On the other hand, Foerster et al. (2013) revealed the improvement of motor performance after anodal tDCS combined with motor imagery, but no effect of training with motor imagery alone was observed. It should be underlined that in our study and in the study of Foerster et al. (2013) and Saimpont et al. (2016) the position of the electrodes, execution of the required task only with the non-dominant hand and the intensity of the current were the same (only the duration of tDCS in our study lasted 15 minutes, while in their studies stimulation lasted 13 minutes). Therefore, results from the above-mentioned studies and our study suggest that the effect of tDCS combined with motor imagery depends more on the amount and quality of motor imagery rather than the duration or intensity of brain stimulation. It should also be noted that individual neuroanatomy might have relevant role in determining the behavioral effects of stimulation. Variability in the efficacy of tDCS may be caused by a variation in electrically generated fields, which can depend on both experimental parameters (e.g., intensity of the current, stimulation duration, etc.) and individual anatomic features of the head and the brain. In the study of Rich et al. (2017), it was revealed that individual variability in brain somatic organization may influence surface scalp localization. In particular, reorganization of the primary motor cortex may occur due to neurologic injury, e.g., after stroke, (Rich, et al., 2017). However, in our study only healthy subjects (without any neurological diseases) were examined, therefore the 10/20 EEG coordinate system (based on the anatomical relationship of skull dimensions to underlying brain anatomy) used in our experiment seems justified. Nevertheless, when examining patients after an injury like a stroke, one should be more cautious in determining the proper stimulation area.

In our analyses, we could also observe the role of motor preparation during learning a motor skill. For sequences that were inhibited in the practice phase, we observed that participants in the test phase became as accurate but not as fast relative to familiar executed sequences. This can be explained by the presence of motor preparation before the NoGo signal, which enables to mentally practice a sequence. Based on the results from the current study, it may be argued that mere motor preparation improves accuracy, but does not affect the speed of motor performance. This result partially corresponds with our previous study (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016), in which we showed that motor preparation may be sufficient to acquire a motor skill. In this study, we showed that the requirement to imagine a motor sequence was not necessary to demonstrate a learning effect (see: (Sobierajewicz, Szarkiewicz, Przekoracka-Krawczyk, Jaśkowski, & van der Lubbe, 2016)). Hence, it can be concluded that not only motor imagery, but also motor preparation may be beneficial for the learning of a fine motor skill (especially with regard to its accuracy), (see also: (Van der Lubbe, Sobierajewicz, Jongsma, & Przekoracka-Krawczyk, 2017, October)).

In summary, this study showed that anodal tDCS improved both the speed and the accuracy of a motor sequence relative to a control group that received no stimulation. Importantly, tDCS did not facilitate the influence of motor imagery on sequence learning. In other words, tDCS did not boost motor performance after motor imagery training. Future studies are needed to clarify the mixed findings of tDCS, for example by determining the underlying mechanisms with the help of EEG.

References

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61*(3), 303-321.

Antal, A., Nitsche, M. A., Kruse, W., Hoffmann, K.-P., & Paulus, W. (2004). Facilitation of visuo-motor learning by transcranial direct current stimulation of the motor and extrastriate visual areas in humans. *European Journal of Neuroscience, 19*(10), 2888-2892.

Aslaksen, P. M., Vasylenko, O., & Fagerlund, J. A. (2014). The effect of transcranial direct current stimulation on experimentally induced heat pain. *Experimental Brain Research, 232*(6), 1865–1873.

Bindman, L. J., Lippold, O. C., & Redfearn, J. W. (1964). The action of brief polarizing currents on the cerebral cortex of the rat (1) during current flow and (2) in the production of long-lasting after-effects. *The Journal of Physiology, 172*(3), 369–382.

Buch, E. R., Santarnecchi, E., Antal, A., Born, J., Celnik, P. A., Classen, J., . . . , et al. (2017). Effects of tDCS on motor learning and memory formation: A consensus and critical position paper. *Clinical Neurophysiology, 128*(4), 589-603.

Carillo-de-la-Peña, M., Galdo-Álvarez, S., & Lastra-Barreira, C. (2008). Equivalent is not equal: Primary motor cortex (MI) activation during motor imagery and execution of sequential movements. *Brain Research, 1226*, 134-143.

