

Time matters
**The effect of time delays before and after goal directed
reaching in visuomotor adaptation**

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Abstract

Through movement, we as humans can interact with our environment. Every movement takes place in a certain temporal context, because the right movement at the wrong time or the right movement coordinated differently in time can lead to a completely different, possibly wrong result. But not only the timing of the individual motor commands is important, also differences in the available time for the neuronal processes underlying the movement, such as movement planning or evaluation, can have an enormous influence. Time itself is often one of the most important variables in behavioral experiments, but also one of the most difficult ones to control.

Thematically, this thesis focuses on the separation of adaptation into an explicit and an implicit component, and how through the manipulation of different time intervals in visuomotor rotation tasks, these can influence computational principles of visuomotor adaptation. First of, drawing on the example of the incomplete asymptote of adaptation, a phenomenon that shows that participants in such trials compensate for perturbation but usually leave a substantial residual error. It has been shown that this residual error is magnified when the time available for planning and preparing the movement is artificially reduced. This thesis shows that prolonging preparation time affects the asymptote in a similar way and can be the solution to overcoming residual errors. Furthermore, some studies have been able to show that a time delay of movement feedback leads to explicit processes becoming prevalent. Under this premise, this thesis investigated the phenomenon of temporal discounting of reward and showed that the explicit component can in fact overcome discounting. As most of the studies use some form of direct methods to measure for the explicit and implicit participation of adaptation, last but not least, this thesis attempted to use EEG, more specifically an event related potential, the feedback related negativity, as a proxy for mapping explicit and implicit processes at the neuronal level.

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List of Abbreviations

ACC	anterior cingulate cortex
AC/DC	alternating current/direct current
Ag	silver
AgCL	silverchlorid
ANOVA	analysis of variance
ASR	artifact subspace reduction
BF	Bayes Factor
Ccw	counterclockwise
Cw	clockwise
CI	confidence interval
cm	centimeter
CNS	central nervous system
CRT	choice reation time
df	degrees of freedom
DT	Dual-task
e.g.	for example (“ <i>exempli gratia</i> ”)
EEG	Electroencephalography
EOG	Electroolfactography
ERP	eventrelated potential
et al.	and others (“ <i>et alii</i> ”)
fMRI	functional magnetic resonance imaging
FRN	feedback related negativity
Hz	hertz
ICA	independent component analysis
i.e.	that is to say (“ <i>id est</i> ”)
ITI	intertrial interval
k Ω	kilo ohm
M	mean
mm	millimeter
ms	milliseconds
PFC	prefrontal cortex
PMC	premotor cortex
PPC	posterior parietal cortex
r	Effect size r

RM ANOVA	repeated-measures analysis of variance
RT	reaction time
s	seconds
SD	standard deviation
SPE	sensory prediction error
ST	Single task
η^2	partial eta squared

List of Figures

Figure 1 Schematic display of the experimental setup (A), possible target presentations and movement directions (B) and overall perturbation schedule (C). Visual stimuli and the cursor were presented on the monitor screen (A). Each trial, one target was presented (B). The cursor was visually displaced according to the perturbation schedule (C). During baseline, cursor and stylus position were veridical, during adaptation, the cursor was rotated 30° clockwise relative to the stylus position. 46

Figure 2 Group averaged mean hand directions for adaptation practice blocks. Eight consecutive single trials were averaged into one trial block, resulting in 40 trial blocks for 320 single adaptation practice trials. Shaded error bands represent standard error of the mean. The dotted line at 30° illustrates perfect compensation. 52

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1. Introduction

I am the one thing in life I can control,
I am inimitable, I am an original.
I'm not falling behind or running late.
I'm not standing still, I am lying in wait.

- Odom Jr., L. (2015). Hamilton: An American Musical [MP3]. Atlantic Records

1.1. Motor learning and motor adaptation

Motor behavior is one of the core elements of what makes a human being – indeed, our diverse set of motor skills and the capacity to learn new ones, is one of our species' hallmarks. The term motor behavior includes everything under the reign of motor control, from involuntary movements like reflexes to goal-directed motor skills that are learned through extensive practice. Movement is how humans are able to interact precisely and skillfully with an ever-changing environment. But in order to keep up with this ever-changing environment, our sensorimotor system needs to be able to adjust and adapt to it and to changes within the body. This process is called motor learning. While learning in general is often defined as "[...] a permanent change in behavior due to experience" (APA Dictionary of Psychology), motor learning can be clearly distinguished from other learning processes, such as experience-dependent perceptual learning or factual rule learning that comes into play when learning to play chess or mastering the grammar of a foreign language (Krakauer et al., 2019). In this thesis, I refer to motor learning as “[...] the study of the acquisition of motor skills, the performance enhancement of learned or highly experienced motor skills or the reacquisition of skills that are difficult to perform [...]” (Magill & Anderson, 2013), to emphasize the versatility of motor learning.

A broad category within the field of motor learning is motor adaptation. Motor adaptation research focuses less on the acquisition of new motor skills, but rather on the adjustments to existing ones, when motor commands for previously acquired motor skills have to be altered. This occurs so that the movement, despite changed circumstances, results in the intended consequences, even if the first calculated commands would not have led to them. Internal changes to the body like fatigue, injuries, or inattentiveness, and also external changes like different dynamics of the environment (e.g., reaching for an object under water) are examples for why short-term adaptations to previously successful motor commands are important. These adaptations are not considered permanent changes, but temporary ones that will subside as soon as situational context allows for it (e.g., the object rises and floats on the water surface).

The example of reaching for the object below the water surface describes the phenomenon of visuomotor adaptation. Because of the refraction of light on the water surface, the position of the object to be reached for appears shifted. The same happens with the hand as soon as it dives below the surface. The water surface perturbs the visual information about position and object,

leading to an adaptation of the motor commands. This adaptation is not assumed to be a unitary process, but has been divided into two main components: the explicit and implicit components of adaptation (Bond & Taylor, 2015; Dawidowicz, Shaine, & Mawase, 2022; Hegele & Heuer, 2010; Heuer & Hegele, 2015; Mazzoni & Krakauer, 2006; McDougle, Bond, & Taylor, 2015; Schween & Hegele, 2017; Schween, Taylor, & Hegele, 2018). This dissociation originated from work on patient H.M. who suffered from anterograde amnesia, caused by a bilateral resection of his medial temporal lobe in 1952 (Corkin, 2002). His symptoms were a complete loss of long-term memory for events that happened after his surgery, impairment in declarative memory tests (Scoville & Milner, 1957) but no other significant intellectual losses, changes in personality or perceptual disorders. Furthermore, his short-term memory remained intact (Milner, Corkin, & Teuber, 1968; Scoville & Milner, 1957). When H.M. was able to consistently improve his performance on a visuomotor skill without remembering that he had done this test before, the first distinctions between procedural, the acquisition of rules and procedures (i.e., “knowing how”), and declarative learning, the acquisition of factual knowledge (i.e., “knowing that”) (Cohen & Squire, 1980), were postulated.

There is no general agreement between researchers about exact definitions for the explicit and implicit components, which leads to them being inconsistently used from study to study. This inconsistency substantially limits the comparability of findings across studies investigating processes dissociation in motor learning. A recent review has focused on this problematic circumstance (Maresch, Werner, & Donchin, 2021b): Within motor learning and adaptation research terms like aware and unaware, explicit and implicit as well as conscious and unconscious are sometimes used interchangeably without necessarily being defined beforehand. Maresch et al. (2021) argue that a stronger characterization of the phenomenology and therefore a clearer definition of the terms used would provide better comparability of research. In this thesis, I use the terms explicit and implicit and to comply with the suggested procedure and I define them in the following section.

1.2. Explicit adaptation

The explicit component of adaptation is often equated with conscious awareness of the imposed transformation. Referring to the idea of “knowing how” versus “knowing what” (Cohen & Squire, 1980), the explicit component would be aligned with “knowing what”, as it is assumed to be responsible for declarative learning and factual knowledge about the transformations that can be expressed through explicitly recalling it (Marinelli et al., 2017).

Research found that the explicit component is largely determined by a specific type of error, the “target error” (Bond & Taylor, 2015; Kim et al., 2018): The target error denotes the visual deviation of the actual action outcome from the visual target. When the movement in a visuomotor

adaptation task places the cursor at target amplitude but 15° off of the target, the target error is 15°. The influence that this type of error has on the explicit component increases the more salient the errors get (i.e. stronger explicit involvement with errors above 25°; (Bond & Taylor, 2015; Kim et al., 2018; Wolpert, Diedrichsen, & Flanagan, 2011)). Evidence suggests that the initial learning phase of a motor skill is the phase with the most and the largest movement errors (Bond & Taylor, 2017). According to the three stage-model of skill learning postulated by Fitts and Posner (Fitts & Posner, 1967), this early stage of learning is called the cognitive stage. According to Fitts' and Posner's model, the learner focuses on improving task performance by decreasing errors, a process that involves in cognitive resources, especially working memory (Anguera et al., 2010; Baddeley, 1992; Benson, Anguera, & Seidler, 2011; Seidler, Bo, & Anguera, 2012). Those cognitive resources are needed to thoroughly attend to movement cues and task characteristics, but are no longer needed with increasing automaticity as learning proceeds out of the cognitive stage (i.e., to the subsequent “associative” and then “autonomous” phases) (Fitts & Posner, 1967). Those characteristics of the explicit component go hand in hand with the Unexpected Event Hypothesis (Frensch et al., 2003) that states that large and unexpected errors in movement outcomes trigger a search for their cause along with the generation of strategies to realign intended and actual movement outcomes. This search for the cause of errors can be directly linked with the development of deliberate compensatory strategies. Strategies are widely conceived as conscious and intentional changes of movement characteristics to serve the goal of task performance improvement. Based on these assumptions, it has been previously argued that the explicit component is located in medio-frontal areas of the brain, with direct access to cognitive resources (Anguera et al., 2007; Anguera et al., 2010; Baddeley, 1992; Benson et al., 2011; Seidler et al., 2012).

1.3. Implicit adaptation

The implicit component of motor learning is often associated with terms like unconscious, unaware or automatic. It refers to procedural, non-declarative memory abilities, which include the “knowing how” (Cohen & Squire, 1980). It is therefore not linked with strategies but rather with skill formation (Marinelli et al., 2017).

Researchers have devoted themselves intensively to study the implicit component of motor adaptation (e.g., (Heuer & Hegele, 2008b; Heuer & Hegele, 2015; Heuer, Hegele, & Sülzenbrück, 2011; Izawa et al., 2008; Maxwell et al., 2001; Mazzoni & Krakauer, 2006)) and with that found that it is based on an internal forward model (Körding & Wolpert, 2004; Wolpert & Kawato, 1998). The accuracy of this model depends on it being constantly updated with new information about the body and the environment. Those studies also showed that the best error signal to train this

model is the sensory prediction error (SPE), a mismatch in the ongoing comparison of predicted and actual sensory consequences of motor commands.

A large number of studies have looked at the localization of such forward models and have agreed that they are most likely residing within the cerebellum and basal ganglia (Held, 1965; Shadmehr, Smith, & Krakauer, 2010; Wolpert et al., 2011). In contrast to the explicit component, the neural processing pathways of the implicit component do not draw on cognitive resources (Seidler & Carson, 2017; Taylor, Klemfuss, & Ivry, 2010). This alleged independence also led to the notion that a cognitively demanding secondary task should have no effect on the implicit component, while it might inhibit the explicit component (Hegele & Heuer, 2010; Mazzoni & Krakauer, 2006).

The explicit and the implicit components can not only be differentiated by their respective dependency on cognitive resources and responses to different error types, they are suggested to also work on different time scales. A study by Smith and colleagues (Smith, Ghazizadeh, & Shadmehr, 2006) revealed that at least two adaptive processes on different time scales, i.e., with different learning and retention rates, govern short-term motor adaptation. One process has a fast learning but a low retention rate, the other process has a slow learning but a higher retention rate (Smith et al., 2006). Since these two components operate on completely different but complementary time scales, an interaction or some kind of exchange must occur to produce a long-term sustainable learning behavior. A previous study has focused on the different time scales and their influence on adaptation behavior (McDougle et al., 2015). As the explicit component is associated with the early learning phase, mostly driven by large target errors, it can be transferred well to the fast-learning process. The implicit component with its association with automaticity can be equated with the slow-learning process. How long and how adaptive behavior is sustained over different durations of time becomes relevant when one wants to go deeper into the topic of savings (Coltman, Cashaback, & Gribble, 2019). Savings are defined as a much faster adaptation performance under re-exposure to a previously experienced perturbation (Huang et al., 2011; Huberdeau, Haith, & Krakauer, 2015).

1.4. Adaptation and its temporal context

In this thesis, I sought to investigate the temporal context of motor adaptation of goal directed movements drawing inspiration from two prominent computational principles of motor control: The speed accuracy trade-off and the temporal discounting of reinforcement. In the following, I describe the relevant time intervals and elaborate on how their manipulation can influence adaptation behavior.

Any form of behavior takes place in a certain temporal context (Hinneberg & Hegele, 2022). Some studies have suggested that adaptation can continue over broad timescales such as days and weeks (Berniker & Kording, 2011; Landi, Baguear, & Della-Maggiore, 2011; McDougle et al., 2015) but there is no discussion that learning itself has taken place since the beginning of time as part of the evolution. Specific to the interest of this thesis, motor learning can take place over the lifespan (Voelcker-Rehage & Willimczik, 2006) and skill learning can last for days or weeks (e.g., (Buitrago et al., 2004; Floyer-Lea & Matthews, 2005; Lohse et al., 2014)). However, since motor adaptation has to take place directly when needed and also subsides quickly as soon as no longer needed, this process is investigated on a very short time scale. It is important within a single experimental session and even within a single trial. The time available for participants to select, plan, perform and evaluate a movement and its movement outcome greatly influences how successful overall adaptation will be. But time available has also influenced how heavily either the explicit or the implicit component participates in the overall adaptation process involved. In some cases, it has been shown that artificially shortened time to react to a stimulus (i.e., reaction time, *rt*) are associated with a slower error reduction rate and a stronger involvement of the implicit component (Fernandez-Ruiz et al., 2011), just as a prolonged time between movement termination and feedback presentation (i.e., feedback delay) decreased the involvement of the implicit component (Brudner et al., 2016; Schween & Hegele, 2017). In addition, adaptation decays with increasing delay between practice and retention trials (Zhou et al., 2017). This illustrates just how versatile the effects of time and timing can be in a visuomotor adaptation task.

The majority of research has focused on different critical time intervals in goal-directed movements, focusing mostly on the intervals immediately before and after the movements (Fernandez-Ruiz et al., 2011; Haith, Huberdeau, & Krakauer, 2015; Miyamoto et al., 2014; Schween & Hegele, 2017; Smith et al., 2006; Zhou et al., 2017). Before the movement, processes of movement preparation and planning take place. After the movement, the result of the movement and the associated motor commands are re-evaluated and the feedback is processed and integrated.

1.4.1. Time Before: The speed-accuracy trade off in action preparation before movement execution interval before the movement

It is a common sensation that rushed movements oftentimes result in erroneous movements. This is true in everyday life and also a well-studied law in psychology called the speed-accuracy tradeoff (SPAT). This tradeoff describes the inverse relationship between the accuracy of an action and the time taken to produce it (Heitz, 2014). Models of SPAT have been around for over a century, able to explain not only economical human decision-making or overall general human behavior across domains from motor control (Fitts, 1954; Plamondon & Alimi, 1997), perception (Grosjean, Shiffrar, & Knoblich, 2007), memory (Hacker, 1980) and mental imagery (Cerritelli et al., 2000)

but also behavior across species from insects (e.g., (Ings & Chittka, 2008)) and rodents (e.g., (Rinberg, Koulakov, & Gelperin, 2006)) to monkeys (Heitz & Schall, 2012). Many studies have examined the SPAT in the context of goal-directed arm movements, but similar to how it is universally valid for different species, it also describes many human movements (Jagacinski & Monk, 1985; Kim, Parnianpour, & Marras, 1996; Michmizos & Krebs, 2014). In the field of perceptual decision-making, the SPAT is often associated with reward maximization, i.e., acting fast and early in order to increase the possibility of more rewards in the future versus waiting for more information to move as precise and accurate as possible (Churchland, Kiani, & Shadlen, 2008; Cisek, Puskas, & El-Murr, 2009; Thura & Cisek, 2017; Thura et al., 2012).

The indications of SPATs in a wide variety of movements indicate that, in order to be performed precisely and accurately, movements require time-consuming planning and preparation (Haith, Pakpoor, & Krakauer, 2016; Hardwick et al., 2021; McDougle & Taylor, 2019). Visuomotor adaptation studies are no exception. In experimental settings, the time interval immediately before movement usually starts after the stimulus appears and is thus titled reaction or response time (RT). Previous adaptation studies have addressed the issue of decreased adaptation performance if RT was artificially abbreviated (Fernandez-Ruiz et al., 2011; Haith et al., 2015; McDougle & Taylor, 2019), thereby indirectly revealing a SPAT. (McDougle & Taylor, 2019) among others postulate that implementing cognitive strategies (i.e., the explicit adaptation component) requires a considerable amount of time and prolongs RT. One approach to explain those results is the phenomenon of analog mental transformations like mental rotation (Shepard & Metzler, 1971). Mental rotation is the ability to mentally rotate representations of two- or three-dimensional objects. In 1971, Shepard and Metzler analyzed RTs and showed that the duration it takes to mentally rotate a cube figure corresponds to an actual rotation in space. In 2019, McDougle and Taylor showed that in a visuomotor rotation task participants may mentally rotate the aiming direction of their reaching movement on each trial by the angle needed to counter the perturbation. Furthermore, the authors suggest that the duration of this rotation is linearly proportional to the magnitude of the perturbation. Therefore, larger perturbation sizes would result in more time-consuming mental rotation, i.e., longer RT (McDougle & Taylor, 2019). Taking up on this mental rotation theory, the results of decreased adaptation performance due to artificially shortened RT might be explained by time consuming cognitive processes, such that a prematurely terminated motor plan results in an insufficient movement adjustment (Leow et al., 2017). Previous studies have focused on artificially shortening RT and found decreased adaptation performance and especially decreased strategy development (Fernandez-Ruiz et al., 2011; Haith et al., 2016; Leow et al., 2017; McDougle & Taylor, 2019). Critically, there is a remaining mystery in adaptation performance: visuomotor adaptation literature shows incomplete adaptation behavior (e.g.,

maximum 40° compensation for a 45° rotation), even when there are no artificial restrictions of the RT. That is, on their own time, participants will learn to compensate for a perturbation but they always leave a significant residual error (Haith et al., 2015; Holland, Codol, & Galea, 2018; Shmuelof et al., 2012; Vaswani et al., 2015).

In my first study, Chapter 2 of this thesis, this phenomenon is called “the incomplete asymptote of adaptation” and will further on be referred to as such. Until the time this study was conducted, there was no investigation whether participants would improve their adaptation performance if they encountered artificially *prolonged* movement preparation times. If adaptation performance increases due to a forced prolonged RT, it would highly suggest that humans are equipped with an internal SPAT that causes incomplete adaptation behavior in unconstricted conditions. Therefore, we wanted to know if participants would be able to overcome this incomplete asymptote of adaptation if they were forced to wait longer than they would without timely limitations during the movement planning interval in a visuomotor rotation paradigm.

1.4.2. Time After: Temporal delays in action evaluation after movement execution

The time interval after a movement was performed and any errors that were/are observed is also critical for learning. For example, time intervals were shown to have dramatic effects in classic associative learning work dating back to Edward Thorndike, Burrhus Frederic (BF) Skinner and Yvan Pavlov. In the 1940s, Skinner complemented Pavlov’s classical conditioning work with Thorndike’s *law of effect*. The law of effect states that behavior is more likely to be repeated if it entails pleasant consequences but avoided if it entails unpleasant consequences (Thorndike, 1927). In this context, Skinner introduced the term reinforcement and punishment. When a behavior is reinforced, it is strengthened and therefore more likely to be repeated. However, when a behavior is punished, it is weakened and will probably not be repeated (Skinner, 1948). Skinner also postulated, that time is of the essence and that “[...] only a few seconds between response and reinforcement destroy most of the effect.” (Skinner, 1954). Skinner’s hypothesis has been increasingly tested and confirmed, mostly with the result that delayed reinforcers indeed reduce the probability of behavior repetition (Sizemore & Lattal, 1977; Williams, 1976). Studies show that if rats and pigeons have to wait a long time for a behavior to be rewarded, they are less likely to repeat it than a behavior that is rewarded sooner (Sizemore & Lattal, 1977; Williams, 1976). Similar to the SPAT and movement preparation time, there are explanatory approaches in decision making theory for a similar phenomenon, to which parallels can well be drawn here: The temporal discount of reward. Temporal discounting refers to the reduction of the magnitude of the subjective value of a reward when it is deferred. It therefore explains the phenomenon that immediately available rewards are oftentimes preferred over larger but delayed rewards. Across different scientific disciplines, researchers have developed two main discounting models: Economists prefer

exponential models (Green, Fristoe, & Myerson, 1994) while neuroscience research tends to assume hyperbolic models of discounting (Haith, Reppert, & Shadmehr, 2012; Shadmehr et al., 2010). Future research could investigate whether there is a cross-disciplinary model or what parameters determine which model to choose.

But how can we transfer insights from this to the field of visuomotor adaptation? Recent studies revealed a significant attenuation of the implicit component of visuomotor adaptation if the movement feedback was artificially delayed (Brudner et al., 2016; Schween & Hegele, 2017). This reinforces the assumption that the implicit component of visuomotor adaptation seems to be particularly dependent on the timing of feedback. A hypothesis drawn from the results of the study by Schween and Hegele is that artificially delaying feedback might decrease the implicit components participation in adaptation. The authors hypothesize that this decrease in the implicit component causes an increase in the explicit component's participation, in order to compensate for the lack of adaptation, suggesting a dependency between explicit and implicit. This could then present the opportunity to overcome temporal discounting of reward, because as Skinner stated, a time delay of the response overrides the effect of the reinforcement, unless "[...] explicit mediating behavior has been set up, [...]" (Skinner, 1954). To test whether feedback delay might actually shift adaptation towards more explicit processes which by extension leads to the fact that it would be a possibility to bypass temporal discounting, the experiment in my second study, in chapter 3 of this thesis, is supplemented with an additional manipulation, a cognitive secondary task. The logic behind this is that if the explicit component engages in cognitive resources, the effects of a cognitive secondary task should be more pronounced on the explicit component (Maxwell et al., 2001; Navon & Miller, 1987; Nissen & Bullemer, 1987; Pashler & Johnston, 1989; Tombu & Jolicoeur, 2002) compared to the implicit component, which is supposed to be unsusceptible to cognitive interference.

1.5. Visuomotor adaptation and EEG: An attempt to use the FRN as a proxy for adaptation processes

Similar to the notion that the terms explicit and implicit are used differently across studies (Maresch, Mudrik, & Donchin, 2021a), the methods used to measure them also vary across studies. It is important to note that different methods yield different results (Maresch et al., 2021b). One possible variation to measure the participation of explicit and implicit components is the direct assessment in the form of postadaptive tests, or posttests. I use this procedure for the first and second study in this thesis. It is a direct method in which participants are asked to either include or exclude a cognitive strategy to compensate for the imposed perturbation. The problem with this procedure, however, is that it affects task features significantly (Heuer & Hegele, 2015; Schween et

al., 2019). Furthermore, in order to perform these tests, the participants must be instructed on what is now expected of them. Thus, the participants' attention is necessarily redirected, which affects the outcomes as well (Newell & Shanks, 2014; Timmermans & Cleeremans, 2015). To avoid such influences in awareness and task design, it would be very helpful, to use indirect methods to assess the explicit and implicit components. Methods, in which no changes are made to the task itself, or that do not stir participants' attention by additional instructions. One possible approach has been touched upon by studies that have linked eye movements to (components of) explicit re-aiming (Bromberg, Donchin, & Haar, 2019; de Brouwer et al., 2018). Eye movements, more specific saccades, are not under arbitrary control and might therefore represent a possible indirect measure for explicit adaptation. However, in the third study, I use another approach. I want to establish a connection to cognitive neuroscience and investigate the inner workings of the explicit and implicit components on a separated, neuronal level.

The feedback related negativity (FRN) is an event-related potential (ERP) which is said to reflect the processing of unexpectedly large, external errors (Krigolson & Holroyd, 2006; Miltner, Braun, & Coles, 1997). Its namesake negative peak is set to occur about 200 ms to 400 ms after movement outcome presentation (Miltner et al., 1997). It is said to be sensitive to temporal delays (Hinneberg & Hegele, 2022) but also to different error sizes (Anguera, Seidler, & Gehring, 2009; Krigolson & Holroyd, 2007b). Therefore, my initial hypothesis for the third study was that certain FRN characteristics, such as latency and amplitude, can be assigned to different participations of the explicit and implicit adaptation processes. Unfortunately, the results from this study are not conclusive, so that I cannot assign specific FRN characteristics to the two components.

2. Prolonged response time helps eliminate residual errors in visuomotor adaptation

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Prolonged response time helps eliminate residual errors in visuomotor adaptation

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Abstract

One persistent curiosity in visuomotor adaptation tasks is that participants often do not reach maximal performance. This incomplete asymptote has been explained as a consequence of obligatory computations within the implicit adaptation system, such as an equilibrium between learning and forgetting. A body of recent work has shown that in standard adaptation tasks, cognitive strategies operate alongside implicit learning. We reasoned that incomplete learning in adaptation tasks may primarily reflect a speed-accuracy tradeoff on time-consuming motor planning. Across three experiments, we find evidence supporting this hypothesis, showing that hastened motor planning may primarily lead to under-compensation. When an obligatory waiting period was administered before movement start, participants were able to fully counteract imposed perturbations (Experiment 1). Inserting the same delay between trials – rather than during movement planning – did not induce full compensation, suggesting that the motor planning interval influences the learning asymptote (Experiment 2). In the last experiment (Experiment 3), we asked participants to continuously report their movement intent. We show that emphasizing explicit re-aiming strategies (and concomitantly increasing planning time) also lead to complete asymptotic learning. Findings from all experiments support the hypothesis that incomplete adaptation is, in part, the result of an intrinsic speed-accuracy tradeoff, perhaps related to cognitive strategies that require parametric attentional reorienting from the visual target to the goal.

Keywords Sensorimotor adaptation · Response time · Motor planning · Asymptote · Explicit strategies

Introduction

One of the persistent curiosities in studying the human mind is the idea of canonical computations, that is that the brain

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applies similar computations to perform a wide range of different tasks. Most examples for such canonical computations (e.g., Carandini & Heeger, 2011; DiCarlo & Johnson, 2000; Miller, 2016; Movshon et al., 1978; Pack & Bensmaia, 2015; Ringach & Malone, 2007) have been identified in the fields of neuroscience and artificial intelligence but have largely eluded scientists in psychology.

One example of a reliable law in psychology is the speed-accuracy tradeoff, the inverse relation between the accuracy of an action and the time taken to produce it (for a review, see Heitz, 2014). The speed-accuracy tradeoff has been shown to shape behavior across domains from motor control (Fitts, 1954; Plamondon & Alimi, 1997) and perception (Grosjean et al., 2007) to memory (Hacker, 1980) and mental imagery (Cerritelli et al., 2000), as well as across species from insects (e.g., Ings & Chittka, 2008) and rodents (e.g., Rinberg et al., 2006) to monkeys (Heitz & Schall, 2012) and humans (Wickelgren, 1977).

Another example is the law of practice, according to which performance improvements are generally larger early during practice before they become systematically smaller as practice

progresses giving rise to a negatively accelerated relationship between performance and the number of practice trials (Crossman, 1959; Chen et al., 2005). Regardless of its actual parameters, all versions of the law of practice postulate that performance improvements asymptote at some point. While it is almost impossible to determine the absolute maximum level of performance for complex skills such as swimming, in experimental paradigms like visuomotor transformation tasks (e.g., force field adaptation or rotations of visual feedback), individual performance improvements are evaluated relative to an absolute maximum. That is, there is a quantifiable level of complete adaptation to the transformation (Shadmehr, Brashers-Krug, & Mussa-Ivaldi, 1994).

Interestingly, one common observation in this context is that of an incomplete asymptote: If individuals are required to make reaching movements while compensating for a visuomotor rotation, their performance curve tends to asymptote below full compensation (Holland et al., 2018; Huberdeau et al., 2015; Haith et al., 2015; van der Kooij et al., 2016), leaving a residual performance error significantly different from zero (Hinder et al., 2010; Shmuelof et al., 2012; Spang et al., 2017; van der Kooij et al., 2015; Vaswani et al., 2015).

One approach to explain this is to leverage state-space models of adaptation, which are incremental Markovian learning algorithms that balance both learning and forgetting during adaptation (Smith et al., 2006). When fit to human learning data, most parameter values can produce a steady-state equilibrium at an arbitrary asymptote. Consequently, these models provide a natural description of the commonly observed undershoot, via an assumption that some amount of forgetting (i.e., reversion to baseline) is inevitable on each trial of the task. This interpretation suggests that incomplete compensation during motor learning is simply a built-in feature of the underlying learning mechanism.

However, Vaswani et al. (2015) demonstrated that humans, in principle, possess the capacity to overcome this incomplete asymptote. In their study, the cursor controlled by the participant moved in a fixed trajectory toward the target or to a nearby location with participants only controlling the amplitude. If the trajectory of the cursor had no variability, individuals appeared to adopt a new learning strategy that allowed them to fully counteract a novel visuomotor transformation. The authors proposed that this exploratory learning mechanism is typically suppressed by error-based learning. The putatively suppressed process only contributes to performance when error-based learning is disengaged, which in their study was caused by a persistent residual error in combination with a contextual change (i.e., the introduction of a lack of natural movement variability).

In the present study, we examined an alternative account of how humans might overcome incomplete asymptotic performance, where the level of performance achieved at later stages of visuomotor adaptation primarily reflects an intrinsic speed-

accuracy tradeoff driven by time-consuming movement planning.

In line with this, research in perceptual decision-making has established that choice reaction time reflects a tradeoff between waiting for more information and acting early in order to speed up the accumulation of (uncertain) rewards on future trials (Churchland et al., 2008; Cisek et al., 2009; Thura et al., 2012; Thura & Cisek, 2017). While visuomotor adaptation tasks traditionally are not studied in the framework of decision-making, recent research has highlighted an important role for volitional decision-making strategies in adaptation tasks (i.e., the explicit re-aiming of movements to counteract perturbations; Bond & Taylor, 2015; Heuer & Hegele, 2009; Heuer & Hegele, 2015; McDougale et al., 2015; Schween & Hegele, 2017; Taylor et al., 2014). Further evidence suggests that in the context of adaptation to a novel visuomotor rotation, such strategies may take the form of mentally rotating the aiming direction of the reaching movement (McDougale & Taylor, 2019), which has been known to require long preparation times (Fernandez-Ruiz et al., 2011; Haith et al., 2015; McDougale & Taylor, 2019). Thus, an incomplete learning asymptote could arise from hurried movement initiation leading to prematurely terminating mental rotation of an abstract aiming trajectory during movement planning (Leow et al., 2017).

We tested our hypothesis over three behavioral experiments where we artificially extended planning time. We predicted that this simple manipulation would alleviate incomplete asymptotic learning (i.e., asymptotic reaching angles that undershoot the ideal angle). In Experiment 1, we introduced a mandatory waiting period between target presentation and movement onset. In Experiment 2, we sought to exclude effects of the total experiment duration by emphasizing the role of within-trial movement planning time versus between-trial consolidation. Finally, in Experiment 3, we used an aiming report method (Taylor et al., 2014) to promote the application of explicit motor learning strategies before movement execution and elucidated their influence on the learning asymptote.

General methods

Participants

A total of 90 neurologically healthy, right-handed students (Experiment 1: N = 36, Experiment 2: N = 36, Experiment 3: N = 18) from the Justus Liebig University Giessen participated in this study. They were recruited as participants and received monetary compensation or course credit for their participation. Written informed consent was obtained from all participants before testing. The experimental protocol was approved by the local ethics committee of the Department of Psychology and Sport Science.

Apparatus

Participants sat on a height-adjustable chair facing a 22-in. widescreen LCD monitor (Samsung 2233RZ; display size: 47.3 cm × 29.6 cm; resolution: 1,680 × 1,050 pixels; frame rate 120 Hz), which was placed at eye level 100 cm in front of them. Their right hand held a digitizing stylus, which they could move across a graphics tablet (Wacom Intuos 4XL). Their hand position recorded from the tip of the stylus was sampled at 130 Hz. Stimulus presentation and movement recording were controlled by a custom-built MATLAB script (R2017b), displayed above the table platform, thus preventing direct vision of the hand (left panel Fig. 1A).

Task

Participants performed center-out reaching movements from a common start location to targets in different directions. They were instructed to move the cursor as quickly as possible from the start location in the direction of the displayed target and “shoot through it.” On the monitor, the start location was in the center of the screen, marked by the outline of a circle of

7 mm in diameter. On the table surface, the start location was 20–25 cm in front of the participant on the body midline. The screen target location, marked by a filled green circle of 4 mm in diameter, varied from trial to trial. Targets were placed on an invisible circle with a radius of 100 mm around the start location; target directions were 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315° (0° is from the start location to the right, 90° is forward, 270° is backward; right panel Figure 1A). On baseline and adaptation trials, visual feedback was given by a cursor (filled white circle, radius 2.5 mm).

Design and procedure

The experiment consisted of three phases: baseline training, training with a 45° clockwise (CW) visuomotor rotation, and post-tests (Fig. 1B). Baseline training had veridical hand-cursor mapping and was organized into three blocks of eight trials each. Each block consisted of a random permutation of the eight target directions without any direction being repeated in successive trials. Training of the visuomotor rotation of 45° CW consisted of 40 blocks of eight trials each.

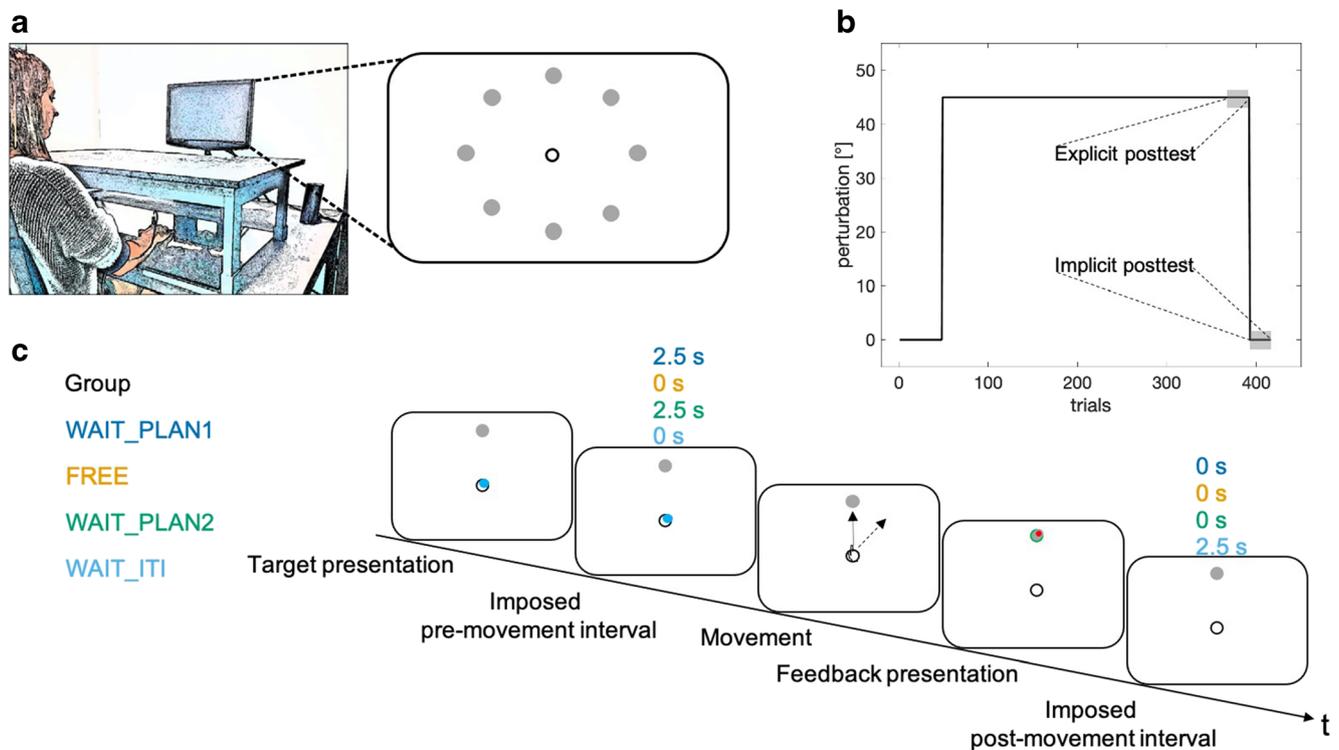


Fig. 1 Schematic display of the experimental setup (A), overall protocol (B), and sequence of one trial (C). Each participant performed center-out reaching movements with a stylus on the tablet. Visual stimuli and the cursor were presented on a monitor. The visual cursor was displaced according to the protocol (B). During baseline, cursor and stylus position were veridical, during adaptation, the cursor was rotated 45° clockwise relative to the stylus position. Within-trial timing differed between groups (C). Group-dependent differences within one trial occurred during either the pre- or the post-movement interval. Whereas the FREE and WAIT_

ITI groups had no specific task during the pre-movement interval, WAIT_PLAN1 and WAIT_PLAN2 groups were required to wait 2.5 s. During the post-movement interval, only the participants in the WAIT_ITI group were required to wait 2.5 s, whereas all other groups continued with the next trial immediately. The AIM group is not presented in this figure as their manipulation did not refer to any time constraints. Panel A is adapted from Schween, Taylor, and Hegele (2018) under CC-BY-4.0 license

The post-test phase consisted of two types of trials: an explicit test (see below) comprising three blocks of eight trials each with each target location occurring once per block, and three blocks of eight after-effect test trials without visual feedback, with the instruction that the cursor rotation would be absent. In the explicit test trials (Hegele & Heuer, 2010; Heuer & Hegele, 2008), start and target locations were presented together with a white line, centered in the start location with its length corresponding to target distance. Initially, the line was presented at an angle of 180° CCW of the respective target's direction. Participants instructed the experimenter to adjust the orientation of the line to match the direction of the movement they judged to be correct for the particular target presented.

Each single-movement trial started with the presentation of the start circle in the center of the screen, serving as the starting position for the subsequent reaching movement. In order to help guide participants' movements back to the start, a white concentric circle appeared after feedback presentation, scaling its radius based on the cursor's distance from the start circle. The cursor was displayed when it was within 3 mm of the start location. Once the start position was held for 300 ms, a tone (440 Hz, 500-ms duration) was presented, followed by a target appearing in one of the eight target positions and the start circle disappeared.

The cursor was visible until it exceeded a movement amplitude of 3 mm, after which it disappeared. When the participant's hand crossed an invisible circle that contained the target, the cursor froze and reappeared in red, providing endpoint feedback for 1,250 ms. Movements that fell outside the range of instructed movement time (MT) criteria ($MT < 100$ ms or > 300 ms) were followed by an error message on the screen and the trial was aborted. Those trials were neither repeated nor used in subsequent analyses. If participants moved too soon in one of the waiting groups (before the appearance of the target or the go cue, see below), they were reminded to wait and the trial was repeated.

Data analysis

The position of the stylus on the tablet surface was recorded and each trial was separately low-pass filtered (fourth-order Butterworth, 10 Hz) using Matlab's *filtfilt* command and then numerically differentiated. Tangential velocity was calculated as the Euclidean distance of x- and y-velocity vectors. Behavior was analyzed in terms of two parameters: response time and endpoint error measured as final hand position. Response time was calculated as the interval between target presentation and movement onset, which was defined when tangential velocity exceeded 30 mm/s for at least five frames (38.5 ms). Endpoint error was calculated as the angular difference between the vector connecting the start circle and the

target, and the vector connecting the start circle and the endpoint position. Endpoint errors were calculated for both training trials and the after-effect trials. The outcome variable of the explicit perceptual judgment test was calculated as the angular difference between the participant-specified line orientation on the screen and the vector connecting the start and target positions.

For each block of training trials and for the post-test, means were computed for each participant following screening for outliers. This screening ensured that single outlier movements were excluded before further analysis. Movements whose endpoint fell outside three standard deviations of the participants' individual mean endpoint in that phase were considered outliers and removed. A total of 1.08% of all trials was detected and eliminated this way. To compare different levels of asymptote, the last five blocks of the training phase were median averaged and compared between groups using a two-sample Wilcoxon's rank-sum test. To interpret the results, an effect size r and its 95% confidence interval were calculated. Statistical analyses were done in Matlab (R2017b) and R (version 3.5.1, <http://www.R-project.org/>). As a normal distribution was not always observed, all results are based on nonparametric tests.

Experiment 1

According to the speed-accuracy tradeoff hypothesis, we expected prolonging response times to have a facilitating effect on adaptation. Experiment 1 investigated this hypothesis by manipulating participants' response times in two groups and comparing their results. We predicted that the dependent variable (final hand position) would display less asymptotic error in a group in which response time was prolonged by the manipulation, relative to a group with no such constraint.

Methods

One group was instructed to move straight to the target after it appeared, with no additional time constraints before moving (FREE, $N = 19$). The other group (WAIT_PLAN1, $N = 17$) was instructed to wait until they heard a high-pitched tone (1,000 Hz, 500-ms duration) that served as a go-signal. Based on previous work indicating that participants were able to aim 90° away from a visual target within ~1.3 s (McDougle & Taylor, 2019), we chose a 2.5-s wait interval to provide ample planning time for the 45° rotation task at hand. The go-signal was presented after this wait interval.

Results

Data from one participant of the FREE group were excluded due to a large number of irregular trials (21% of premature

Table 1 Mean and standard deviation for each experimental group at asymptote level, for the explicit judgment and the implicit after-effect post-tests

Group	Mean	SD
Asymptote		
FREE	41.15	8.28
WAIT_ PLAN1	46.66	5.85
WAIT_ PLAN2	46.33	3.99
WAIT_ITI	43.96	3.01
AIM	46.63	4.12
Explicit Judgment		
FREE	24.78	5.45
WAIT_ PLAN1	30.65	8.33
WAIT_ PLAN2	30.88	10.21
WAIT_ITI	30.53	8.57
AIM	28.32	10.95
Implicit After-Effects		
FREE	9.99	3.81
WAIT_ PLAN1	9.35	3.67
WAIT_ PLAN2	7.63	3.87
WAIT_ITI	8.45	4.77
AIM	8.87	3.29

movement initiations, moving too fast or too slow). Including this participant in the analyses (not shown) did not alter the results qualitatively.