Cho, H., Kim, J., & Lee, G. (2013). Effects of motor imagery training on balance and gait abilities in post-stroke patients: a randomized controlled trial. *Clinical Rehabilitation, 27*(8), 675-680.

Ciechanski, P., & Kirton, A. (2016). Transcranial Direct-Current Stimulation Can Enhance Motor Learning in Children. *Cerebral Cortex, 27*(5), 2758–2767.

Cuypers, K., Leenus, D., van den Berg, F. E., Nitsche, M. A., Thijs, H., Wenderoth, N., & Meesen, R. L. (2013). Is Motor Learning Mediated by tDCS Intensity? *PLoS ONE, 8*(6):e67344.

De Kleine, E., & Van der Lubbe, R. H. (2011). Decreased load on general motor preparation and visual-working memory while preparing familiar as compared to unfamiliar movement sequences. *Brain and Cognition, 75*(2), 126-134.

Debarnot, U., Clerget, E., & Olivier, E. (2011). Role of the primary motor cortex in the early boost in performance following mental imagery training. *PLoS ONE, 6*(10):e26717.

Driskell, J. E., Copper, C., & Moran, A. (1994). Does mental practice enhance performance? *Journal of Applied Psychology, 79,* 481-492.

Foerster, Á., Rocha, S., Wiesiolek, C., Chagas, A. P., Machado, G., Silva, E., . . . Monte-Silva, K. (2013). Site-specific effects of mental practice combined with transcranial direct current stimulation on motor learning. *European Journal of Neuroscience, 37*(5), 786-794.

Gentili, R., Papaxanthis, C., & Pozzo, T. (2006). Improvement and generalization of arm motor performance through motor imagery practice. *Neuroscience, 137*(3), 761-772.

Jackson, P. L., Lafleur, M. F., Malouin, F., & Richards, C. (2001). Potential Role of Mental Practice Using Motor Imagery in Neurologic Rehabilitation. *Archives of Physical Medicine and Rehabilitation, 82*(8), 1133-1141.

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage, 14,* 103-109.

Kaminski, E., Hoff, M., Sehm, B., Taubert, M., Conde, V., Steele, C. J., . . . Rogert, P. (2013). Effect of transcranial direct current stimulation (tDCS) during complex whole body motor skill learning. *Neuroscience Letters, 552*, 76– 80.

Kang, E. K., & Paik, N.-J. (2011). Effect of a tDCS electrode montage on implicit motor sequence learning in healthy subjects. *Experimental & Translational Stroke Medicine, 3,* 4.

Keele, S. W., Ivry, R., Mayr, U., Hazeltine, E., & Heuer, H. (2003). The Cognitive and Neural Architecture of Sequence Representation. *Psychological Review, 110*(2), 316–339.

Kidgell, D. J., Goodwill, A. M., Frazer, A. K., & Daly, R. M. (2013). Induction of cortical plasticity and improved motor performance following unilateral and bilateral transcranial direct current stimulation of the primary motor cortex. *BMC Neuroscience, 14*, 64.

Lebon, F., Collet, C., & Guillot, A. (2010). Benefits of motor imagery training on muscle strength. *Journal of Strength and Conditioning Research, 24*(6), 1680-1687.

Maillet, A., Fraix, V., Thobois, S., Derost, P., Bloem, B., Pollak, P., & Debû, B. (2013). Kinesthetic imagery of gait in advanced Parkinson`s disease. *EDP Sciences, 82*, 115-128.

Malenka, R., & Nicoll, R. (1999). Long-term potentation - a decade of progress? *Science, 285*, 1870-1874.

Miyaguchi, S., Onishi, H., Kojima, S., Sugawara, K., Tsubaki, A., Kirimoto, H., . . . Yamamoto, N. (2013). Corticomotor excitability induced by anodal transcranial direct current stimulation with and without non-exhaustive movement. *Brain Research, 1529*, 83-91.