As shown in Fig. 2A, the FREE group displayed the typical incomplete asymptote ($M = 41.15$, $SD = 8.28$) (Table 1), whereas the WAIT_PLAN1 ($M = 46.66$, $SD = 5.85$) group achieved a greater asymptote ($W = 244$, $p = 0.001$, $r = -0.42$, $CI = [-0.67, -0.13]$). Hand directions late during practice were significantly less than 45° in the FREE ($W = 32.5$, $p = 0.02$, $r = -0.61$, $CI = [-0.84, -0.21]$) group, while the WAIT_PLAN1 group did not differ significantly from 45° ($W = 108$, $p = 0.62$, $r = 0.12$, $CI = [-0.33, 0.53]$) (Table 2).

In the explicit judgment test (Fig. 2G), the FREE group estimated the rotation to be significantly smaller relative to the WAIT_PLAN1 group ($W = 83$, $p = 0.04$, $r = -0.36$, $CI = [-0.62, -0.031]$). Implicit after-effects (Fig. 2G) did not differ significantly between the groups ($W = 179$, $p = 0.59$, $r = 0.09$, $CI = [-0.24, 0.39]$) (Table 2).

Discussion

Forcing participants to prolong their response time before movement onset on each trial led to an increase in asymptotic learning. Furthermore, this also led to an increase in

accumulated explicit knowledge. While these results are consistent with our speed-accuracy tradeoff hypothesis, they cannot rule out an unspecific effect of time on task.

Experiment 2

To further investigate whether the elevated asymptote from Experiment 1 was a nonspecific effect of time or in fact due to longer planning times, Experiment 2 aimed to delineate this by comparing two groups with matched intertrial intervals. According to the speed-accuracy tradeoff hypothesis, we predicted that, similar to Experiment 1, the outcome measure of final hand position would show less residual error in a group with prolonged response time compared to a group with an imposed post-movement intertrial interval even though total trial length was matched.

Methods

Experiment 2 manipulated the trial duration in two groups: the WAIT_PLAN2 group ($N = 22$) was a replication of the WAIT_PLAN1 group in Experiment 1. Participants in the second group (WAIT_ITI, $N = 20$) could initiate movements as soon as the target had appeared on the screen replicating the planning interval of the FREE group from Experiment 1. Critically, the WAIT_ITI experienced an additional 2.5 s waiting period after the presentation of the endpoint feedback. Thus, the two groups, WAIT_PLAN2 and WAIT_ITI, had matched trial lengths but different planning intervals. During the 2.5-s inter-trial delay in the WAIT_ITI group, only the target was visible on the screen and participants were told to maintain their final hand position.

Results

Inserting waiting time into the planning phase led to an asymptote not significantly different from 45° ($M = 46.33$, $SD = 3.99$), whereas inserting the waiting time into the intertrial interval led to an asymptote significantly less than 45° ($M = 43.96$, $SD = 3.01$) (Table 1). Those two asymptotes were significantly different from each other ($W = 311$, $p = 0.01$, $r = -0.34$, $CI = [-0.59, -0.05]$) (Table 2).

On the post-test for explicit knowledge (Fig. 2H), the temporal locus of the additional waiting time did not have a significant effect: Both groups appeared to accumulate equivalent amounts of explicit knowledge ($W = 231$, $p = 0.79$, $r = 0.04$, $CI = [-0.25, 0.36]$), but showed greater explicit estimations than the FREE group in Experiment 1 (FREE, WAIT_PLAN2: $W = 85$, $p = 0.03$, $r = -0.37$, $CI = [-0.63, -0.06]$; FREE, WAIT_ITI: $W = 93$, $p = 0.03$, $r = -0.37$, $CI = [-0.63, -0.08]$), whose trial structure did not contain any additional waiting interval. Furthermore, after-effects in

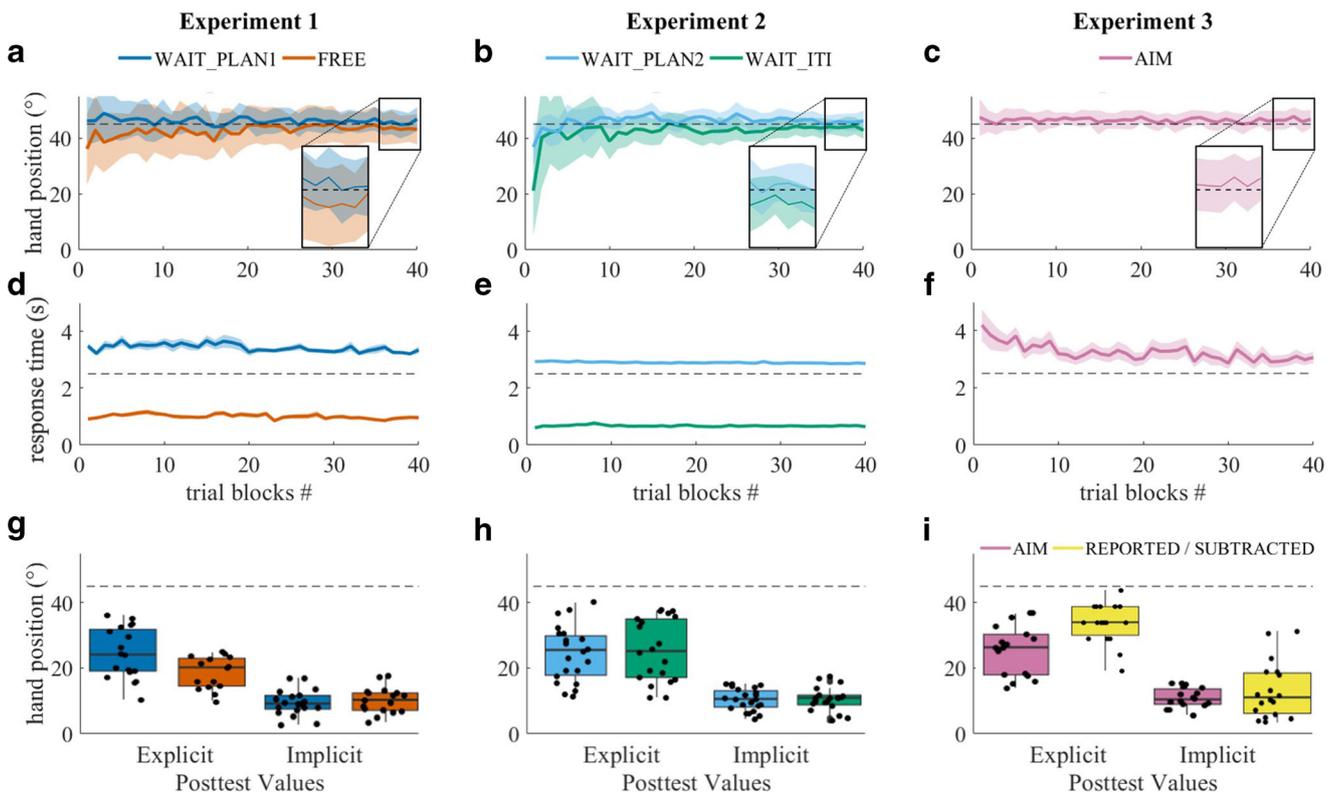


Figure 2 Mean hand direction (panels A-C) and mean movement response times (panels D-F) during practice plotted separately by experiments and groups. Panel G-I show the median hand direction during explicit and implicit posttests, separately and the individual data from single participants. The horizontal dashed lines in panels A-C and H-I

indicate ideal compensation for the 45° cursor rotation. In panels D-F, they indicate the imposed waiting times of 2.5 seconds in the WAIT_PLAN groups. Shaded error bands in panels A-F represent standard deviation of the mean.

Experiment 2 did not differ significantly between groups ($W = 214$, $p = 0.89$, $r = -0.02$, $CI = [-0.34, 0.36]$, Fig. 2H).

Discussion

The absence of significant asymptotic error in the WAIT_PLAN2 group replicated the effect of additional planning time observed in Experiment 1. Comparing the WAIT_ITI group with the FREE group across experiments suggests that extending the intertrial interval may have had an unspecific effect on learning as indicated by greater explicit learning in the WAIT_ITI group.

Importantly, the significant difference between groups and the fact that the WAIT_ITI group displayed an incomplete asymptote shows that most of the benefit of added time in Experiment 1 was not a mere consequence of a prolonged intertrial interval, suggesting a specific benefit of additional time for movement planning in line with our speed-accuracy tradeoff hypothesis.

Experiment 3

As both preceding experiments hinted toward an unspecific effect of time on task on learning due to accumulating more

explicit knowledge, this experiment sought to account for the possibility that it is in fact not time *per se* but the increased participation of explicit processes that raises the level of asymptote. To this end, we used the reporting paradigm as this procedure requires active explicit engagement during the planning interval. We hypothesized that the dependent variable of final hand position would thus show close to no residual error.

Methods

A single group of participants (AIM group, $N = 18$) was asked to report their aiming direction prior to movement initiation (Bond & Taylor, 2015; McDougle et al., 2015; Taylor et al., 2014). The participants in this group saw a numbered ring of visual landmarks. The numbers were arranged at 5.63° intervals with the current target positioned at the 0° position. Clockwise the numbers became larger and counterclockwise the numbers became smaller (up to 32°, -32°, respectively), forming a circle 20 cm in diameter. Participants were instructed to verbally report the number they were aiming their reach at before moving (see Taylor et al., 2014, for further information on this task). Verbal reports were manually registered by the experimenter on each reporting trial. In Experiment 3, baseline training included three additional

Table 2 Parameters for Wilcoxon's rank-sum tests between groups (compared groups are separated with a comma) and against 45° (complete compensation). Two-sided alternatives are represented with an unequalsign (\neq), directed hypotheses are marked with a greater or smaller than symbol ($>$ or $<$).

Wilcoxon's rank-sum Test	W	p	Effect size r	95% confidence interval
Asymptote				
FREE, WAIT_PLAN 1	244	0.001	-0.42	[-0.67, -0.13]
Free < 45	32.5	0.02	-0.61	[-0.84, -0.21]
WAIT_PLAN1 \neq 45	108	0.62	0.12	[-0.33, 0.53]
WAIT_PLAN2, WAIT_ITI	311	0.01	-0.34	[-0.59, -0.05]
WAIT_PLAN2 \neq 45	235	0.28	0.25	[-0.18, 0.66]
WAIT_ITI < 45	63	0.02	-0.44	[-0.75, -0.05]
AIM > 45	125	0.05	0.41	[-0.08, 0.75]
Explicit Judgment				
FREE, WAIT_PLAN 1	83	0.04	-0.36	[-0.62, -0.031]
WAIT_PLAN2	231	0.79	0.04	[-0.25, 0.36]
WAIT_ITI				
FREE, WAIT_PLAN2	85	0.03	-0.37	[-0.63, -0.06]
FREE, WAIT_ITI	93	0.03	-0.37	[-0.63, -0.08]
AIM, FREE	197.5	0.03	0.39	[0.05, 0.60]
AIM, WAIT_PLAN1	160.5	0.76	-0.05	[-0.36, 0.27]
AIM, WAIT_PLAN2	160	0.57	-0.09	[-0.39, 0.22]
AIM, WAIT_ITI	190.5	0.85	-0.03	[-0.34, 0.28]
AIM \neq 45	0	< 0.01	-0.88	[-0.88, -0.87]
Implicit After-Effects				
FREE, WAIT_PLAN 1	179	0.59	0.09	[-0.24, 0.39]
WAIT_PLAN2, WAIT_ITI	214	0.89	-0.02	[-0.34, 0.36]
FREE, WAIT_PLAN 2	227.5	0.08	0.29	[-0.02, 0.58]
FREE, WAIT_ITI	256.5	0.05	0.34	[0.03, 0.62]
AIM, FREE	140.5	0.69	-0.07	[-0.39, 0.27]
AIM, WAIT_PLAN1	167.5	0.93	-0.02	[-0.35, 0.31]
AIM, WAIT_PLAN2	221	0.24	0.19	[-0.11, 0.52]

blocks in which participants had to report their aiming direction prior to movement onset.

Results

Participants in the AIM group completely compensated the rotation. Adaptive shifts in hand positions were significantly larger than 45° ($M = 46.63$, $SD = 4.12$, $W = 125$, $p = 0.05$, $r = 0.41$, $CI = [-0.08, 0.75]$) (Table 2), suggesting that adaptation at asymptote was complete and, in fact, some participants overcompensated for the rotation (Fig. 2C). Explicit judgments of required compensation (Fig. 2I) were significantly less than 45° ($M = 28.32$, $SD = 10.95$, $W = 0$, $p < 0.01$, $r = -0.88$, $CI = [-0.88, -0.87]$) (Table 2).

To test whether the reporting task influenced the outcome of the explicit judgment tests, we compared the post-test values between the AIM group and those of the other groups in Experiments 1 and 2. There was a significant difference in the explicit judgments between the AIM group and the FREE

group from Experiment 1 ($W = 197.5$, $p = 0.03$, $r = 0.39$, $CI = [0.05, 0.60]$). Across the AIM group and WAIT_PLAN2 ($W = 160.5$, $p = 0.76$, $r = -0.05$, $CI = [-0.36, 0.27]$) and WAIT_ITI ($W = 190.5$, $p = 0.85$, $r = -0.03$, $CI = [-0.34, 0.28]$) groups in Experiment 2, there were no differences in the explicit judgment tests (Table 2).

Discussion

By instructing participants to verbally report their movement aim prior to movement execution trial-by-trial (Taylor et al., 2014), we potentially primed the explicit component of adaptation by getting subjects to attend to angular deviations. We reasoned that this would serve as an opportunity to replicate our findings, in that requiring active explicit reporting also extends the planning interval. Our results suggest that experimentally querying the explicit process of adaptation does not qualitatively alter the explicit learning balance, but does act to

improve the adaptation asymptote by promoting planning and prolonging the movement planning interval.

Concluding discussion

This study was designed to investigate whether previously reported findings of incomplete asymptotic visuomotor learning may be reframed as an instantiation of the speed-accuracy tradeoff. In line with this hypothesis, artificially prolonging the waiting period prior to goal-directed movement onset elevated asymptotic learning and appeared to eliminate residual errors. This benefit was specific to prolonging motor planning (prior to a go-signal). Prolonging the interval between visual feedback and the start of the next trial did not provide the same benefit. Our results suggest that time-consuming planning processes are a major cause of incomplete asymptotic learning.

Why did hasty planning result in consistent undershooting rather than, for example, increased movement variability? We suggest that parametric mental computations might explain this phenomenon: In visuomotor rotation tasks, participants' response times increase linearly with the magnitude of imposed rotations (Georgopoulos & Massey, 1987; McDougle & Taylor, 2019), reflecting a putative mental rotation process (Shepard & Metzler, 1971). A previous study by McDougle and Taylor (2019) demonstrated that reaction time in a free condition appeared to decompose into a ~ 1 -s baseline reaction time plus ~ 200 ms for a $\sim 45^\circ$ mental rotation (their Fig. 4b). Thus, the potential savings by rotating incompletely may seem small; however, it is consistent with our response-time results (Fig. 2D), and it is also consistent with decision-making research that shows similar amounts of time being saved in reward-based speed-accuracy tradeoff tasks (Thura, Cos, Trung, & Cisek, 2014). Interestingly, in another experiment by McDougle and Taylor (2019), participants reliably rotated movements to around $\sim 75^\circ$ when a forced total reaction time of ~ 350 ms was imposed for a 90° perturbation. This may indicate that urgency imposed by the forced response task independently modulates the baseline preparation time. Overall, this mental rotation interpretation is further supported by the results of our third experiment, in which emphasizing the application of explicit aiming strategies prior to movement initiation led to qualitatively similar asymptotic learning as in the groups with prolonged response times. Finally, we note that delaying movement initiation did not only cause full compensation, but induced overcompensation, suggesting perhaps that implicit processes superimposed onto an accurate explicit rotation strategy may have caused reach angles to drift, gradually adapting the hand further in the direction of compensation (cf. Mazzoni & Krakauer, 2006).

The idea of a speed-accuracy tradeoff prematurely interrupting putative mental rotation processes during motor

planning also provides an explanation for previously observed age-related differences in visuomotor learning: Hegele and Heuer (2013) used explicit instructions and cognitive pretraining prior to learning a novel visuomotor rotation to boost explicit knowledge of the transformation. Older adults with full explicit knowledge of the transformation turned out to be less efficient in applying it for strategic corrections of their aiming movements. This age-related difference with respect to the behavioral exploitation of explicit knowledge became manifest only when participants had almost perfect explicit knowledge, but not when they had only poor explicit knowledge and showed minimal strategic adjustments. Given the present results, one could speculate that the reduced exploitation of explicit knowledge for strategic corrections in older participants is due to a combination of age-related slowing in mental rotation and the premature termination of (slowed) mental rotation during motor planning.

Traditionally, the incomplete asymptote phenomenon has been explained by state-space models of adaptation (Smith et al., 2006). As subsequent studies indicated that this model alone is insufficient for explaining incomplete asymptotic behavior, alternatives were proposed: among others, that spatial error-based learning processes suppress other mechanisms that could drive full compensation (Shmuelof et al., 2012; Vaswani et al., 2015). In our study, participants in all groups received similar spatial error feedback. Thus, a potential suppression should have affected all groups equally, making this explanation insufficient to explain the modulations in asymptote we observed.

Another approach to the state-space model suggests that residual errors in adaptation paradigms are caused by implicit processes that tune the motor system's sensitivity to errors until it reaches an equilibrium with constant forgetting (Albert et al., 2019). These authors manipulated the variability of the perturbation and found that residual errors increase with the perturbations' variance. Without having considered this a priori, we note that our hypothesis could potentially be adapted to account for these variations in asymptote (e.g., experiencing perturbation variability could affect the benefit that learners expect from planning, and thus the time they spend on it). However, in one experiment that study also showed a speed-accuracy tradeoff by obtaining larger residual errors when the reaction time was artificially shortened compared to free response times, regardless of the variance of perturbation. Thus, we believe that additional planning time is an essential element in eliminating residual errors to achieve full compensation, though it is likely not the only thing determining the exact asymptotic value.

Moreover, we also note that consistent undershooting relative to the perturbation, as observed here and in previous studies, is critically not seen in experimental paradigms designed to isolate the implicit component of visuomotor adaptation (Morehead et al., 2017) – indeed, even when rotational

perturbations are as small as $\sim 1.75^\circ$, implicit adaptation appears to asymptote around $\sim 15^\circ$ (Kim et al., 2018). In the current study, results from the implicit post-test were unaffected by changes in the response-time interval. Thus, it may be that incomplete compensation relative to the visual error mainly involves explicit cognitive processes that succumb to speed-accuracy tradeoffs, whereas asymptotic dynamics of the implicit system require a separate explanation.

Recent accounts have framed motor planning as a time-consuming optimization process from which a reduction in movement accuracy arises naturally when constraints are imposed (Al Borno et al., 2019). Our findings suggest that similar principles apply when one is intentionally choosing to perform a movement in another direction than the one implied by the target presented, and that learners naturally constrain their planning time even in seemingly unconstrained conditions. Haith and colleagues (Haith et al., 2016) recently showed that movement preparation and initiation are independent, i.e., that, instead of complete preparation triggering movement initiation, humans appear to determine a time for movement initiation based on when they expect planning to be completed. This view naturally implies the possibility for premature movement initiation. The planning time chosen may therefore trade off the achieved accuracy within a given time and the urgency to move on (Churchland et al., 2008; Cisek et al., 2009; Thura & Cisek, 2017).

Many of the common explanations for incomplete asymptote outlined above imply that it is a fundamental property of learning. Psychology and kinesiology traditionally distinguish performance effects (the behavioral act of executing a skill at a specific time in a specific situation) from learning effects (the change in the unobservable underlying capability to perform a skill, which is indirectly inferred from a relatively permanent improvement of performance). For example, with respect to the asymptotic reaching behavior of two groups in our experiments, their underlying knowledge could be identical while retrieval processes in specific test conditions can lead to different performance profiles (Magill & Anderson, 2017; Schmidt & Lee, 2011). Even though our experiments were not specifically designed to distinguish learning from performance, our findings suggest that both may contribute to an incomplete asymptote in adaptation: If our results reflected a performance effect alone, the manipulation should have affected behavior in the adaptation phase but not in the post-test results. In Experiment 1, however, explicit estimates of the rotation magnitude were increased with added response time, suggesting that perhaps some of the benefit of longer response times may be due to learners honing their explicit knowledge. However, the observation that explicit knowledge was similarly increased regardless of whether additional time was added at the beginning or end of a trial in Experiment 2 indicates that this learning effect may be a non-specific consequence of longer intertrial intervals (it is), and that the

remaining increase in asymptote is indeed a performance effect. A recent paper analyzing preparatory neural states in rhesus monkeys performing visuomotor learning tasks also found that longer preparation times not only yielded smaller variance on the current trial, but also smaller errors on the subsequent trial, supporting a learning effect (Vyas et al., 2020). Future research could attempt to better delineate learning from performance effects in human motor adaptation. Moreover, the post-tests reported here should be interpreted with caution: Recent work suggests that measurements of explicit visuomotor learning components are contingent on the methodology used (Maresch, Werner, & Donchin, 2020).

Lastly, we emphasize that we are not claiming that other learning mechanisms cannot contribute to asymptotic behavior (Albert et al., 2019; Emken et al., 2007), nor that a state-space model with gradual decay towards zero is invalid (Brennan & Smith, 2015). What we do suggest is that a potentially major aspect determining the magnitude of asymptotic errors in visuomotor learning is a speed-accuracy tradeoff. Since this decision process is likely to be relevant across a broader range of motor tasks, we speculate that our results extend beyond motor adaptation, and that simple interventions, like explicitly prolonging response times to allow for complete planning, could improve asymptotic performance in a range of motor learning tasks.

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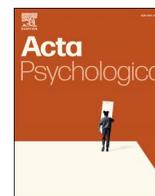
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3. Additional cognitive load decreases performance but not adaptation to a visuomotor transformation

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Additional cognitive load decreases performance but not adaptation to a visuomotor transformation

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ABSTRACT

Dual-task paradigms are procedures for investigating interference with two tasks performed simultaneously. Studies that previously addressed dual-task paradigms within a visuomotor reaching task yielded mixed results. While some of the studies found evidence of cognitive interference, called dual-task costs, other studies did not. We assume that dual-task costs only manifest themselves within the explicit component of adaptation, as it involves cognitive resources for processing. We suspect the divergent findings to be due to the lack of differentiation between the explicit and implicit component. In this study, we aimed to investigate how a cognitive secondary task affects visuomotor adaptation overall and its different components, both during and after adaptation. In a series of posttests, we examined the explicit and implicit components separately. Eighty participants performed a center-outward reaching movement with a 30° cursor perturbation. Participants were either assigned to a single task group (ST) or a dual-task group (DT) with an additional auditory 1-back task. To further enhance our predicted effect of dual-task interference on the explicit component, we added a visual feedback delay condition to both groups (ST/DT_{DEL}). In the other condition, participants received visual feedback immediately after movement termination (ST/DT_{NoDEL}).

While there were clear dual-task costs during the practice phase, there were no dual-task effects on any of the posttest measures. On one hand, our findings suggest that dual-task costs in visuomotor adaptation tasks can occur with sufficient cognitive demand, and on the other hand, that cognitive constraints may affect motor performance but not necessarily motor adaptation.

1. Introduction

Catching a fish below the water surface with a spear, drifting through the curve in a game of Mario Kart or guiding an endoscope to perform an incision during microsurgery; these three tasks seem to be completely different in their characteristics, but they all comprise operating a tool that requires mastery of a more or less complex sensorimotor transformation.

A mirrored screen, a broken joystick or strong waves can misguide the targeted movements considerably. In such scenarios, humans need to adapt to a new situation by adjusting the mapping between sensory inflow and motor outflow, thus adapting their sensorimotor

transformation. The human ability to adjust to new sensorimotor transformations has been a topic of interest for more than 150 years (Stratton, 1896; von Helmholtz, 1867; Welch, 1978). One of the most popular paradigms to study this ability in the laboratory is adaptation to visuomotor rotations (Bond & Taylor, 2017; Cunningham, 1989; Hegele & Heuer, 2010; Heuer & Hegele, 2008; Mazzoni & Krakauer, 2006; Schween & Hegele, 2017; Shabbott & Sainburg, 2010; Taylor, Ivry, 2011b; Taylor & Ivry, 2012; Taylor & Ivry, 2014). In this paradigm, participants control the movements of a computer cursor on a screen by hand movements. The relationship between hand and cursor motion is then changed in a way that the movement direction of the cursor is rotated relative to the hand movement. In analogy to the tools outlined

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above, this allows investigating the adaptation to novel or altered sensorimotor transformations. Despite considerable methodological differences, these studies consistently show that humans are able to adapt their hand movements after having practiced reaching a target with the novel visuomotor transformation present.

The apparent simplicity of the change in the visuomotor mapping by rotating cursor motion belies the subtlety of the underlying adaptation, which is not a unitary phenomenon, but requires the interplay of several components. Based on previous studies, a major distinction can be drawn between explicit and implicit components (Hegele & Heuer, 2010; Heuer & Hegele, 2015; Mazzoni & Krakauer, 2006; McDougle et al., 2015; Schween et al., 2018; Schween & Hegele, 2017; Taylor & Ivry, 2014).

The implicit component is thought to reflect the adjustment of an internal model of the respective sensorimotor transformation. Its development is thought to be mainly driven by sensory prediction errors originating from (future) state estimation in the cerebellum (Held, 1965; Wolpert et al., 2011). The effect of these prediction errors and their influence on the development of an internal model has been shown to depend on sensory feedback about the consequence of the performed action (Izawa & Shadmehr, 2011; Wolpert & Miall, 1996). More specifically, previous studies have shown a distinct attenuation of the implicit component, when outcome feedback was delayed (Brudner et al., 2016; Schween & Hegele, 2017). A very important and interesting aspect of the implicit component from the point of view of behavioral experiments is, that it has been suggested that its processing does not engage cognitive resources in general (Seidler & Carson, 2017) and should therefore be more likely to remain unaffected in dual-task paradigms.

The explicit component, on the other hand, is thought to be driven primarily by target (outcome) errors (Taylor, Ivry, 2011a; Wolpert et al., 2011). This explicit component refers to explicit knowledge of the transformation that develops within a conscious focus on the unexpectedly erroneous movement under the new transformation (Frensch et al., 2003). Through this focus, hypotheses are generated about the underlying visuomotor transformation, which are evaluated and refined over the course of practicing the novel transformation. This facilitates the implementation of compensatory strategies of otherwise spontaneously executed movements towards the respective target. One could, for example, point to the side of a visual target knowing that the resulting feedback of the controlled cursor on the computer screen is shifted relative to the hand movement. In contrast to the observed attenuation of implicit adaptation with delayed outcome feedback, explicit adjustments have been shown to either remain unaffected (Brudner et al., 2016) or being facilitated by additional temporal delays in the availability of outcome feedback (Schween & Hegele, 2017). It is argued to be processed in working memory demanding cognitive resources (Anguera et al., 2010; Benson et al., 2011; Seidler et al., 2012), which should make it susceptible to cognitive interference in dual-task paradigms.

One way to assess the need for cognitive resources is to measure differences in adaptation between single task conditions (ST), in which only the adaptation task had to be performed, and dual-task conditions (DT), in which an additional secondary task has to be performed simultaneously to the primary adaptation task. The resulting interference between the two tasks is commonly called *dual-task cost* (Eversheim & Bock, 2001; Galea et al., 2010; Taylor & Thoroughman, 2007; Taylor & Thoroughman, 2008). In cognitive psychology, such dual-task interference is frequently used as a tool to examine the contribution of what are assumed to be capacity-limited cognitive resources and processes (Navon & Miller, 1987; Pashler & Johnston, 1989; Tombu & Jolicoeur, 2002).

In visuomotor adaptation experiments, adding a secondary task has yielded inconsistent results: whereas some studies did report dual-task costs (Eversheim & Bock, 2001; Galea et al., 2010; Hesse et al., 2012; Taylor & Thoroughman, 2007), others did not find any indication for impaired adaptation in the presence of a secondary task (Im et al., 2016;

Song & Bédard, 2015). For example, Eversheim and Bock (2001) asked participants to track a moving target with up-down reversed visual feedback on a computer screen. They observed decrements in tracking accuracy when participants had to simultaneously engage in a manual reaction-time task and concluded that attentional resources used for a secondary task attenuate performance especially in early stages of adaptation, during which attention-demanding processes are needed to adjust the spatial relationship between sensory inflow and motor outflow. Similar performance effects of a secondary task on visuomotor adaptation have been reported by Galea et al. (2010). Using a more cognitive secondary task (participants had to vocally shadow an auditory stimulus), they found reduced adaptation rates in response to both a gradually introduced visuomotor rotation of 30° as well as a step-wise rotation of 30° adaptation.

In stark contrast to the two aforementioned studies, Song and Bédard (2015) and Im et al. (2016) conducted a series of dual-task studies, in which they did not find any evidence for dual-task costs on visuomotor memory. In their experiments, participants performed a secondary rapid serial visual presentation task, while adapting to a 45° visually rotated cursor. Contrary to the authors' original hypothesis, they found no attenuation of adapted performance during practice.

Here, we provide and test the tentative hypothesis that these diverging findings might be explained by the differential involvement of explicit and implicit components of visuomotor adaptation across studies. Specifically, we assume that explicit adaptation requires the use of cognitive resources to develop explicit knowledge about the visuomotor rotation (Mazzoni & Krakauer, 2006; Taylor et al., 2014). Hence, a cognitively engaging secondary task should impair explicit adaptation. In contrast to this, feedback corrections based on the same sensory prediction errors that drive implicit adaptation have been found immune to cognitive interference (Taylor & Thoroughman, 2007). We therefore assume that implicit adaptation should be unimpaired by a cognitively engaging secondary task. Assuming that explicit and implicit components of adaptation are approximately additive in producing overall adaptation, variations in task designs across studies that affect the contribution of explicit and implicit components could therefore explain the differential impairment of overall adaptation by secondary tasks. Notably, there might be doubt about our above reasoning based on the fact that implicit learning of motor sequences was attenuated when a secondary cognitive task was performed simultaneously (Frensch et al., 1998; Hsiao & Reber, 2001; Stadler, 1995; Stadler, 1997). We believe that this does not invalidate our assumption that implicit adaptation is immune to interference from a cognitive secondary task. According to recent models of motor control and adaptation (Diedrichsen & Kornyshova, 2015; Ikegami et al., 2021; Wong et al., 2015) the selection of sequential actions is distinct from the adaptation of individual action components to the current spatial and dynamic requirements. Following this reasoning, implicit, prediction error-based adaptation is situated at a lower level of a motor hierarchy (Schween et al., 2019) and thus likely remote from cognitive interference that affects implicit sequences learning.

To summarize, previous studies have shown different results in relation to dual-task costs on visuomotor adaptation. However, these studies did not consider explicit and implicit components of adaptation, separately. Hypothesizing that the two components respond differently to a secondary cognitive task, we will monitor the influence of a cognitive secondary task on practicing a novel visuomotor transformation and quantify the resulting adaptive behavioral changes with respect to its explicit and implicit components. More specifically, we use a series of posttests (adaptive shifts = overall adaptation, aftereffects = implicit adaptation, explicit shifts = explicit adaptation) that (a) dissociate explicit and implicit adaptive components and (b) assess adaptation under single-task conditions to elucidate whether the presence/absence of a secondary task during practice had modulated adaptation. We predict that adaptation is attenuated after practicing with a secondary task whenever the explicit component is able to contribute to

visuomotor adaptation. For our test of aftereffects that is thought to exclusively measure implicit adaptation (see methods for a more thorough description of the design and reasoning behind this set of post-tests), we do not expect any difference between groups that had practiced with or without a secondary task. Furthermore, as both, explicit and implicit components contribute to performance during practice, we also predict dual-task costs to appear during practice of the visuomotor rotation. As a secondary task, we use an auditory 1-back task, which has been shown to be loading working memory and cognitively demanding. To increase the involvement of the explicit component and thus make the design even more sensitive to dual-task interference, we additionally incorporate groups who practiced the visuomotor rotation with delayed outcome feedback as this has shown to attenuate implicit, but facilitate explicit adaptation (Schween & Hegele, 2017).

2. Methods, setup & protocol

2.1. Participants & experimental groups

80 neurologically healthy, right-handed participants with normal color vision and normal or corrected-to-normal visual acuity were recruited via the Ludwig-Maximilians-University's email distribution list. Handedness was assessed prior to the experiment (Büsch et al., 2009). All participants were either students from the Ludwig-Maximilians-University or the Technical University of Munich. The study was approved by the local ethics committee and all participants gave written informed consent before testing. Participants received monetary compensation or course credit for their participation.

Participants were randomly assigned to one of four experimental groups - single task condition with added feedback delay (ST_{DEL}), single task condition without added feedback delay (ST_{NODEL}), dual-task condition with added feedback delay (DT_{DEL}), dual-task condition without added feedback delay (DT_{NODEL}) – implementing a 2 × 2 factorial design.

One participant from the DT_{DEL} group was excluded from analysis, as they did not finish the experiment due to scheduling issues, resulting in a total number of 79 participants.

2.2. Apparatus

Participants were seated in a dark room on a height-adjustable chair facing a vertically oriented 22-in., 120 Hz LCD-Screen (Samsung 2233RZ) approximately at head height in 1 m distance. Movements were performed in the horizontal plane on a graphic tablet (WACOM Intuos 4 XL; 62 cm × 46.5 cm × 3 cm) using a graphic stylus. The tablet was placed in a custom-made occluder so that participants could not see their hand during the experiment. The tablet tracked the coordinates of the tip of the stylus with a sampling frequency of 130 Hz. Data collection and stimulus presentation were controlled and generated in a custom Matlab script (2015a, 32 Bit) using the Psychophysics toolbox (Brainard & Vision, 1997; Pelli, 1997).

2.3. Task

Instructions for the whole experiment were presented as written text on the screen. The participants were able to read through the instructions at their own pace and scroll back, if necessary, before starting the actual task. This was to ensure that they really understood the task required of them. A schematic representation of the task is shown in Fig. 1.

2.4. Motor task

The primary motor task was a center-out reaching task towards one of two possible target locations (−22.5° or −67.5°, with 0° corresponding to horizontal rightward movement and a negative sign

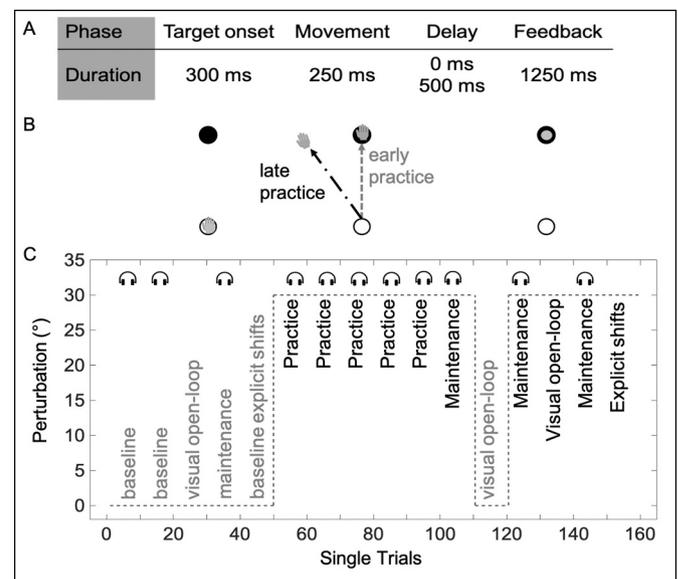


Fig. 1. Schematic representation of the experiment, divided into the temporal sequences (A), visual stimuli and movement subtasks (B) within one trial and across the whole experiment (C). Panel A shows the individual segments of one single trial in their chronological order and their maximum duration. The delay between movement termination and feedback presentation differed between delay groups (NO DEL vs. DEL) and was either 0 ms or 500 ms. Panel B shows the visual feedback presented on the screen with its associated hand movements, each vertically aligned to its respective phase segment from panel A. During target onset (left hand panel), the participant saw the trial target and kept their hand and visible visual cursor within the starting position. During movement (middle pane) participants were required to perform reaching movements to the target in the absence of concurrent visual feedback about their cursor. Arrows represent hand movement. The light grey arrow shows hand movement early during practice, when no compensatory behavior is adapted, while the darker arrow represents hand movement at the end of practice, when participants had developed a compensatory behavior for the cursor manipulation. Panel C shows the perturbation present in the experiment over the individual trials. In addition, the labels of the individual trial phases are inserted in a block-like manner. The shaded phase descriptions represent cursor perturbation (lighter grey for no manipulation, darker grey for a 30° manipulation). To illustrate the schedule of the secondary task, headphones are drawn in the blocks with secondary task above the phase label. In the blocks with no headphones above the phase label, participants did not have to complete a secondary task. For a more detailed description of the individual trial types and segments within one trial, see the methods section - experimental protocol.

indicating counterclockwise rotation from 0°). Participants started with a black screen and the starting position in the center of the screen (outline of a white circle with 3.5 mm radius). The cursor was presented as a white concentric circle, the radius of which depended on the distance of the current hand position to the starting position. As soon as the participants placed the cursor within the starting position (within 3.5 mm of the center of the screen) and kept the stylus still for at least 300 ms, the concentric circle vanished and the cursor turned into a cyan filled cursor (2.4 mm radius) at hand position. At the same time a white, filled circle serving as the trial target (2.8 mm radius) appeared in one of the two locations at a target amplitude of 90 mm. The task goal in every trial was to perform a fast and smooth movement on the tablet, “slicing” the cursor through the target. During maintenance and practice trials, the cursor was present before movement onset, while resting in the starting position. It disappeared upon movement onset and reappeared after movement termination and group specific feedback delay at the intersection of movement trajectory and target amplitude. During visual open-loop trials, the cursor did not reappear at target amplitude but remained completely invisible.

2.5. Cognitive task

The secondary task for dual-task groups was an auditory–verbal 1-Back task. They received written instruction together with the instructions for the motor task to ensure that they understood both tasks before starting the experiment. Over headphones, participants listened to an audio file that reported digits in a mechanical voice in standardized speed and volume while practicing the visuomotor adaptation task. The digits were pseudorandomized for each participant. Participants were required to verbally report whenever they judged a digit to be the same as the preceding one (1-Back) and their responses were collected by the experimenter. Participants did not receive any feedback about correctness of their answer. The secondary task was present during all maintenance and practice trials, independent of the cursor manipulation. In contrast to other studies (Im et al., 2016; Song & Bédard, 2015), our secondary task was not tied to the timing of movement but was applied freely throughout movements and inter-movement intervals. In order to assess explicit and implicit adaptation in the absence of potential performance-attenuating effects of the secondary task, the 1-Back task did not occur in any test sessions, neither in pre- nor in posttests. Participants in the single task groups also received auditory input over headphones. They heard two differently pitched sounds. A high-pitched sound signaled the start of the trial and one low pitched sound signaled the end of the trial. The headphones were noise-cancelling headphones (Bose Quiet Comfort 15).

2.6. Procedure

The experiment was divided into five phases: familiarization, baseline, pretest, practice and posttests. The first 72 trials were used to familiarize participants with the procedures. For this, participants performed the center-outward reaching movements of the main task in self-selected directions, with no cursor perturbation and no specific reaching target. Data in this phase was not recorded. For all following phases, trials were segmented into blocks of ten consecutive trials, five movements to each target location. For analysis, values were averaged within one block.

During baseline, visual cursor positions corresponded to the actual stylus positions (i.e., no perturbation). The baseline phase consisted of two blocks of practice trials in which the dual-task groups also had to complete the secondary task. This was then followed by two test blocks in the pretest phase. The pretests were divided into two test types, neither of which was accompanied by a secondary task: visual open-loop trials and explicit shift test trials. In visual open-loop test trials, visual feedback of the cursor was withdrawn. The task itself remained the same as during the baseline practice trials, with participants being required to perform fast center-outward reaching movements, trying to slice the then invisible cursor through the target, without being informed about their movement outcome. For the explicit shift test (Hegele & Heuer, 2010; Heuer & Hegele, 2008), participants were asked to put down the stylus and place their hand on their thigh. A target, and a straight white line (90 mm length) with the origin in the white starting circle appeared on the screen. The experimenter rotated the line clockwise around the starting circle until the participant judged the line to resemble the movement path to that particular target in baseline or maintenance trials in previous phases.

In five blocks of practice trials, the direction of the cursor's path was manipulated so that it was at a 30° angle to the stylus's movement path, which required the participants with the task of adjusting their own movement in a compensatory manner, as they were instructed to make sure, they continued to slice the cursor through the target. Dual-task groups were also continuously asked to perform the secondary task throughout the whole practice phase.

The posttests were similar to the pretests in baseline: It started with two visual open-loop tests, where the cursor remained invisible even after movement termination. For the first visual open-loop test block,

the participants were instructed to perform the same movement as in the baseline trials. They were also informed, that the cursor would remain invisible but that it would veridically follow the path of their hand. For the second visual open-loop test, the participants were instructed, that the cursor's path would again be manipulated in the same way, as they experienced during the practice phase. The last test block was the explicit shift test, in which the participants were also informed about the manipulation they would need to consider for their judgement.

Between each posttest block, participants performed a block of maintenance trials, that were the same as practice trials with perturbation. The secondary task was present during maintenance trials for dual-task groups (DT_{NoDEL}/DT_{DEL}).

Movement termination was defined as the instance when the stylus had the same coordinates in at least two consecutive frames. Participants in delay groups (ST/DT_{DEL}) received task feedback in form of a static cursor at target amplitude 500 ms after movement termination. Participants in the no delay groups (ST/DT_{NoDEL}) received task feedback immediately after movement termination. If participants performed dynamically irregular movements, like not reaching the desired movement-termination in time, or if they moved too fast (<200 ms) or too slow (>500 ms), they received an error message (in German “Zu schnell!” or “Zu langsam!”, respectively) on the screen and the trial was aborted. No messages were displayed when movement criteria were appropriate.