Mondini, V., Mangia, A. L., & Cappello, A. (2018). Single-session tDCS over the dominant hemisphere affects contralateral spectral EEG power, but does not enhance neurofeedback-guided event-related desynchronization of the non-dominant hemisphere’s sensorimotor rhythm. *PLoS ONE, 13*(3): e0193004.

Nitsche, M. A., & Paulus, W. (2001). Sustained excitability elevations induced by transcranial DC motor cortex stimulation in humans. *Neurology, 57*(10), 1899-1901.

Nitsche, M. A., Nitsche, M. S., Klein, C. C., Tergau, F., Rothwell, J. C., & Paulus, W. (2003). Level of action of cathodal DC polarisation induced inhibition of the human motor cortex. *Clinical Neurophysiology, 114*(4), 600–604.

Nitsche, M., & Paulus, W. (2000). Excitability changes induced in the human motor cortex by weak transcranial direct current stimulation. *Journal of Physiology, 527*, 633-639.

Nitsche, M., Schauenburg, A., Lang, N., Liebetanz, D., Exner, C., & Paulus, W. (2003). Facilitation of implicit motor learning by weak transcranial direct current stimulation of the primary motor cortex in the human. *Journal of Cognitive Neuroscience, 15*(4), 619–626.

Nuzum, N. D., Hendy, A. M., Russell, A. P., & Teo, W.-P. (2016). Measures to Predict The Individual Variability of Corticospinal Responses Following Transcranial Direct Current Stimulation. *Frontiers in Human Neuroscience, 10,* 487.

Pascual-Leone, A., Nguyet, D., Cohen, L. G., Brasil-Neto, J. P., Cammarota, A., & Hallett, M. (1995). Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *Journal of Neurophysiology, 74*(3), 1037-1045.

Purpura, D. P., & McMurtry, J. G. (1965). Intracellular activities and evoked potential changes during polarization of motor cortex. *Journal of Neurophysiology, 28,* 166-185.

Quartarone, A., Morgante, F., Bagnato, S., Rizzo, V., Sant`angelo, A., Aiello, E., . . . Girlanda, P. (2004). Long lasting effects of transcranial direct current stimulation on motor imagery. *NeuroReport, 15*(8), 1287-1291.

Reis, J., Schambra, H. M., Cohen, L. G., Buch, E. R., Fritsch, B., Zarahn, E., … Krakauer, J. W. (2009). Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation. *Proceedings of the National Academy of Sciences of the United States of America, 106*(5), 1590–1595.

Rich, T. L., Menk, J. S., Rudser, K. D., Chen, M., Meekins, G. D., Peña, E., … Gillick, B. T. (2017). Determining Electrode Placement for Transcranial Direct Current Stimulation: A Comparison of EEG- Versus TMS-Guided Methods. *Clinical EEG and Neuroscience, 48*(6), 367–375.

Ruitenberg, M. F., De Kleine, E., Van der Lubbe, R. H., Verwey, W. B., & Abrahamse, E. L. (2011). Context-dependent motor skill and the role of practice. *Psychological Research, 76*(6), 812-820.

Saimpont, A., Mercier, C., Malouin, F., Guillot, A., Collet, C., Doyon, J., & Jackson, P. L. (2016). Anodal transcranial direct current stimulation enhances the effects of motor imagery training in a finger tapping task. *European Journal of Neuroscience, 43*(1), 113-119.

Sobierajewicz, J., Przekoracka-Krawczyk, A., Jaśkowski, W., & van der Lubbe, R. H. (2017). How effector-specific is the effect of learning by motor execution and motor imagery? *Experimental Brain Research, 235*(12), 3757-3769.

Sobierajewicz, J., Przekoracka-Krawczyk, Jaśkowski, W., Verwey, W. B., & van der Lubbe, R. (2017). The influence of motor imagery on the learning of a sequential motor skill. *Experimental Brain Research, 235*(1), 305-320.

Sobierajewicz, J., Szarkiewicz, S., Przekoracka-Krawczyk, A., Jaśkowski, W., & van der Lubbe, R. (2016). To what extent can motor imagery replace motor execution while learning a fine motor skill? *Advances in Coginitive Psychology, 12*(4), 179-192.