2.7. Data analysis

X and Y position data of the stylus were continuously tracked. In order to filter out high-frequency noise, which for biomechanical reasons could not have originated from the movement, but rather reflected artifacts from the dispersion from the measurement system, a smoothing filter was used. An algorithm that is frequently used for this kind of smoothing is the Butterworth filter. We filtered the data with Matlab's own functions “butter” and “filtfilt” using a 4th order Butterworth filter and a cutoff frequency of 10 Hz. Movement onset was measured as the first frame in which the sensor position reached Euclidean distance to the center of the start larger than 1 mm. Movement end was detected when two exact identical sensor positions occurred in succession. Those had to be at least 45 mm away from the start in order to be detected as movement termination. Movements with extreme durations (<200 ms or > 500 ms) were excluded from analysis. The primary outcome measure was *hand direction* relative to the target. It was calculated as the angular difference between the vector connecting the start position with the hand position at target amplitude and the vector connecting the start position with the actual target position. This procedure was the same in all movement trials. For the *explicit shift* pre-and posttest trials, the angular difference of the orientation of the vector connecting the start position with the target position and presented white line was calculated. The hand directions from the posttest phase were used to determine the change in behavior in the separate adaptation components caused by repeatedly compensating for the cursor perturbation during practice. The outcome variable for the posttest phase was obtained by baseline-correcting hand directions. For this, values from baseline blocks were subtracted from the values of the respective posttest blocks. We thus had three different, continuous, dependent variables, one for *implicit aftereffects*, one for *adaptive shifts* and one for *explicit shifts*. The variable implicit aftereffects measured values from the visual open-loop test without cursor path manipulation, which measure the implicit component of adaptation. The variable adaptive shifts measured values from the visual open-loop test with cursor path manipulation, in which the combined influence of explicit and implicit components was effective. The explicit shift test examined the verbally recallable compensation strategy the participants used to encounter the cursor rotation as a proxy for the explicit component.

For statistical analysis, each of the outcome measures were averaged into trial blocks for each participant, resulting in five average measures

for practice, and one average measure for each posttest. For further analysis, averaged measures were used as dependent variables while delay (DEL and NoDEL) and condition (ST and DT) served as independent between-subject variables, all together resulting in a 2-by-2 factorial design.

Measures were tested for distribution of normality and the assumption of homogeneity of variance using the Shapiro-Wilk test and Levene's test, respectively. Where these assumptions were met, we tested for significant differences using either repeated measure or one way analysis of variance (RM-ANOVA) with between subject factors delay (DEL and NoDEL) and condition (ST and DT) and within subject factor practice block. Where assumptions were violated, we used the ANOVAS non-parametric counterparts. In the case of differences during practice, this was a f_2 - l_d - f_1 analysis, which is a non-parametric alternative to a RM-ANOVA (Noguchi et al., 2012). For the posttests, we used the frequentist ANOVA provided by JASP (JASP Team 2021, Version 0.15). All statistical analyses were done in Matlab (2017b), R and JASP (JASP Team 2021, Version 0.15). For dual-task effects on adaptation, the hypothesis predicted the same effect direction in all three posttests: due to dual-task interference during practice, the DT groups should show smaller adaptive adjustments in the posttests than the single task groups. When the frequentist approach revealed non-significant results for one of the group comparisons, for which we hypothesized the occurrence of dual-task effects on adaptation, we additionally computed Bayes Factors (BF_{01}) reflecting the probability of the null model (i.e., no dual-task costs present) conditionally on the observed data. To this end, we computed directed independent sample t -Tests to obtain an estimate of whether the non-significant findings would count against our hypothesis or merely indicate data insensitivity.

For delay effects in the aftereffects, the hypothesis was directed in that we expected lower implicit aftereffects, but larger explicit shifts in the delay groups. No difference was expected for the adaptive shifts, which comprise both explicit and implicit components (Schween & Hegele, 2017).

3. Results

3.1. Differences during adaptation practice

Fig. 2 shows the whole practice phase. Participants in both delay groups of the respective task condition show a similar level of performance already at the beginning of the practice phase. This is due to the fact that the practice blocks represent the mean value of ten consecutive trials and thus the increase in performance gain from the first couple of trials is not visible in this figure. Furthermore, a differentiation over the course of the practice phase between dual-task and single task is clearly visible, not so much so for the delay groups within the same task

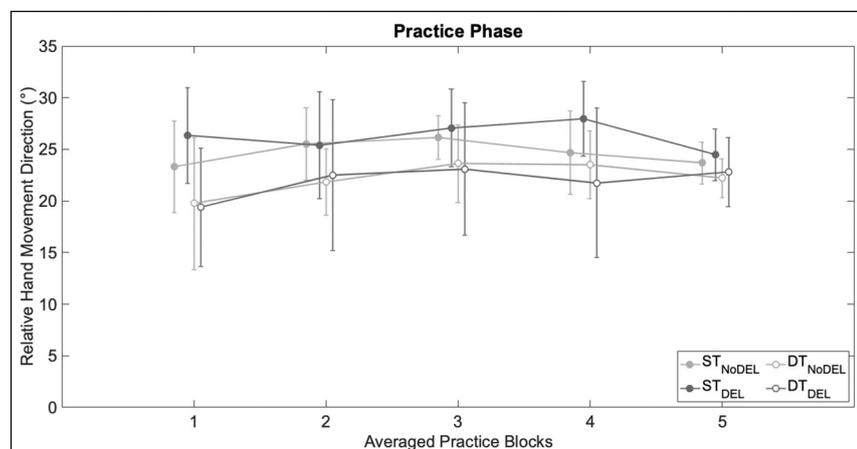


Fig. 2. Results for hand movement direction relative to trial target during practice. Lines with solid markers are single task groups with and without feedback delay. Lines with hollow markers are dual-task groups with and without feedback delay. Lighter grey represents the groups without feedback delay, both in the single and dual-task condition, while darker grey represents both condition groups with feedback delay. Values for final hand movement direction are median averaged for each practice block (10 consecutive trials, 5 to each target). Error bars show median absolute deviation (mad).

condition. At the end of the practice phase, all four groups had achieved a similar level of performance. We used a non-parametric version of a 2 (single- or dual-task) \times 2 (delay or no delay) \times 5 (time-point) mixed ANOVA with hand position as the dependent variable. We found a significant main effect for practice block (ANOVA Type Statistic = 9.088, $df = 3.30$, $p < 0.01$). We hypothesized that the dual-task groups would show decreased performance during practice, revealing dual-task costs. In support of this hypothesis, ST groups did indeed show better performance during practice, as indicated by a significant main effect of task condition (ANOVA Type Statistic = 5.977, $df = 1$, $p < 0.01$). There was no significant effect of feedback delay, nor any significant interaction for the practice phase.

3.2. Differences during posttest phase: overview

After the practice phase, participants performed a series of posttests in the absence of the secondary cognitive task. Those tests provided measures for implicit aftereffects, adaptive shifts reflecting overall adaptation and explicit shifts. Results for all three posttests are shown for each group in Fig. 3.

3.2.1. Implicit aftereffects

For implicit aftereffects, we calculated a 2 (single- vs. dual-task) \times 2 (delay vs. no delay) between-subjects ANOVA with relative hand movement direction as dependent variable. In line with previous studies (Brudner et al., 2016; Schween & Hegele, 2017), the feedback delay attenuated implicit aftereffects. The ANOVA revealed a significant main effect for delay, $F(1,75) = 17.399$, $p < 0.01$, $\eta^2 = 0.188$, confirming a reduced contribution of the implicit component of adaptation in the delay groups compared to no delay groups. There was, however, no effect for task condition, $F(1,75) = 0.621$, $p = 0.433$, $\eta^2 = 0.008$. Even though we had no prior expectation for dual-task effects on implicit aftereffects, we took inspiration from prior studies in cognitive psychology using serial reaction time tasks that showed dual-task costs for implicit sequence learning (Frensch et al., 2003; Hsiao & Reber, 2001) and computed a directed Bayesian independent samples t -Test to further probe the non-significant effect of a concurrent secondary task during practice on the implicit component of adaptation. This analysis yielded a Bayes Factor (BF_{01}) of 6.971 indicating that the data were almost 7 times more likely under the null hypothesis of no dual-task costs in the implicit aftereffects. There was no significant interaction (Fig. 3 left panel).

3.2.2. Adaptive shifts

The adaptive shifts posttest is assumed to comprise both explicit and implicit components of adaptation. The explicit component was predicted to be more susceptible to cognitive interference. Therefore, we expected to find significant differences between single task and dual-

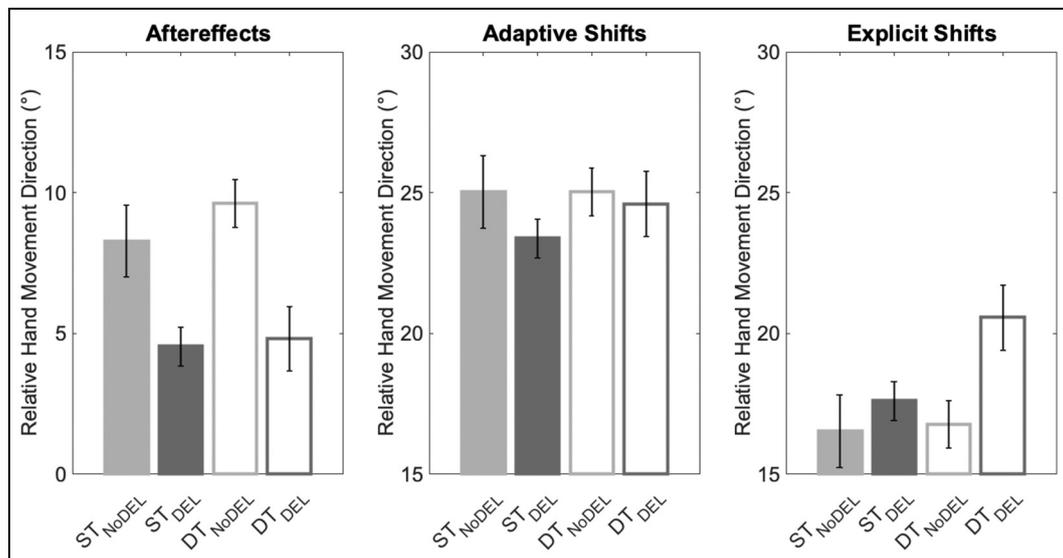


Fig. 3. Change of hand direction relative to target direction from pre to posttest. Error bars represent standard error of the mean (SEM).

task groups within this posttest. We calculated a 2 (single- vs. dual-task) \times 2 (delay or vs. delay) between-subjects ANOVA. Even though we did find evidence for dual-task costs during practice, there was no main effect for task condition, $F(1,75) = 0.091$, $p = 0.764$, $\eta^2 = 0.001$. The absence of dual-task effects on adaptive shifts was further supported by a directed Bayesian independent samples t -Test that yielded moderate evidence against dual-task interference in adaptive shifts ($BF_{01} = 5.309$). Further, there was no significant main effect for delay, $F(1,75) = 0.268$, $p = 0.606$, $\eta^2 = 0.003$; $BF_{01} = 3.786$ (non-directed) and no significant interaction, $F(1,75) = 0.091$, $p = 0.764$, $\eta^2 = 0.001$ (Fig. 3 middle panel).

3.2.3. Explicit shifts

A previous study, from which the current experimental design was adapted, postulated the idea of a push and pull relationship between the explicit and the implicit component, meaning that whenever certain manipulation causes the implicit participation to decrease, the explicit process will proportionally increase to compensate for the reduced contribution from implicit processes (Schween & Hegele, 2017). We calculated a 2 (single- vs. dual-task) \times 2 (delay vs. no delay) between-subjects ANOVA with perceptual judgments of hand movement directions appropriate to reach a specific target as dependent variable. We used the feedback delay manipulation to promote the explicit component and to further highlight the dual-task effects to be expected in this component. In contrast to our assumption, our results showed that delay had no impact on explicit contributions to visuomotor adaptation ($F(1,75) = 1.464$, $p = 0.230$, $\eta^2 = 0.019$). Following up on this non-significant result with a directed Bayesian independent samples t -Test yielded a Bayes Factor (BF_{01}) of 1.327 suggesting that the explicit shifts posttest was not sensitive enough to provide empirical evidence for either hypothesis. In addition, and also contrary to our predictions, we did not find any dual-task effects in the explicit shifts' posttests, $F(1,75) = 0.619$, $p = 0.434$, $\eta^2 = 0.008$. Contrary to the follow-up analysis of the delay factor, however, a Bayes Factor of 6.933 (BF_{01}) obtained from the directed Bayesian independent samples t -Test provided moderate evidence against an effect of dual-task interference on the explicit components of adaptation.

4. Discussion

The aim of this study was to investigate whether a secondary cognitive task would differentially interfere with explicit and implicit components of visuomotor adaptation. This would provide a potential

explanation for inconsistent findings by previous studies, which did not control for the contribution of explicit and implicit processes. We hypothesized that a cognitive secondary task should interfere with the explicit component of adaptation, while the implicit component should remain unaffected. Assuming that the explicit component was susceptible to dual-task interference, we expected to find dual-task effects on adaptation (i.e., less accurate reaching) whenever the explicit component dominated the adaptive adjustments. Accordingly, we expected to see dual-task costs during the practice phase, when potentially both explicit and implicit processes are at work, as well as dual-task effects during the posttests for adaptive shifts and explicit shifts. However, we did not expect to see dual-task effects on the implicit aftereffects.

While the present results clearly show dual-task costs in the performance of a novel visuomotor transformation, our posttests failed to provide any evidence of dual-task effects on visuomotor adaptation. Bayesian analyses of the posttest data with respect to the main effect of presence/absence of a secondary task during practice yielded moderate evidence for the null hypothesis suggesting that the absence of dual-task effects in all of the posttests was not primarily due to the data just being insensitive, but rather reflects the absence of dual-task interference with respect to implicit, and surprisingly also explicit adaptation. Analyzing performance during practice, however, revealed clearly observable dual-task costs, which disappeared once the secondary task was removed in the posttest phase.

While it is admittedly hard to argue for evidence of absence based on the absence of evidence, we believe this particular study to be informative as we obtained some evidence in support of the absence of evidence (see above) and also designed our study to maximize the chances of detecting dual-task effects, if there were any, specifically in the explicit component of visuomotor adaptation.

Firstly, we not only compared single- and dual-task practice of a visuomotor rotation. In order to increase the experiment's sensitivity for observing potential dual-task effects on the explicit component, we included feedback delay as an additional between-participants factor. Delaying outcome feedback has been previously shown to shift adaptation towards using explicit strategies (Schween & Hegele, 2017). We thus expected higher chances to detect dual-task effects on the explicit component as we hypothesized that performance in the delayed condition would be more susceptible to dual-task interference. But even with delayed feedback, we did not observe any dual-task effects on adaptation as measured in our posttests after practice. Note however, that while the present study successfully replicated the previously observed attenuation of implicit adaptation under conditions of delayed outcome

feedback, indicating that this is a rather robust empirical finding probably associated with the temporal discounting of error information or the temporal decay of prediction errors in the implicit adaptation system, we could not replicate the delay effect on the accumulation of explicit knowledge of the transformation, probably due to insufficient sensitivity of our data.

Another measure to assess dual-task interference in visuomotor adaptation was that we examined a larger sample of participants ($N = 79$), compared to previous studies on this topic (Eversheim & Bock, 2001; Im et al., 2016; Song & Bédard, 2015; Taylor & Thoroughman, 2008). This led to an increase in statistical power allowing us to identify dual-task costs on performance during the practice phase.

Furthermore, we sought to maximize the potential effects of a concurrent secondary task on visuomotor adaptation by employing the secondary task throughout the entire practice phase, not limiting it to trial on- and offset. This ensured that participants in the dual-task groups had to attend to both the primary motor task and the secondary cognitive task throughout the entire practice phase. Thus, there was no opportunity for them to focus only on the motor task during the intertrial interval. As we found clear evidence for dual-task interference during practice, we consider the secondary task chosen in this paradigm to be effective in engaging cognitive resources. Having a cognitive demanding secondary task present throughout the whole practice phase might be critical as it has been shown that a few seconds of pause are sufficient to allow for consolidation of the acquired motor task (Bönstrup et al., 2020; Reis et al., 2008). Having only a cognitive secondary task during the execution of the motor task, but not within the inter trial interval might also explain why Im et al. (2016), and Song and Bédard (2015), found no dual-task costs in their studies.

Thus, the design features of the experiment were informed choices to reinforce and differentiate the dual-task effects on the explicit component of adaptation. Therefore, we consider the null results of this study to be meaningful. Given the results of the follow-up Bayesian analysis of the non-significant group differences with respect to dual-task cost, which provided moderate evidence in favour of accepting the null hypotheses, this indicates that visuomotor adaptation, at least under certain conditions, does not necessarily depend on cognitive resources. However, if future research develops studies that are even more specifically adjusted for finding dual-task interference, we expect that these effects will be extremely small, if they exist at all. However, it is not entirely out of the question that other factors may have led to us not finding dual-task effects on adaptation in the posttests, which are discussed below.

Firstly, the posttest phase in our study was preceded by an instruction phase of about two to five minutes giving participants enough time between the last trial of the motor task with cognitive interference and the first posttest trial to let offline gains occur. This would imply that humans can keep relevant feedback information from practice of the visuomotor rotation in memory and use it for learning once cognitive resources become available. From theoretical reasoning, we would expect such offline gains only to affect the explicit component, since the implicit component already decays with a 500 ms feedback delay (Brudner et al., 2016; Schween & Hegele, 2017) and is therefore unlikely to be consolidated offline.

A second explanation for the absence of dual-task effects on adaptation in our posttests is the length of the practice phase. Because there were only two targets, it is possible that participants quickly reached a ceiling effect in the motor task. Since we did find dual-task costs during the practice phase, it is possible that those costs reflect participants in the dual-task groups taking longer to reach the same level of adaptation as the participants in the single task groups, but the practice phase was sufficiently long for participants in the dual-task group to eventually overcome those differences.

It is also worth noting that our results contrast previous studies that claimed that performance in visuomotor tasks does not suffer from cognitive dual-task interference (Liu et al., 2008; Singhal et al., 2007).

The findings from our study contradict this claim and add a further paradigm (the visuomotor rotation task) to the growing list of visuomotor tasks for which dual-task interference has been demonstrated (Göhringer et al., 2018; Hesse et al., 2012; Hesse & Deubel, 2011; Janczyk & Kunde, 2010; Kunde et al., 2007; Löhr-Limpens et al., 2020).

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4. The feedback-related negativity (FRN) as a proxy for explicit and implicit components of visuomotor adaptation

4.1. Introduction

Humans adapt their behavior according to changes in the environment - e.g., changing one's gait on an icy path of pavement – or within the body – caused by fatigue or injuries. More than a hundred years of research have revealed that especially the human visuomotor system possesses a remarkable degree of plasticity (Köhler & Klein, 1964; von Helmholtz, 1867; Welch, Choe, & Heinrich, 1974). Amongst others, such plasticity enables humans to adapt to novel visuomotor gains and rotations. While visuomotor gains refer to novel ratios of visually perceived distances and the associated amplitudes of body movements, visuomotor rotations refer to altered relations between the visually perceived direction of a target and the associated movement of an end effector. Such adaptive behavior is thought to involve at least two qualitatively distinct components: a slow developing, implicit component, which is based on sensorimotor remapping, and a fast-developing explicit component, which allows for rapid error reduction by using conscious strategic corrections (Hegele & Heuer, 2010; Heuer & Hegele, 2015; Mazzoni & Krakauer, 2006; McDougle et al., 2015; Schween & Hegele, 2017; Schween et al., 2018; Taylor, Krakauer, & Ivry, 2014).

Previous research suggests that one difference between the explicit and implicit components is the sensitivity to time, including their operations on distinct time scales. The explicit component has previously been defined as the control mechanism behind deliberate strategic motor behaviors, such as consciously re-aiming one's reach to compensate for a salient visual perturbation. It has been suggested that such deliberate strategies may be based on time-consuming manipulations such as mental rotation (Shepard & Metzler, 1971). McDougle and Taylor have put forward the idea that previously to executing the movement, participants mentally rotate the movement to compensate for the perturbation (McDougle & Taylor, 2019). Such processes are associated with cognitive resources such as the working memory (Fernandez-Ruiz et al., 2011; Haith et al., 2015). Explicit processes arise from target errors, rather than sensory prediction error, and are driven primarily by salient errors larger than 25° (Bond & Taylor, 2015; Kim et al., 2018). In line with the Unexpected Event Hypothesis (Frensch et al., 2003), large and unexpected errors in movement outcomes trigger a search for their causes along with the generation of strategies to realign intended and actual movement outcomes. In adjusting to a novel visuomotor transformation, for instance, self-generated explicit knowledge of the transformation is used to induce deliberate changes in aiming direction of the subsequent movement. On the other hand, previous studies have linked the implicit component to sensory prediction errors (SPE, (Miall et al., 1993; Schlerf et al., 2013)), a mismatch between predicted and actual sensory feedback during (ie. concurrent feedback (Hinder

et al., 2008a; Sülzenbrück & Heuer, 2011)) and immediately after (ie. terminal feedback (Bernier, Chua, & Franks, 2005; Heuer & Hegele, 2008a)) movement execution. Theory shows that sensory prediction is the correct form of error for training an internal forward model (Körding & Wolpert, 2004; Wolpert & Kawato, 1998).

In recent years, research has focused on quantifying and experimentally dissociating the relative contributions of each of these underlying components to motor adaptation (Hegele & Heuer, 2010; Morehead et al., 2017; Taylor & Ivry, 2014; Taylor et al., 2014). Specifically, visuomotor rotation tasks, in which participants are asked to reach for a target and adjust their movement to compensate for an imposed rotation of visual feedback of their manually controlled cursor, offer a range of methods to estimate the explicit and implicit contribution to adaptation. These methods can be divided into two classes. In direct methods, participants are explicitly asked or cued to include or exclude conscious strategies they might have developed based off on accumulated explicit knowledge of the transformation. This class includes a measure of the implicit component called aftereffects, or exclusion, in which participants are asked to aim straight towards the target without receiving visual feedback of their movement. This measure can occur either throughout adaptation or at the end of it. Participants will typically produce a residual error of around 10° up to 30° in compensatory direction (Hegele & Heuer, 2010; Taylor et al., 2014), indicating the amount of sensorimotor recalibration that took place. For the explicit components, participants can simply be asked to report their intended aiming direction – either concurrently (Taylor et al., 2014) or by means of post adaptive perceptual judgments (i.e., posttests) (Hegele & Heuer, 2010).

These two types of directly assessing explicit and implicit contributions to visuomotor adaptation each have their advantages and disadvantages. Reporting one's aiming direction before each movement during adaptation (Taylor et al., 2014), for example, has the advantage that the process is directly assessed at the time of testing. However, since it requires overt instructions and time, these methods shift participants' attention towards what is being measured. This attentional shift can affect participants' behavior and lead to confounds in the measurements (Newell & Shanks, 2014; Timmermans & Cleeremans, 2015). Explicit re-aiming, for example, can be reinforced by participants being repeatedly reminded of the perturbation (Maresch et al., 2021a). Differentiated posttests for the explicit and implicit component circumvent the problem of stirring attention, but at the cost of not being able to assess adaptation as it unfolds over time (Hegele & Heuer, 2010; Hegele & Heuer, 2013). In addition, studies utilizing posttests introduce changes in task context from trials, in which adaptation is induced, to trials, in which the final levels of adaptation are assessed in the absence of visual feedback. Previous studies have indeed shown that subtle changes in task features modulated the extent of explicit and implicit adaptation (Heuer & Hegele, 2015; Schween et al., 2019). Accordingly, changing contextual features of the previously learned task for

testing purposes might eliminate some cues or features associated with implicit adaptation. To accurately reflect the contributions of explicit and implicit processes during adaptation, indirect methods that do not change task features are desirable. Such indirect methods describe another class of tests used to measure the contribution of explicit and implicit processes to overall adaptation by extracting information from behavioral proxies for explicit and implicit adaptation that neither change task contexts nor bias participants' attention towards specific features of the experiment. In this context, several studies have linked eye movements to (components of) explicit re-aiming (Bromberg et al., 2019; de Brouwer et al., 2018), because they found a systematic connection between features of the explicit component and certain eye movements emerged. For example, participants who fixated a point off target before movement initiation, that approximately described the compensatory strategy, also showed faster adaptation and larger error corrections (de Brouwer et al., 2018). Another approach to shed light into the inner workings of those dissociated behavioral components would be to map out the neural correlates of explicit and implicit processing.

Previous research on the neural correlates of performance monitoring in motor learning has identified two event-related potentials (ERP) in the EEG that are most closely associated with error processing and the trial-to-trial adjustments required to master novel sensorimotor transformations. The error-related negativity (ERN) was first reported by two independent research groups in the early 1990s as neurophysiological evidence for error monitoring in choice reaction time tasks (Falkenstein et al., 1991; Gehring et al., 1993). The effect window of the ERN was set around 50 ms - 100 ms after movement and elicited in medio-frontal areas of the brain. In the years following the initial report of the ERN, it has been reliably replicated and has become a standard ERP for error monitoring (e.g., (Joch et al., 2017; Krigolson & Holroyd, 2006; Krigolson & Holroyd, 2007a; Krigolson & Holroyd, 2007b; Maurer, Maurer, & Müller, 2015)). A few years after the ERN was reported, another ERP became relevant in the field of error monitoring, the feedback-related negativity (FRN). As the name states, it is characterized by a negativity that is set to occur shortly (200 – 400 ms) after feedback presentation of movement outcomes (Miltner et al., 1997). It is primarily localized in fronto-central areas of the brain, mostly within the anterior cingulate cortex (ACC). Whereas the ERN is mostly associated with it being sensitive to internal error detections, the FRN is supposed to reflect processing of external errors (Krigolson & Holroyd, 2006; Miltner et al., 1997), rendering it possibly useful for assessing error monitoring in visuomotor adaptation paradigms.

In order to investigate the potential of the FRN as a proxy for explicit or implicit components of visuomotor adaptation, we focus on two characteristic features of explicit and implicit adaptation and examine how the FRN reacts to experimental modulations of these two features. The first

characteristic feature by which explicit and implicit adaptation could be distinguished in previous studies is the susceptibility to temporally delayed outcome feedback. Previous studies showed (Brudner et al., 2016; Langsdorf et al., 2022; Schween & Hegele, 2017) that delaying outcome feedback by as few as 200 ms attenuated implicit adaptation. One study by Schween and Hegele (2017) even found support for the notion that delaying outcome feedback facilitated explicit adaptation thus compensating for the attenuated implicit component and keeping overall adaptation on the same level regardless of feedback delay. Therefore, we reasoned that manipulating the temporal availability of feedback about a movement's outcome, while keeping all contextual features including error size, error type and motor output identical between groups, would selectively bias visuomotor adaptation to rely more on either implicit or explicit component. Thus, delay-induced modulations of the FRN should tell us something about its use as a proxy for either explicit or implicit adaptation. More specifically, if the FRN was primarily reflecting the implicit part of error processing within visuomotor adaptation, we would expect the FRN to decrease with increasing feedback delay. If, on the contrary, the FRN was reflecting action monitoring within the explicit component of visuomotor adaptation, we would expect it to increase with increasing feedback delay.

Besides biasing adaptation to rely more on either component by delaying movement outcome feedback, error sensitivity might be another way to differentiate between the explicit and the implicit component of adaptation (Bond & Taylor, 2015; Wei & Körding, 2009). Target errors are greatest in the initial stage of learning, leading to large variability in the beginning but also to the most significant error corrections. These eventually lead to a rapid increase in behavioral performance with resulting changes in conscious strategies that are proportional to the size of the error, no matter how large. Bond and Taylor (2017) for instance showed, that explicit learning scaled with respect to the size of the visuomotor rotation to which participants had to adapt. The error sensitivity of the implicit component of adaptation, on the other hand, was shown to saturate at error sizes below 15° (Bond & Taylor, 2015; Kim et al., 2018; Morehead et al., 2017). Based on these previous studies, we sought to test whether the FRN would also proportionally scale with error size mirroring the error sensitivity of explicit adaptation or whether the FRN would remain disproportional to error size in a similar way that implicit learning has been shown to be. Accordingly, we predict an increase in the FRN with increasing outcome errors if the FRN primarily reflected processing of the explicit component adaptation and conversely a stable FRN across different error sizes in case of the FRN reflecting the workings of the implicit components of adaptation.

4.2. Methods and Materials

4.2.1. *Participants*

A total of 55 healthy participants, between 18 and 30 years of age participated in this study. All participants were self-declared right-handers and had normal or corrected-to-normal visual acuity. Prior to testing, participants gave written informed consent according to the general experimental protocol, approved by the local ethics committee of Department for Psychology and Sport Science at Justus Liebig University, Giessen. Participants were randomly assigned to one of three experimental groups, which differed in terms of the time delay between movement termination and the occurrence of outcome feedback (knowledge-of-results, KR). Participants in the No-Delay group (12 women, 6 men, mean age 23.72 years) received KR as soon as possible after the movement (we estimate the minimal system-inherent delay to be approximately 12 ms). Participants in the Short-Delay (13 women, 5 men, mean age 23.56 years) and the Long-Delay groups (13 women, 6 men, mean age 22.73 years) had to wait an additional time interval of 200 ms or 1500 ms, respectively, for outcome feedback to appear on the screen. Group assignment was accomplished by block randomization balanced for sex. Data of participants who produced a considerable number of irregular trials were excluded from the analysis ($N = 4$, 2 in the Long-Delay group, 1 in the Short-Delay group and 1 in the No-Delay group. See below for criteria to identify irregular trials). Participants received course credit or a monetary compensation (8 € per hour) for their participation.

4.2.2. *Apparatus*

The experimental apparatus is depicted in Figure 1. Participants sat on a height-adjustable chair facing a 22-inch, 120 Hz LCD-screen (Samsung 2233RZ), which was placed on a table approximately at head height at a distance of about 100 cm from their eyes. Participants performed straight reaching movements by drawing straight lines on a graphic tablet (WACOM Intuos 4 XL; 62 cm × 46.5 cm × 3 cm) using a digitizing stylus. The tablet was placed in the horizontal plane on the table, surrounded by an opaque occluder, that prevented participants' direct vision of their hand. Data collection and stimulus presentation were controlled by custom scripts in MATLAB (2019a) using the Psychophysics toolbox (Brainard & Vision, 1997; Pelli, 1997).

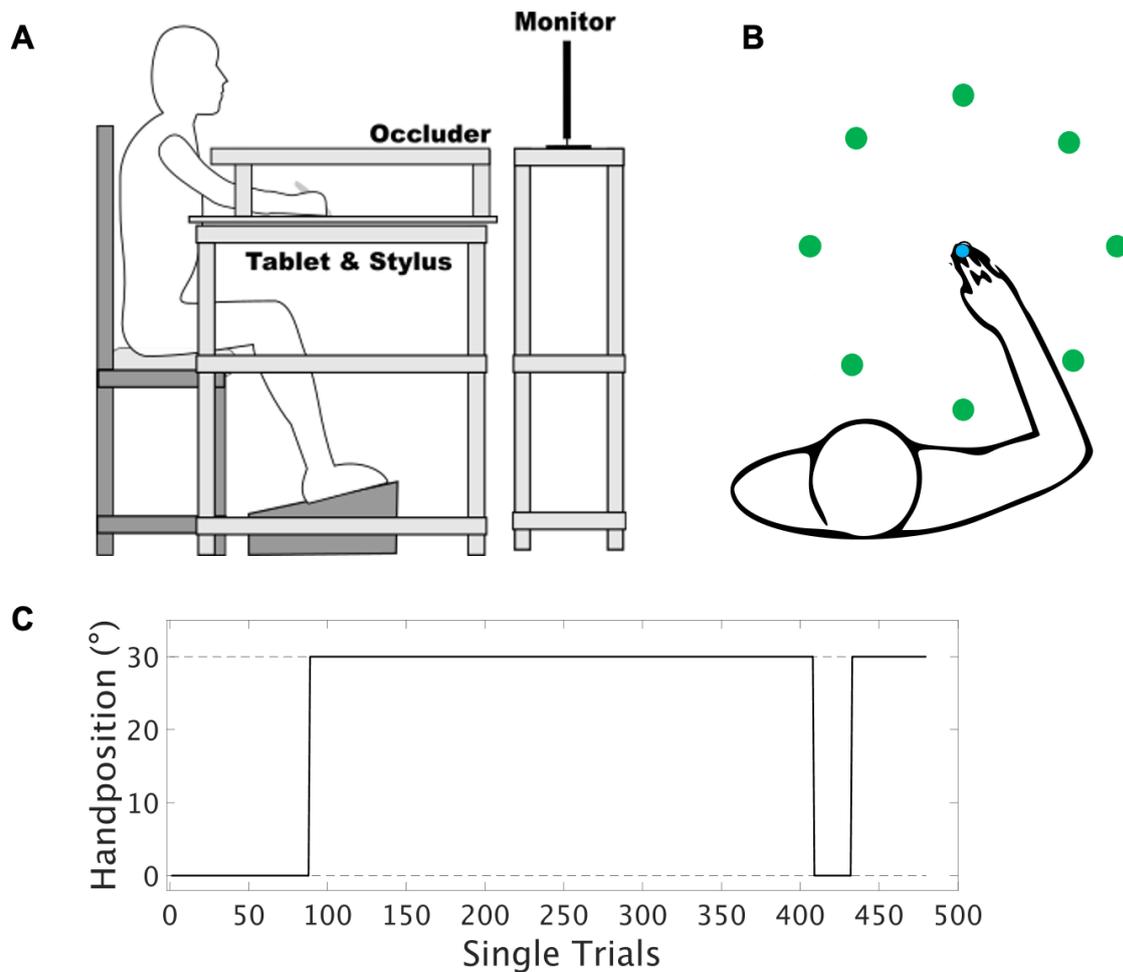


Figure 1 Schematic display of the experimental setup (A), possible target presentations and movement directions (B) and overall perturbation schedule (C). Visual stimuli and the cursor were presented on the monitor screen (A). Each trial, one target was presented (B). The cursor was visually displaced according to the perturbation schedule (C). During baseline, cursor and stylus position were veridical, during adaptation, the cursor was rotated 30° clockwise relative to the stylus position.

4.2.3. Task

Participants were told to perform uncorrected, ballistic movements from a predefined starting location toward a target, not necessarily ending their movements on, but rather “shooting through” the target. On the monitor, the starting location was presented as a circle outline in the middle of the screen (7 mm diameter). On the tablet surface, the starting circle was about 250 mm in front of the participant and laterally displaced from the median plane by 50 mm. The respective target location was a white filled circle of 5.6 mm diameter presented in one of the eight possible target positions. Targets were placed on a circle with a radius of 100 mm, around the start location. Target directions were 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315° (with 0° corresponding to a rightward, 180° to a leftward, 90° to an upward and 270° to a downward movement). The stylus that tracked the hand position was presented as a cursor on the screen, a filled cyan circle of 4.8 mm in diameter. In all trials, visual feedback of the cursor was not visible during movement execution toward the respective target. Thus, the visual cursor will disappear upon movement onset and reappear for a duration of 1000 ms, 0 ms, 200 ms or 1500 ms after movement termination (KR;

depending on the assigned group). To compensate for different trial durations, a black screen will be shown after feedback presentation (for 1500 ms, 1300 ms or 0 ms, respectively). The color of the start circle on the monitor served as a cue to indicate the presence or absence of a visuomotor rotation of 30° CCW. A yellow start circle indicated the absence of the rotation, a blue color its presence. As soon as the start circle turned blue for the first time (adaptation practice phase, see below), the participants were informed that the circle had been yellow so far and that the cursor was controlled exactly by their hand movement. The participants were then instructed that a blue starting circle meant that cursor movement would differ relative to hand movement. However, they were not instructed about the exact perturbation.

4.2.4. Design & Procedure

The design and experimental protocol were based on a previous study by Schween and Hegele (2017). The whole experiment consisted of four phases: a baseline practice phase with only unperturbed movement trials, a pretest phase consisting of unperturbed tests trials, an adaptation practice phase, in which participants had to compensate for a visuomotor rotation of 30° CCW and a posttest phase, which tested for overall adaptation and the participation of explicit and implicit components of adaptation in isolation. All phases were divided into blocks of trials. In order to eliminate directional biases of the targets, each block contained eight consecutive trials, one to each target direction in a pseudorandomly permuted order without any target direction being repeated in successive trials. Baseline practice consisted of five blocks; the pretest contained two blocks of visual open-loop tests (i.e., without KR) with unperturbed movements, serving as a baseline for both the implicit aftereffects and the overall learning tests during the posttest phase. The pretest phase concluded with two blocks of explicit judgement tests serving as the baseline for the explicit judgement with perturbation during the posttest phase. During explicit judgement tests, participants were instructed to put down the digitizing stylus and position the right hand on their thigh. The purpose of this was to ensure that participants did not simulate the previously performed movement and therefore included motor recollection in their judgement. The screen displayed the starting circle, a target, and a straight white line, 100 mm long, on one end attached to the middle of the starting circle and pointing in the direction opposite the current target. The experimenter then rotated this line and participants were asked to verbally instruct the experimenter to place the line to represent their hand movement, if they were controlling the cursor. Participants could then instruct the experimenter to change the selected direction in 1° increments until they were satisfied with the result and the final selected direction was noted. In all pretest trials, the starting circle was yellow to cue the absence of the visuomotor rotation.

The adaptation practice phase with the visuomotor rotation of 30° lasted for 40 blocks of eight movements each, for a total of 320 trials. The start location was colored blue to cue the

presence of the transformation. Posttests contained two blocks of visual open-loop trials in the absence of the visuomotor rotation (aftereffects), two blocks of visual open-loop trials in the presence of the visuomotor rotation (adaptive shifts) and two blocks of explicit judgement trials also in the cued presence of the transformation in this order.

Each single-movement trial began with the presentation of the starting circle in the trial specific color and a white concentric circle outline whose radius depended on the distance of the cursor from the starting circle. In order to reach the starting position, participants were instructed to minimize the circle outline. When they placed the stylus within 3 cm distance from the starting position, the cursor appeared instead of the concentric circle to represent the hand position and assisting participants to accurately place the cursor inside the starting circle. Once they reached the starting position and held the stylus stationary in it for at least 300 ms, they heard a high-pitched sound, signaling the start of the current trial (trial onset). After a randomized interval (between 500 ms, 900 ms and 1300 ms) to prevent rhythmic anticipation of the movement, one of the eight possible targets appeared (target onset) and participants had to execute their ballistic aiming movements towards the respective target within a movement time between 100 ms and 300 ms. Movement onset was measured as the first frame in which the sensor position reached Euclidean distance to the center of the start larger than 3 mm. Movement end was defined as the first instant, when two exact identical stylus positions occurred in succession, at least 45 mm away from the starting circle. Only correctly executed trials were considered for analysis. Failure to execute movements within the predefined timing criteria resulted in an error message displayed on the screen and the trial being aborted.

4.2.5. Behavioral data recording and preprocessing

X and Y coordinates of the tip of the stylus were tracked at 130 Hz and then low-pass filtered with a fourth-order Butterworth filter and a cut-off frequency at 10 Hz, using MATLABs “butter” and “filtfilt” command to avoid introducing phase lags and differentiated by a two-point central difference algorithm. The primary outcome measure for the behavioral data was the final hand direction (hand position at target amplitude) calculated as the angular difference between the vector connecting the starting circle with the target and the vector connecting the starting circle with the final hand position. All movement directions used for further analysis were expressed relative to target directions so that normal averaging procedures rather than circular means could be used. Following a screening for outliers, in which movements with large direction errors ($< -120^\circ$ or $> 120^\circ$) were excluded from further analyses, for each participant, mean averages were computed for each block of practice trials and tests. For the No-Delay group 121 trials were excluded, for the Short-Delay group 100 trials and for the Long-Delay group 72 trials. For RM

ANOVA of adaptation practice, the 40 trial blocks were averaged into five for comprehensive blocks.

4.2.6. EEG data recording and preprocessing

Data acquisition. EEG and EOG data were recorded continuously at a temporal resolution of 1,000 Hz using a 32-channel AC/DC LiveAmp amplifier with active scalp electrodes (Ag/AgCl) and BrainVision Recorder software (Brain Products, Munich, Germany). Electrode placement followed the 10-20 EEG system using the actiCAP electrode cap by Brain Products. Signals from the 'Fp1', 'Fz', 'F3', 'F7', 'FT9', 'FC5', 'FC1', 'C3', 'T7', 'CP5', 'CP1', 'Pz', 'P3', 'P7', 'FCz', 'P4', 'P8', 'CP6', 'CP2', 'Cz', 'C4', 'T8', 'FT10', 'FC6', 'FC2', 'F4', 'F8' and 'Fp2' electrodes were recorded for data analysis. The ground electrode was placed on the Fpz position. The reference electrode was placed on the TP9 position (left mastoid) for online reference. Vertical eye movements were recorded by two electrodes positioned under and above the left orbit (blinks; 'LVEGo', 'LVEGu'), horizontal eye movement were recorded by one electrode on the external canthi of the right eye (saccades; 'HeR'). Electrode impedance was held below 10 k Ω .

EEG preprocessing. The EEG and EOG data were preprocessed offline using MATLAB and EEGLab. Continuous data were re-referenced to averaged mastoids (TP9 and TP10), down sampled to 250 Hz and bandpass filtered between 1 Hz and 100 Hz. Obviously noisy and erroneous data segments were discarded by visual inspection. Afterwards, an automatic, EEGLab custom algorithm called “clean_artifacts” further rejected bad channels and corrected continuous data. The algorithm is an all-in-one function for artifact removal, including the correction of the continuous data (subspace reconstruction; ASR). It was set to categorize channels as abnormal and thus reject them, if they had a flatline duration of 5 s or more (“FlatlineCriterion”), had a correlation less than 0.8 with other channel estimates (“ChannelCriterion”), or had line noise more than 4 times the standard deviation relative to their signal (“LineNoiseCriterion”). After artifact rejection, removed channels were interpolated from this corrected data and then submitted to ICA (runica algorithm). After ICA, the ICLabel algorithm (Pion-Tonachini, Kreutz-Delgado, & Makeig, 2019), a plugin in the EEGLab software, assigned the components to either one of seven possible categories: brain, muscle, eye, heart, line noise, channel noise and other. It also assigned it a score, which indicates how much percentage the assigned category represented of the total recorded activity. Only components with more than 70 % brain activity (Miyakoshi, 2022) were then selected to reconstruct the EEG signal on a channel basis. From this newly constructed continuous EEG data, epochs around -3000 ms to +1500 ms of feedback onset were extracted and baseline corrected using the average activation from trial onset to target presentation.