Stagg, C. J., Jayaram, G., Pastor, D., Kincses, Z. T., Matthews, P. M., & Johansen-Berg, H. (2011). Polarity and timing-dependent effects of transcranial direct current stimulation in explicit motor learning. *Neuropsychologia, 49*(5), 800–804.

Van der Lubbe, R., Sobierajewicz, J., Jongsma, M., & Przekoracka-Krawczyk, A. (2017, October). To what extent does motor imagery resemble motor preparation? *Psychophysiology, 54.* Poster session presented at the meeting of The Society for Psychophysiological Research, Vienna, Austria.

Verwey, W. B., & Wright, D. L. (2014). Learning a keying sequence you never executed: Evidence for independent associative and motor chunk learning. *Acta Psychologica*, *151*, 24-31.

5. SUMMARY AND CONCLUSIONS

Motor imagery can be considered as a cognitive process during which motor actions are internally simulated without producing an overt action. Several studies revealed that motor imagery can help with the acquisition of motor skills when people are not or less well able to physically practice these skills, for example, due to a disease (e.g., stroke, cerebral palsy, Parkinson`s disease etc.). Additionally, research showed that motor imagery may enhance motor skills, for example for musicians or athletes. Discovery that motor imagery involves similar neural pathways as those involved in actual movement suggest that motor imagery may also influence learning a fine motor skill. However, the effects of motor learning by motor imagery appear less strong than the effects of motor learning by motor execution. The aim of this thesis was to increase our understanding of what motor imagery actually is, and to establish whether a fine sequential hand motor skill can be acquired with the help of motor imagery. Below, the contributions of *Chapters 2 – 4* to our understanding of the role of motor imagery in learning sequential fine motor skills are summarized.

In order to go to the conclusions from all chapters, it should be reminded that the Go/NoGo discrete sequence production task was used in all research. This task allows to examine the effectiveness of motor imagery and motor execution during learning of a sequential motor skill. In all chapters two phases were distinguished to establish the learning effects. First, the practice phase (the training phase is used interchangeably) was used, in which participants carried out the required task, either by executing a sequence, by using motor imagery, or by inhibiting the execution of a sequence. After the practice phase, the test phase was carried out within which all sequences were physically executed. This procedure enabled to compare behavioral learning effects (i.e., response times and accuracy) between motor execution, motor imagery, and motor inhibition. Moreover, in the practice phase (i.e., during motor execution, motor imagery, and motor inhibition) EMG was recorded in order to confirm that a specific effect is really due to motor imagery instead of any overt movements or peripheral (muscle) activation. In other words, recording of EMG enabled to control whether only required movements (i.e., button presses) were carried out during motor execution.

This dissertation attempted to clarify whether learning a sequential motor skill with motor imagery induces sequence-learning effects. It is crucial to distinguish between sequence-a-specific and sequence-specific learning effects as sequence-a-specific learning involves the development of a sequencing skill in general while sequence-specific learning concerns the learning of a particular sequence, which was detailed in *Chapter 1*. In order to establish whether motor imagery induces sequence-specific learning effects, familiar practiced sequences and familiar imagined sequences with new (unfamiliar) sequences were compared in the final test phase (in each experiment). In all chapters (2-4) it was investigated whether motor execution and motor imagery during learning might induce sequence-specific learning. Results revealed that motor imagery indeed induces sequence-specific learning of a fine motor skill, because participants responded faster and more accurately while executing familiar imagined and familiar executed sequences relative to unfamiliar sequences in all studies.

In *Chapter 2*, the question which was addressed concerned how effector-specific the effect of learning a sequential fine motor skill is. It has been argued that motor sequences are processed at two different levels: cognitive and motor, which are related with the notion that motor skill learning is initially effector-independent (when spatial representation of a motor sequence develops at the cognitive level), while with practice it becomes effector-dependent (when motor representation of a motor sequence develops at the motor level). In this study, it was examined how motor-specific the effect of motor execution and motor imagery on motor learning is by varying the execution mode during a practice and a test phase. Results demonstrated that motor skill learning with motor execution and motor imagery is effector-independent. In both cases of learning (i.e., either with motor execution or motor imagery), results suggested the development of spatio-temporal representations at a cognitive level instead of a motor level. These results indicate that learning of a sequential motor skill by motor imagery is not muscle specific; in other words, it is effector-independent. However, it should be noticed that the number of practiced sequences (more long-term practice) and the involved effector (i.e., hand, arm, leg etc.) could play a relevant role in the development of the effector-dependent component. Nevertheless, our results (showing that both motor execution and motor imagery used during learning a motor skill are effector-independent) are relevant to be implemented in the case of therapy, for example for patients after stroke. Even if a patient is unable to perform particular movement due to paresis, he can imagine doing it, which is crucial to develop a spatio-temporal pattern of a particular sequence.