Event-related potentials. For analyzing the FRN, data from the FCz site were integrated with data from the adjacent FC1 and FC2 sites to reduce noise and to increase statistical power. Trials

were pooled and averaged according to feedback delay (no, short, long) and error size (small, medium, large). Based on previous findings from Maurer et al. (Maurer et al., 2015), an effect window for the FRN was set a priori at 200 ms to 400 ms after feedback presentation (Eff_{FRN}). The trajectory of a perfect hit trial would connect the center of the starting circle and the center of the target with a straight line. A hit trial was defined as a trial in which the final cursor position achieved at least a minimum pixel overlap with the target. Due to the respective sizes of cursor and target, this resulted in movement directions with final positions ranging from 26.29° up to 33.71° , with 30.00° being perfect compensation. Erroneous trials were thus defined as all movements in which no pixel overlap occurred, i.e., movements that ended outside this defined 3.71° radius hit range.

To test the hypothesis that the amplitude of the FRN scales with the error size, scaled difference curves for the different error sizes were computed. A distinction was made between small, medium and large errors. The increment of the different error sizes was a multiple of the hit radius. A trial was considered a small error trial, if the final cursor position was within one hit radius away from the hit range ($[22.57, 26.28^\circ; 333.71^\circ, 7.42^\circ]$), a medium error trial, if its final cursor position was within three times the hit radius away from hit range ($[15.14^\circ; 44.85^\circ]$) and a large error, if it was outside of any of those bounds ($[< 15.14^\circ; > 44.85^\circ]$).

The difference-curve FRN (FRN_{diff}) was defined as the largest negative peak in the difference curve (negative feedback minus positive feedback) occurring between 200 and 400 ms after feedback presentation at electrodes FCz, FC1 and FC2. In addition, a peak-based FRN (FRN_{peak}) was computed based on the average hit, small error, medium error and large error EEG curves. It computed the peak-to-peak difference between the first positive peak after feedback presentation and the first following largest negative peak in the EFF_{FRN} . To yield a relative peak-to-peak difference for each error size, peak-to-peak values of error trials were also subtracted from peak-to-peak values of hit trials (FRN_{peak_delta}).

4.2.7. Analysis of Behavioral and EEG Data

Statistical analyses were done in MATLAB (2019a) and JASP (Version 0.16.1). The requirements for parametric testing, data normality and equality of variance were checked with the Shapiro-Wilk test and the Levene's test, respectively. Additionally, Q-Q-plots of residuals allowed for visual inspection of normal distribution. If the data were not normally distributed, they were transformed using a square root transformation that was designed to work well with negatively skewed data ($\sqrt{\max(x + 1) - x}$). If other assumptions were not met, non-parametric alternatives for analytic testing were conducted. The alpha level of significance was set at .05. Behavioral data were examined for influence of the different delay conditions using an ANOVA with between-participant factor delay (no, short, long). Based on Schween & Hegele (2017), aftereffects were expected to become smaller with increasing delay, whereas explicit shifts were supposed to grow

larger with increasing delay. No significant difference was expected for the adaptive shifts posttest. The specific hypotheses for the three isolated posttests were tested using a mixed factor ANOVA. When the frequentist approach revealed non-significant results, a follow-up analysis computed Bayes Factors (BF_{01}) in order to assess the probability of the null model. Bayes Factors (BF) were interpreted according to (Goss-Sampson, 2020). BFs 1 – 3 were interpreted as anecdotal evidence for the alternative hypothesis, 3 – 10 as moderate, 10 – 30 as strong, 30 – 100 as very strong and BFs > 100 as decisive evidence.

For FRN data, two separate RM-ANOVA, with between subject factor delay (no, short, long) and within subject factor error size (small, medium, large) were conducted. For difference-curve FRN (FRN_{diff}), the largest negative peak values of the FRN effect window (200 ms – 400 ms after feedback presentation) were compared. To yield insights and compare changes in amplitudes across adaptation and error sizes, the second RM ANOVA was performed with the relative peak-to-peak-difference (FRN_{peak}) of the three separated error size trials to hit trials.

4.3. Results

4.3.1. Behavior

Adaptation practice. The adaptation practice is shown in Figure 2. An RM ANOVA with between subject factor delay (0 ms, 200 ms, 1500 ms) and within subject factor block showed no effect of delay ($F(2, 52) = 1.426, p < .250, \eta^2 = .032$). As expected, it did show a significant effect of block ($F(4, 208) = 2.663, p < .034, \eta^2 = .018$), indicating that participants in all groups adapted more and more over the course of adaptation practice. The Bayes Factor of the model including delay as the predictor provides anecdotal evidence in favor of the null hypothesis ($BF_{01} = 2.195$), indicating that the lack of a delay effect was not primarily due to an underpowered sample size.

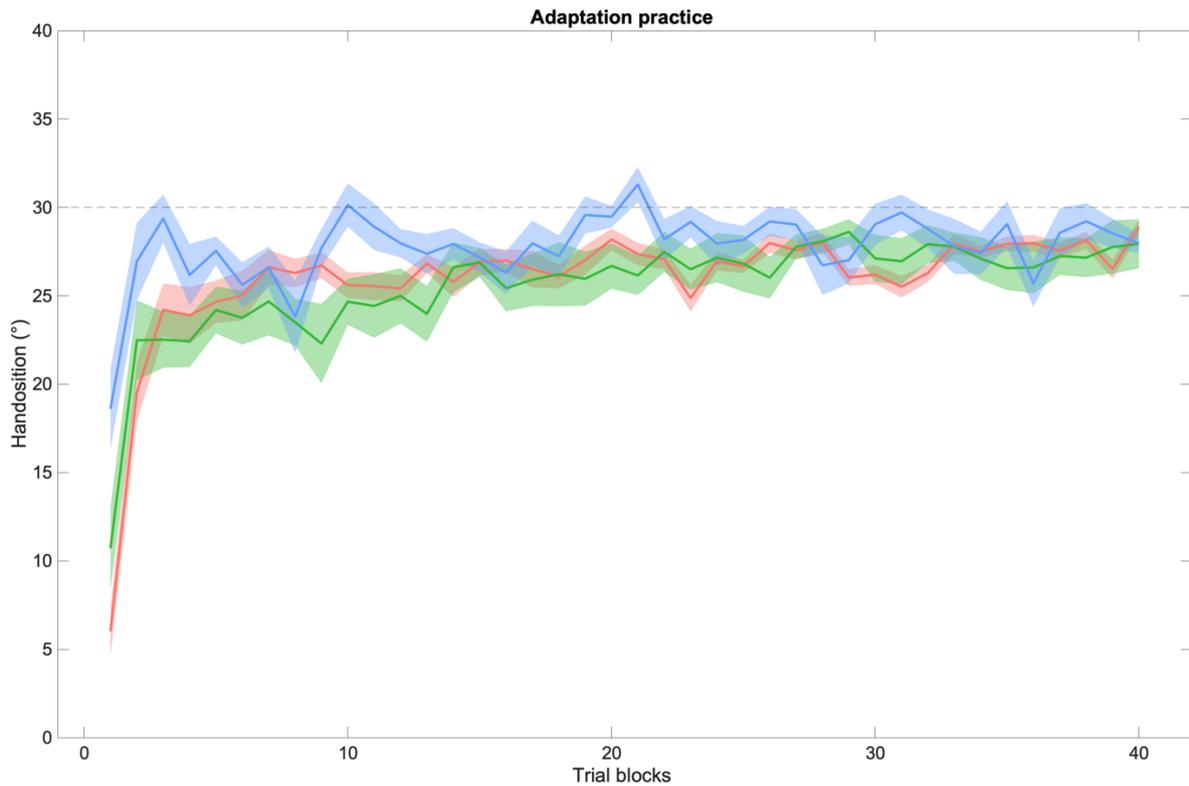


Figure 2 Group averaged mean hand directions for adaptation practice blocks. Eight consecutive single trials were averaged into one trial block, resulting in 40 trial blocks for 320 single adaptation practice trials. Shaded error bands represent standard error of the mean. The dotted line at 30° illustrates perfect compensation.

Adaptive shifts, aftereffects, and explicit shifts. The baseline corrected mean adaptive shifts, aftereffects, and explicit shifts are shown in Figure 3. They were all positive, except for the aftereffects of the Long-Delay group, showing that participants mostly compensated for the visuomotor perturbation. Adaptive shifts comprised both explicit and implicit components of adaptation. As in the previous study by Schween and Hegele (2017), there was no difference in adaptive shifts as a function of delay ($F(2, 52) = 0.161, p = .851, \eta^2 = .006$). A follow-up Bayesian ANOVA revealed moderate evidence in favor of the null hypothesis ($BF_{01} = 6.206$), indicating that the null effect was not primarily due to an underpowered sample size.

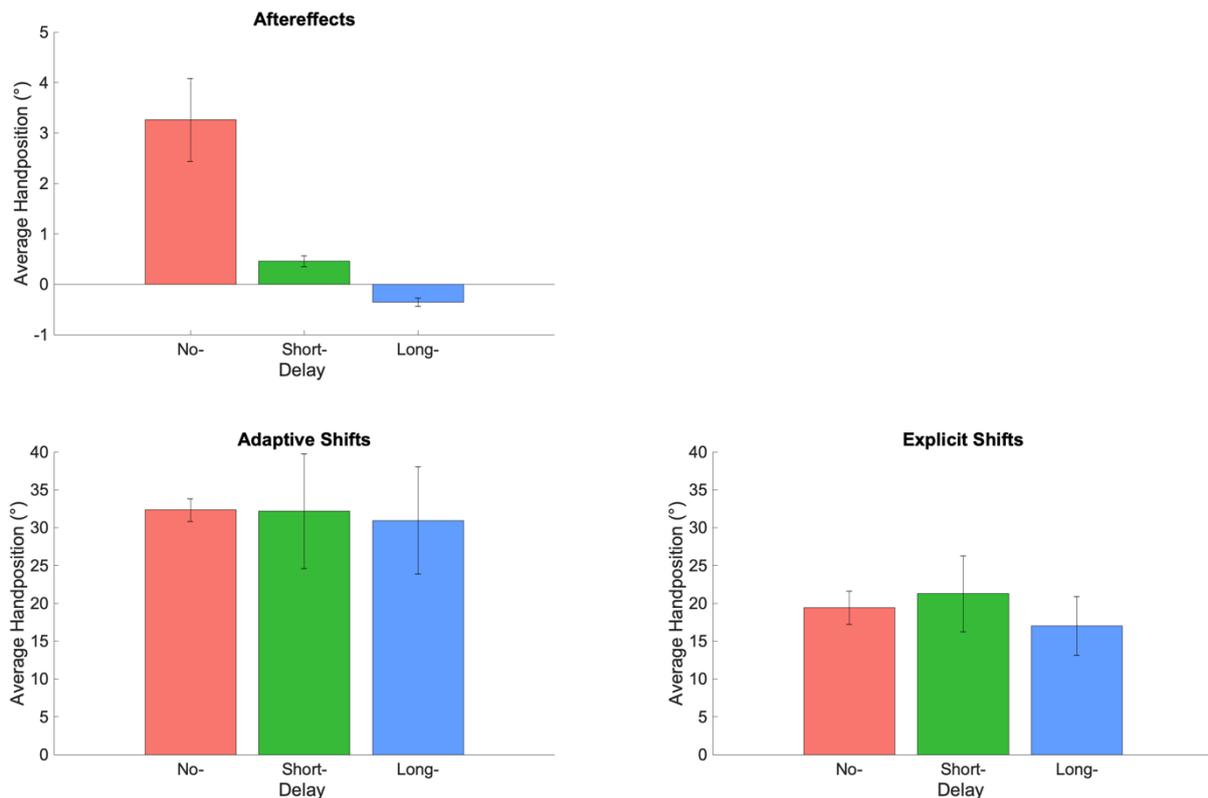


Figure 3 Mean averaged hand positions separated by delay group and posttest. The upper lefthand panel shows remaining implicit aftereffects, the lower righthand panel shows results for the explicit shifts posttest and the lower lefthand panel shows the results for the adaptive shifts posttest. Error bars represent standard error of the mean.

The mean aftereffects reflecting the implicit component of adaptation were rather small but differed systematically between groups. The statistical analysis showed a highly significant effect of delay ($F(2, 52) = 11.123$, $p < .001$, $\eta^2 = .299$). Bonferroni corrected posthoc tests revealed significant differences between No-Delay and Short-Delay ($p = .007$) as well as between No-Delay and Long-Delay ($p < .001$). There was no significant difference between the Short-Delay and Long-Delay groups ($p = .340$). Bayesian Factor revealed anecdotal evidence in favor of the null hypothesis ($BF_{01} = 1.066$).

Finally, the mean explicit shifts exhibited a pattern similar to the adaptive shifts with no systematic differences across delay groups, $F(2, 52) = .032$, $p = .968$, $\eta^2 = .001$, and the follow-up Bayesian ANOVA revealed moderate evidence in favor of the null hypothesis ($BF_{01} = 6.821$).

4.3.2. EEG

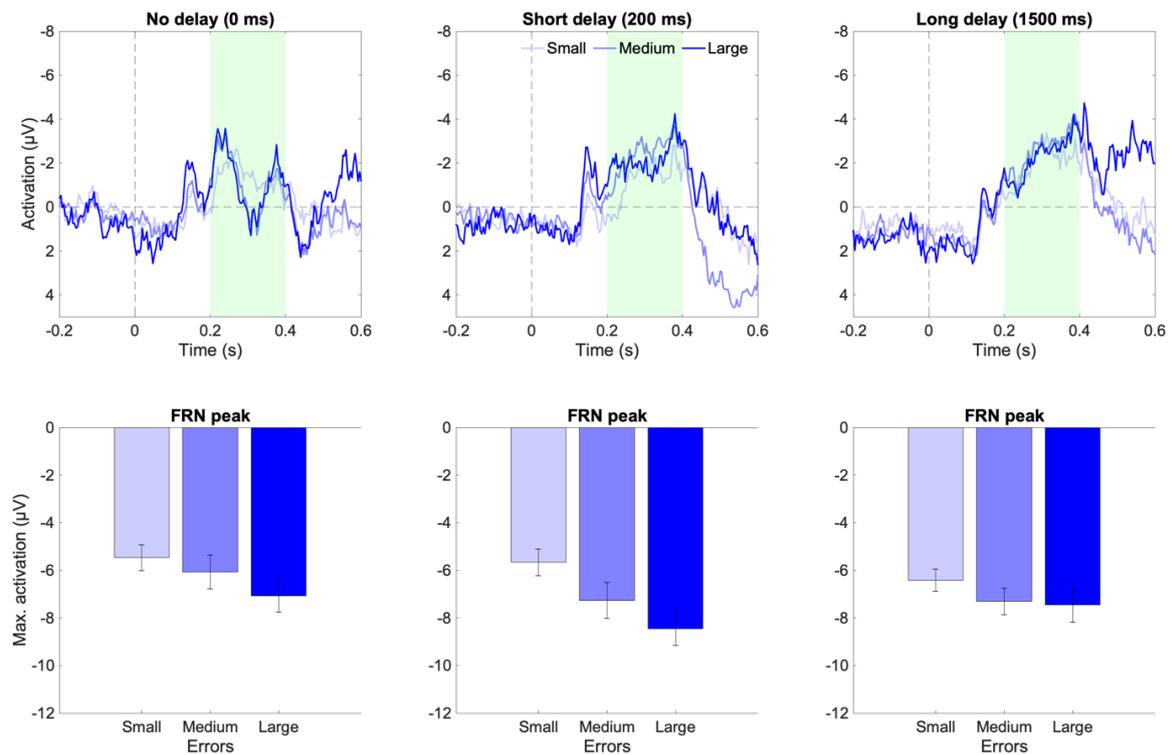


Figure 4 Group mean averaged difference curves (hit trial data subtracted from error trial data) for all three error size trials (upper row) and largest negative peak within the effect window (lower row) for all three delay conditions. In the upper row, the time participants received feedback is displayed as the dotted line at 0 s. The blue of the line becomes opaquer with increasing error size of the behavioral data, resulting in light blue for small error trials, more vibrant blue for medium error trials and bright blue for large error trials. The green shaded area from 0.2 s to 0.4 s represents the FRN effect window, for which both the mean peak (FRN_{diff}) and the peak-to-peak differences (FRN_{peak} and FRN_{peak_delta}) were calculated and used for analysis. In the lower row, the bar plots represent the group mean averaged peak value of the FRN within the effect window. The nuanced shades of blue represent the same error size trials as above. Error bars represent standard error of the mean.

Difference-curve FRN. The RM ANOVA for the difference-curve FRN (FRN_{diff}) supported the hypothesis, that FRN amplitude in fact scales with error size $F(2, 98) = 14.057$, $p < .001$, $\eta^2 = .049$. Post hoc p-values were adjusted using the Bonferroni correction. There were significant differences in the largest negative peak between all three error sizes, increasing with increasing error size. The negative peak within the effect window was significant larger for medium and large errors compared to small errors ($p = .018$, $p < .001$, respectively), and the negative peak was larger for large errors compared to medium errors ($p = .04$). There was no significant delay effect ($F(2, 49) = 1.157$, $p = .232$, $\eta^2 = .035$) and no significant interaction between delay and error size, ($F(4, 98) = .892$, $p = .472$, $\eta^2 = .006$). Compared to the null model, the model including the delay condition provided anecdotal evidence for the null hypothesis ($BF_{01} = 2.018$).

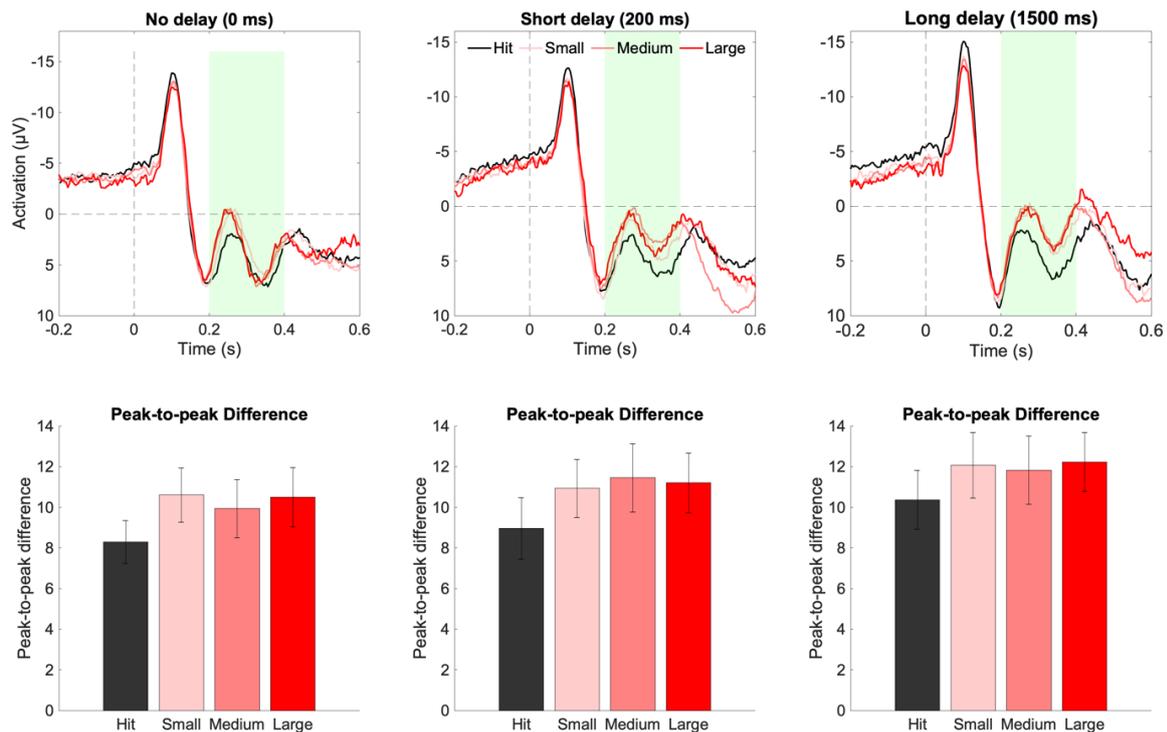


Figure 5 Grand average curves of the hit and error trials (upper row) and the group mean averaged peak-to-peak differences of the respective error trials compared to hit trials (lower row) in all three delay conditions. In the upper row, the time participants received feedback is displayed as the dotted line at 0 s. The black line illustrates mean averaged hit trials, the red of the other lines becomes opaquer with increasing error size of the behavioral data, resulting in light red for small error trials, more vibrant red for medium error trials and bright red for large error trials. The green shaded area from 0.2 s to 0.4 s represents the FRN effect window, for which both the mean peak (FRN_{diff}) and the peak-to-peak differences (FRN_{peak} and FRN_{peak_delta}) were calculated and used for analysis. In the lower row, the bar plots represent the group mean averaged of the peak-to-peak difference between the first positive and the first negative peak after feedback presentation. The nuanced shades of red represent the same error size trials as above. Error bars represent standard error of the mean.

Peak-to-Peak FRN. The peak based approach (FRN_{peak} and FRN_{peak_delta}) was used to quantify the changes in FRN amplitude over the adaptation phase. The RM ANOVA of the peak-to-peak difference (FRN_{peak}) showed no significant effect of delay ($F(2, 49) = .348, p = .708, \eta^2 = .013$) nor a significant effect of error size ($F(2, 98) = .166, p = .847, \eta^2 = .001$). However, relative to the respective hit trial peak-to-peak difference (FRN_{peak_delta}), a RM ANOVA revealed a significant effect of delay ($F(2, 49) = 3.869, p = .028, \eta^2 = .106$). The Short-Delay group shows a significant lower peak-to-peak difference compared to the No-Delay group ($p = .035$), whereas there was no statistical difference between the No-Delay and the Long-Delay groups ($p = .128$), nor between Short-Delay and Long-Delay ($p = 1.0$). All post hoc comparisons were corrected using the Bonferroni method. The RM ANOVA yielded a not significant effect for the within factor error size ($F(2, 98) = 2.946, p = .057, \eta^2 = .012$). The Bayes Factor provided moderate evidence in favor of the null hypothesis that there was in fact no effect of error size ($BF_{01} = 3.404$).

4.4. Discussion

In the present study we sought to not only test the viability of electroencephalography (EEG) as a tool to assess explicit and implicit contributions to visuomotor adaptation, but also if the feedback-related negativity (FRN) can serve as a proxy for explicit and implicit components. We reasoned that if the FRN predominantly reflects processing of the explicit component, it should increase with increasing outcome error size, whereas it should remain consistent across varied error sizes if it primarily reflects implicit processes of adaptation. To behaviorally dissociate between the explicit and implicit component, we manipulated the timing of movement outcome feedback presentation. Previous studies were able to bias visuomotor processing and therefore dissociate between explicit and implicit components using such delayed feedback (Brudner et al., 2016; Schween & Hegele, 2017). The FRN has been suggested to be similarly sensitive to feedback delay and additionally error size. For this purpose, participants were randomly assigned to three different feedback delay groups (No-Delay, Short-Delay, Long-Delay), and furthermore, behavioral data within participants were divided into three different error size categories (small, medium, large). Based on previous research on the FRN, a negativity in the EEG signal was expected in fronto-central sites between 200 ms and 400 ms after feedback presentation for all delay groups and error sizes. If the FRN rather reflects the explicit processing, we would expect the FRN to increase with increasing error size and longer feedback delay. Representation of the implicit component would be associated with stable FRN patterns across error sizes and delay conditions.

To quantify the difference-curve FRN (FRN_{diff}), the signal of hit trials was subtracted from the signal of all error size categories. The largest negative peak in the resulting difference curve was used for analyses. The peak-to-peak difference (FRN_{peak}) was computed based on the peak-to-peak difference between the first positive and the first negative peak within the FRN effect window (200 ms – 400 ms after feedback). This value was computed for hit and all three error size categories. To obtain the relative peak-to-peak difference used for analyses, the peak-to-peak difference of all three error categories was subtracted from the peak-to-peak difference of the hits.

Results showed that the negative peak of the FRN difference curve was strongest for the large errors and decreased with decreasing error size. However, contrary to our expectations, we found no delay effect. On peak-to-peak difference, similar to the behavioral results by Schween and Hegele (2017), the EEG data revealed a significant effect of delay between No-Delay and Short-Delay but no effect between No-Delay and Long-Delay or even Short-Delay and Long-Delay. Regarding the behavioral data, we did not detect any delay effects, neither during adaptation practice nor during the posttest phase. The only significant delay effect manifested itself in the, already untypically low, aftereffects. We expected this attenuation of the implicit aftereffects due to feedback delay, but based on previous studies (Brudner et al., 2016; Schween & Hegele, 2017),

but we also expected that this attenuation would be accompanied by an increase in the explicit component in order to maintain overall level of adaptation., i.e., an increase of the delayed conditions in the adaptive and the explicit shifts posttest. However, this increase, and thus also any other delay effect on a behavioral level failed to emerge. Thus, based on these data, we cannot say whether the FRN reflects explicit or implicit processing of visuomotor adaptation or whether it is even a favorable proxy for neural visualization of visuomotor adaptation.

Similar to a previous study that had a different primary focus (Langsdorf et al., 2022), we found no delay effects in the adaptive and the explicit shifts posttests. As argued in the other study, it is quite possible that our design is not sensitive enough to produce the delay effects in the explicit component. We had short break after adaptation practice, during which the experimenter instructed the participants for the posttest phase. If there were any offline gains during this time, e.g., due to consolidation, we would expect them only influence the explicit component, since the implicit component starts to decay after 500 ms (Brudner et al., 2016; Miyamoto et al., 2014; Schween & Hegele, 2017).

Since the delay effect did not occur at the behavioral level, it seems reasonable that it also did not occur at the neuronal level. One argumentation for this would be that the manipulation apparently did not work. Even though we found a difference in the peak-to-peak differences (FRN_{peak}) between the Short-Delay and No-Delay group. If looking closely at the grand averages (upper row, Figure 5), one can see that the pattern of the grand averages differs between the delay groups. With increasing delay, it seems to develop into a two-peaked curve in the FRN effect window, with only a small positive dip at about 350 ms. The second negativity is located outside the effect window but might be worth investigating. Our statistics did not confirm any significant differences, but we can't rule out the possibility that there is something meaningful in this negativity after 400 ms, nor that these are ultimately motion artifacts that we couldn't clean up. However, approaching these null effects on the neuronal level theoretically, another explanation could be that the FRN represents a process that is higher up in the processing hierarchy. Thus, it could be that the expressed behavior measured in the adaptation practice is subject to further, subsequent processes that are not included in the FRN. Previous studies suggested internal forward models to be located within the cerebellum (Miall et al., 1993; Schlerf et al., 2013). But also sites like the posterior parietal cortex (PPC) have been postulated as a locus for forward models (Desmurget & Grafton, 2000; Grafton, 2010; Scott, 2012; Shadmehr & Krakauer, 2008) and have been associated with learning processes involved in tasks like prism adaptation (Fernandez-Ruiz et al., 2011) as well as adaptation to rotations (Clower et al., 1996; Diedrichsen et al., 2005; Inoue et al., 1997; Inoue et al., 2000; Krakauer et al., 2004). Another study suggested that introducing a visuomotor perturbation even leverages connections from the PPC to the motor cortex (Tanaka, Sejnowski, &

Krakauer, 2009). While no studies, to our knowledge, have specifically investigated the neural correlates of the deliberate, explicit component, some fMRI results have been interpreted as evidence for explicit component location within frontal lobe regions including lateral and medial aspects of the prefrontal cortex, as well as the premotor cortex (Krakauer et al., 2004; Seidler et al., 2012). Further, working memory functions like mental rotation, as well as many other higher cognitive processes like planning and performance monitoring, are also primarily associated with the prefrontal cortex, as well as a broader network that includes parietal and motor cortices (Anguera et al., 2007; Anguera et al., 2010; Baddeley, 1992; Benson et al., 2011; Seidler et al., 2012). The assumption that the working memory-based computations of conscious motor realignment require cognitive resources, whereas the implicit motor adaptation process does not, led to the idea that there ought to be separate neural correlates for the two components. But maybe the FRN is not the right proxy for this endeavor. The FRNs' sensitivity to feedback delay was one of the key motivators in this study. A recent review has elaborated on the FRNs sensitivity to feedback delay (Hinneberg & Hegele, 2022). The review compares studies that define a feedback delay range from immediate feedback (500 ms to 1000 ms), up to long delays (about 7000 ms). The common trend in all those studies, no matter how different they were in their methodology and the actual task, is that the FRN amplitude decreased the longer the feedback was delayed, under the premise, that feedback was conducive to learning per se (see (Hinneberg & Hegele, 2022) for full review). Contrary to those results, for our study, we hypothesized that the FRN amplitude would increase, if it reflected the explicit component. It is quite possible that amplitude reduction is also associated with stronger involvement of the explicit component. In any case, we would expect a change. However, it is not certain that the results of these studies can be applied to our specific research question, as motor tasks are not equivalent to cognitive decision tasks in their neuronal processing. In addition, the short feedback delays used in these studies are larger than any of the feedback delays used by us or Schween and Hegele (2017).

To conclude, the based on the experiments designed for this study we cannot state whether the FRN is a proxy for either explicit or implicit components of visuomotor adaptation. However, we were able to find an FRN and furthermore establish that this FRN is sensitive to different error sizes in a visuomotor adaptation task. This is an important finding, since basic information on EEG parameters in visuomotor adaptation is still very scarce. Therefore, it would be important for future research to record behavioral experiments together with EEG data to establish systematic relationships between behavioral phenomena and neural correlates. This would provide enormous insight into the processes of not only of visuomotor but also of sensorimotor adaptation and the whole field of motor learning.

5. Summary

Inspired by two computational principles of motor control, this thesis sought to elucidate if and how manipulating the time intervals before and after the execution of goal-directed aiming movements would affect explicit and implicit components of visuomotor adaptation. All in all, participants in all three studies were sensitive to time manipulation, either before or after the movement. In the first study, prolonging movement preparation times enhanced visuomotor performance. In the second study, delaying movement feedback attenuated implicit aftereffects and disabled temporal discounting. Similar to the second study, the implicit component was attenuated by delayed feedback in Chapter 4, the third study.

Just like every other kind of behavior, goal directed reaching movements take place in a temporal context with the crux that, unlike most movements that are often examined in behavioral studies, time itself cannot be manipulated (Schween, R., Personal Communication). One way, however, to approximate the influence of time on such studies is to manipulate different time intervals. In the field of motor adaptation that is the ability to adapt ones' behavior to new circumstances, research has taken advantage of the different susceptibilities of the two main components of adaptation, the explicit and implicit component, to temporal manipulations and used them to dissociate between them (Bond & Taylor, 2015; Dawidowicz et al., 2022; Hegele & Heuer, 2010; Heuer & Hegele, 2015; Mazzoni & Krakauer, 2006; McDougale et al., 2015; Schween & Hegele, 2017; Schween et al., 2018). The explicit component is associated with deliberate behavioral changes and strategy development that is driven largely by target errors and engaged in cognitive resources, whereas the implicit component is greatly associated with the sensory prediction error (SPE) and its unconscious manifestation in skill formation. On methodological levels, temporal manipulations, such as a prolonged movement feedback delay (e.g. Brudner et al., 2016; Schween & Hegele, 2017) or shortened movement preparation times (e.g. Haith et al., 2016; Leow et al., 2017) could differentiate between the contribution of either the explicit or the implicit component on overall adaptation. However, time matters not only on a methodological, but also on a conceptual level.

The phenomenon that movements selected and performed immaturely are usually less accurate than those for which more time has been taken is the main focus of chapter 2. We interpret this as a SPAT, the inverse relation between the accuracy of a movement and the time taken to produce it. When participants in a visuomotor rotation task are free to move as soon as they like after target presentation, their performance level ends up well below full compensation. However, the results in chapter 2 show that if participants are forced to wait for 2.5 s between target presentation and their allowed movement onset, performance level goes up and reach full compensation. To gain more insight into the causes of these differences in adaptation performance,

I attempted to determine through posttests how much of the adaptation performance was due to explicit and how much was due to implicit gains. However, based on my results and the data collected, I could not answer this inquiry validly. One hypothesis that I have is that incomplete adaptation during adaptation practice is more likely to be a performance effect rather than a manifested learning effect. I understand a performance effect as a process in which knowledge about the transformation is accumulated in the background, but there is not enough capacity to implement this knowledge directly in the performance. This knowledge is accumulated in equal amounts in all groups, which could then also explain why all groups show similar values in the final posttest. However, I did find a small, but not statistically significant increase in the explicit component for the participants with prolonged response time in experiment 1, hinting towards the hypothesis that a little more explicit knowledge builds up. A recent study by (Vyas et al., 2020) also suggests that prolonging preparation times can have beneficial effects on motor learning and not just performance. It might therefore be interesting to investigate how time influences explicit processing during movement preparation and movement initiation, two not necessarily dependent processes (Haith et al., 2016).

Chapter 3 investigated whether artificially shifting visuomotor adaptation onto explicit processes due to delaying movement feedback might be an opportunity to avoid temporal discounting. To verify that the observed behavior is indeed explicit in nature, we introduced a cognitive secondary task. Due to the different dependence on cognitive resources and therefore the different neural processing pathways of the explicit and implicit component, in an explicitly driven adaptation behavior there should also be a decrease in motor performance called dual-task costs.

While dual-task costs are a robust phenomenon in the cognitive psychology literature, the visuomotor literature has yielded many contradictory results in this regard. Some studies find dual-task costs, others do not. The results provided in chapter 3 do show, contrary to some beliefs (Im, Bédard, & Song, 2016; Song & Bédard, 2015), that if a task is cognitively demanding enough, it can have a significant impact on adaptation. This impact does not however transfer into the posttest phase, again suggesting an effect of performance rather than learning. But the temporal delay did only decrease implicit adaptation, not overall or explicit adaptation, which might suggest, that the more explicit participation for the explicit and adaptive shifts may have nullified the temporal discounting, while the implicit component was fully exposed to it.

Chapter 4 was not so much aimed at revealing a novel phenomenon as at elucidating whether EEG was a viable tool to gain more insights into the process dissociation between explicit and implicit. We used the findings from Chapter 3 and assumed that delayed feedback should decrease the contribution of the implicit and might increase the involvement of the explicit

component in adaptation behavior. To create as little casual interference as possible, we used the same experimental design of the behavioral experiment from previous studies (Schween & Hegele, 2017), but supplemented it by additionally recording continuous EEG data. Our hypothesis was that the feedback-related negativity (FRN), a fronto-central component reflecting the error processing of unexpected, external errors, might be a viable neural proxy for covert processing of either the explicit or implicit component of visuomotor adaptation. I intended to reveal it by manipulating the temporal availability of the outcome feedback.

There are only a few studies that have examined visuomotor adaptation in conjunction with EEG (Darch et al., 2020; Jahani et al., 2020; Savoie et al., 2018). These studies suggested, that there are both spatially and functionally distinct neuronal networks for the explicit and implicit components (Jahani et al., 2020). While we were able to verify a clear FRN, that scaled across different behavioral error sizes, we were not able to use it for a specific process dissociation. Further, our manipulation of delayed movement feedback only revealed a systematic attenuation of implicit, but no facilitation of explicit adaptation on a behavioral level. It is therefore reasonable that we did not find separated neural correlates, because we did not find behaviorally distinct component expressions of them in the first place. However, it remains possible that EEG, if investigated further, will be a suitable tool for a process dissociation.

6. Outlook

The concept of cognitive interference in the form of dual-task paradigms was briefly touched upon in chapter 3. Experiments investigating this phenomenon oftentimes include a main motor task and a secondary task, often of a different modality. Using a cognitive secondary task such as solving mental arithmetic problems or remembering items from a previously recited list decrease motor performance in the primary motor task. Such errors in the primary motor task are expected as the secondary task takes up cognitive resources that would be necessary for error-free movement execution. The concept of dual adaptation on the other hand refers to the fact that humans can develop different and separate adaptations if the situation requires it (Welch et al., 1993). However, if two opposing transformations are scheduled to alternate without any indication of which transformation is present, interferences will occur. This results in the participant being unable to perform either transformation appropriately (Bock, Schneider, & Bloomberg, 2001; Shadmehr, Brashers-Krug, & Mussa-Ivaldi, 1994). It is now very well understood that sufficient contextual separation of the two transformations can lead to a reduction of this interference and separate motor memories can be formed (Schween et al., 2019). These contexts may refer to separate physical or visual workspaces (Forano & Franklin, 2020; Howard, Wolpert, & Franklin, 2013),

action outcome effects (Schween et al., 2019) and different lead-in (Howard et al., 2012) or follow-through movements (Howard, Wolpert, & Franklin, 2015).

In a previous dual adaptation study, Schween and colleagues (Schween et al., 2019) investigated whether different context cues, such as different visual cursors on the screen or different action effects would result in distinct implicit motor memories. The authors found no evidence for this hypothesis. The only context cue in this study that actually yielded separate implicit motor memories were different executing limbs. Previous studies have already suggested that only context cues directly related to the state of the body can establish separate, context-dependent motor memories (Howard et al., 2013). However, innovative technical procedures such as tool-assisted microsurgery or modern video games show clearly that humans are capable of successfully remembering different motor memories even though the tools share the same body state. Up to now, studies consistently fail to find such cues (Hinder et al., 2008b).

In the previous chapters, I elaborated on how manipulations to the different time intervals affect adaptation behavior. This may raise the question of whether the influences of these time intervals can not only affect adaptation, but also act as a context cue for generating separate motor memories. To investigate this inquiry, a dual adaptation experiment, similar to those stated above (Forano & Franklin, 2020; Howard et al., 2012; Howard et al., 2013; Howard et al., 2015; Schween et al., 2019; Schween et al., 2019), might need to consider using either prolonged or abbreviated response time or prolonged feedback delay intervals, each associated with a certain transformation and apply them consequently over a longer practice time. Meanwhile, posttests or EEG data might be an opportunity to monitor adaptation processing.

This could be another piece in the puzzle of how exactly adaptation is processed. Until today, visuomotor adaptation is mostly studied on a behavioral level. And although in chapter 4 I tried to join the groups that have already combined EEG with visuomotor adaptation, forming a bridge to cognitive psychology, there are not yet many enlightening findings for neural correlates of adaptation, especially with regard to process dissociation between the explicit and implicit components of adaptation. Therefore, future research should investigate neuronal activity more during visuomotor adaptation. This could clarify many, still unanswered questions about adaptation and adaptation performance, including whether the performance effect phenomenon is not due to another explanation as well. Neurological or even imaging techniques (e.g., fMRI) may provide further insight into how it is that participants show clear signs of interference in training phases but no longer in the posttests, a phase in which we as researchers define how much has been learned, as was the case in particular in the second study. In the context of this thesis, the distinction between learning and performing a visuomotor adaptation task has been defined in the sense that a person has acquired a certain amount of knowledge, but does not necessarily express this

knowledge. Examples like this can be found in literature describing *latent learning* as gaining knowledge not yet apparent (Malone, 2012). For example, Tolman and Honzik (1930) showed that rats' performance on a maze task did not change with practice, but was clearly revealed when they were motivated with a food reward. Similarly, it is quite possible that the participants in both studies know exactly what the optimal compensatory strategy should be, but there may be several reasons why this potential knowledge is not implemented in the movement that is observed during adaptation. Under the phenomenon of a speed-accuracy tradeoff (SPAT), one explanation could be that implementing the complete compensational strategy would be too time-consuming and thus poses a possible risk to future rewards. If the cognitive resources for solving a secondary task already have to be used, a further explanation would be that there are insufficient cognitive resources left to adequately implement the knowledge about the perturbation.

However, those possible explanations do not contradict the possibility of knowledge about the perturbation accumulating in the background and thus explain how all groups yield similar results in the posttests.

Finally, I would like to point out that the methods chosen for those posttests have also had a great influence on how the results are to be interpreted and are thus directly interwoven with the difference between learning and performing. All experiments in this thesis have a dissociated posttest phase in which the explicit and implicit components were measured independently. Maresch and colleagues have mentioned that the definition of what is considered explicit and implicit differs for the most part from study to study (Maresch et al., 2021a). Moreover, recent work by the same authors suggests that the methodology used has a very strong influence on how the measurement of especially the explicit visuomotor learning components turns out (Maresch et al., 2021b). The authors propose to break down the explicit component further and suggest to differentiate between awareness, explicit knowledge and declarative knowledge (Maresch et al., 2021a). In doing so, the authors question the previous definition of the explicit as declarative and verbalizable. For visuomotor adaptation studies that might mean that participants develop some form of a procedural explicit knowledge: They know how to perform their compensatory strategy, but do not know how to express it in another modality such as speech (Stanley & Krakauer, 2013). Researchers for future studies should have in mind the extent to which the distinction between explicit and implicit is practical and method-driven, but for functional explanatory approaches of human behavior, a more theory-driven approach may be required (Hadjiosif & Krakauer, 2021; Maresch et al., 2021a). Furthermore, future studies should also include several ways to better distinguish between learning and performing, as there seem to be still many confounds about each process and their interaction.

7. References

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8. Declaration of independence

I hereby declare that I have prepared the thesis at hand independently and without undue aid or the use of any resources other than indicated within the thesis. All parts of my thesis taken either verbatim or analogously from the published or unpublished works of or based on oral communications with others are indicated as such. Regarding all aspects of my scientific enquiries as they appear in my thesis, I have upheld the tenets of good scientific practice as laid out in the "Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis" and complied with the precept of ethics, data protection and animal welfare. I declare that I have neither directly nor indirectly given monetary or any other valuable considerations to others in connection with the thesis at hand. I declare that I have not presented the thesis at hand, either in an identical or similar form, to an examination office or agency in Germany or any other country as part of any examination or degree. All materials from other sources as well as all works performed by others used or directly referenced within the thesis at hand have been indicated as such. In particular, all persons involved directly or indirectly in the development of the thesis at hand have been named. I agree with the screening of my thesis for plagiarism via offline or online detection-software.

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