In *Chapter 3*, the influence of expertise on learning sequential motor skill with motor imagery was examined. Assuming that musicians have to train a fine motor skill significantly more often than novices, it was examined whether learning such a skill would be more efficient for musicians than for non-musicians due to extensive practice. It has been proposed that a spatial representation of a motor sequence will develop among novices, whereas both spatial and motor representations can be developed among musicians due to an increased expertise. Behavioral results showed that learning a fine motor skill was more effective for professional musicians as compared with non-musicians. Our results from the test phase showed better sequence-a-specific learning effects (i.e., faster response times and increased accuracy) for musicians than for non-musicians. It has been shown that non-musicians benefit more from physical execution while learning a required motor sequence, whereas sequence-specific learning effects due to learning with motor imagery were very similar for musicians and non-musicians. Additionally, it has been questioned whether increased expertise may be reflected in electrophysiological changes in brain activation above cortical brain areas while imaging and executing a movement relative to non-musicians. EEG analyses revealed similar lateralized activity during learning a motor skill for both groups. In other words, it has been demonstrated that music experience did not influence electrophysiological brain activation above motor brain areas during learning a fine motor skill. It should be underlined that the EEG signal was examined only above the primary motor area, thus the possibility that activation in other brain areas (e.g., the prefrontal cortex) depends on increased expertise should not be ruled out.

Based on the notion that previous studies revealed that tDCS and motor imagery independently affect motor learning, the main aim of the *Chapter 4* was to investigate whether learning a fine motor skill with motor execution and motor imagery combined with tDCS would influence the sequence-learning effects. Four group of participants were involved in this study: anodal, cathodal, sham, and control group. Results showed that the anodal tDCS improved both the speed and the accuracy of a motor sequence relative only to the control group (who received no stimulation at all). The effects of anodal tDCS were already developing during the practice phase, which is relevant in the context of timing of tDCS (whether it should be applied during the practice or before the practice). Importantly, no significant difference in motor performance was observed in the case of cathodal or sham stimulation as compared with control group, suggesting that a placebo effect cannot be ruled out. Moreover, it has been revealed that tDCS does not facilitate the influence of motor imagery on sequence learning. Hence, our findings showed that tDCS and motor imagery independently affect motor learning, but tDCS does not increase the influence of motor imagery on sequence learning. However, the efficacy of tDCS during learning a motor skill may depend on several factors, e.g., experimental parameters (intensity of the current, stimulation duration, etc.), individual anatomic features of the head and the stimulated brain area. In our study, we focused on stimulation of the primary motor cortex. Even though, the primary motor cortex participates in motor skill learning, other brain areas (such as: the prefrontal cortex, the supplementary motor area, the premotor cortex) may be more relevant in acquiring new motor skill the primary motor cortex.

Overall, the results reported in this dissertation indicate that motor imagery has a beneficial effect on the learning a fine sequential motor skill. All studies showed that motor imagery induces sequence-specific learning effects. Based on this thesis, the following major outcomes were identified:

- Both motor imagery and motor execution induce sequence-specific learning of a fine motor skill.
- Not only motor imagery, but also mere motor preparation seems to be sufficient to learn a motor skill.
- Motor skill learning with motor execution and motor imagery is in both cases effector-independent, indicating that learning effects can be generalized to an untrained effector system.
- Motor skill learning with motor execution and motor imagery is related to the development of spatial representation of a motor sequence rather than to the development of a specific motor pattern.
- Using a different execution mode during learning a sequential motor skill has an influence on particular processing phases of sequence skill, i.e., on the initiation phase which is related with the selection and preparation of a sequence.
- Learning a fine motor skill depends on increased expertise only in the case of learning with motor execution.
- Learning a fine motor skill with motor imagery appears to be independent of increased expertise.
- A-specific motor learning was more efficient for musicians as compared with non-musicians, whereas similar sequence-specific learning effects were observed in both groups.

- A comparison of electrophysiological activation during learning a fine motor skill between professional musicians and non-musicians revealed similar lateralized activity in both groups.
- ERLs revealed similarities between motor imagery and motor execution as more negativity was present for these condition as compared with motor inhibition. In the case of motor inhibition, a polarity reversal was observed indicating the inhibition of activity in the contralateral motor cortex.
- tDCS affects only a-specific learning effects, but not sequence-specific learning effects.
- It has been revealed that tDCS does not facilitate the influence of motor imagery on sequence learning.
- Similar motor performance between cathodal, sham, and control group was observed, suggesting the role of a placebo effect.

The idea behind this thesis was to provide an overview of the role of motor imagery for learning a fine hand motor skill (including the role of effector-dependent component, an increased expertise, and additional application of tDCS). Above-mentioned outcomes of this thesis increase our understanding of what motor imagery actually is. All these results have relevant consequences for therapies using mental practice, for example, for children with cerebral palsy, patients after stroke, in the case of inability of physical practice or disease, but it may also be used to enhance specific motor skills, e.g., by musicians or athletes.

This thesis does not exhaust the topic of motor imagery. Some possible ways to improve our understanding of motor imagery include (i) clarifying the specific effects of motor imagery training among professional musicians and other experts (ii) clarifying the mixed findings of tDCS, for example by determining the underlying mechanisms with the help of EEG (iii) clarifying whether learning with motor execution and motor imagery with other effectors (like the arms or legs) is also effector-independent. Further research in this area can possibly lead to a universal model that is needed for therapies using mental practice.

List of figures and tables

1. General Introduction

2. How effector-specific is the effect of learning by motor execution and motor imagery?

3. Do musicians learn a fine hand motor skill differently than non-musicians?

4. Does transcranial direct current stimulation affect the learning of a fine sequential hand motor skill with motor imagery?

Appendix

Sequences of five key presses used in the experiment:

6 structures of the sequence, 4 versions each
1-**a**, 2-**s**, 3-**d**, 4-**f**
1-**;**, 2-**l**, 3-**k**, 4-**j**

Structure 1

Version_1: Left hand: **a s f d s** (12432) Right hand: **; l j k l** (12432)
Version_2: Left hand: **s d a f d** (23143 Right hand: (23143)
Version_3: Left hand: **d f s a f** (34214) Right hand: (34214)
Version_4: Left hand: **f a d s a** (41321) Right hand: (41321)

Structure 2

Version_1: Left hand: **a d f s d** (13423) Right hand: (13423)
Version_2: Left hand: (24134) Right hand: (24134)
Version_3: Left hand: (31241) Right hand: (31241)
Version_4: Left hand: (42312) Right hand: (42312)

Structure 3

Version_1: Left hand: **a f s a d** (14213) Right hand: (14213)
Version_2: Left hand: (21324) Right hand: (21324)
Version_3: Left hand: (32431) Right hand: (32431)
Version_4: Left hand: (43142 Right hand: (43142)

Structure 4

Version_1: Left hand: **a d s f a** (13241) Right hand: (13241)
Version_2: Left hand: (24312) Right hand: (24312)
Version_3: Left hand: (31423) Right hand: (31423)
Version_4: Left hand: (42134) Right hand: (42134)

Structure 5

Version_1: Left hand: **a f d a s** (14312) Right hand: (14312)
Version_2: Left hand: (21423) Right hand: (21423)
Version_3: Left hand: (32134) Right hand: (32134)
Version_4: Left hand: (43241) Right hand: (43241)

Structure 6

Version_1: Left hand: **a f d a s** (21431) Right hand: (21431)
Version_2: Left hand: (32142) Right hand: (32142)
Version_3: Left hand: (43213) Right hand: (43213)
Version_4: Left hand: (14324) Right hand: (14324)