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# Does the Uncertainty of Prior Knowledge affect Sensorimotor Adaptation?

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## Abstract

The question of how our brain deals with uncertain sensory information to compute an appropriate behaviour is fundamental for a comprehensive understanding of human information processing. In the past decades, the idea that it might follow a form of Bayesian inference has been supported by a growing body of evidence. In the context of visuomotor adaptation, it has been shown that, in line with Bayesian principles, the amount of uncertainty in sensory information influences sensorimotor adaptation. However, the second prediction of the Bayesian account, namely that a higher degree of uncertainty in prior knowledge should lead to less adaptation as well, remains largely unexplored. The purpose of the present thesis is therefore to examine whether the second prediction also proves valid in human sensorimotor adaptation. Focusing on the feedforward component of adaptation only, a behavioural between-subjects visuomotor rotation study has been conducted to investigate whether the amount of uncertainty in a prediction influences learning. More specifically, we investigated its impact on learning rate, washout rate and generalisation width. We hypothesised that, if adaptation follows Bayesian principles, a higher amount of uncertainty in prior knowledge should lead to slower learning. Data was acquired for three different variance conditions ( $\sigma_0 = 0^\circ$ ,  $\sigma_1 = 4^\circ$ ,  $\sigma_2 = 12^\circ$ ), where the mean of the imposed rotations was  $\mu = 15^\circ$  across all groups. Following the convention in the literature, imposed rotations were counterbalanced for a clockwise (CW) and a counterclockwise (CCW) rotation condition. Surprisingly, reaching behaviour differed between those two rotation conditions, requiring us to conduct the analysis separately for CW and CCW participants. For CW participants, results speak in favour of our hypothesis, though post-hoc Bayes factor analyses suggest that the halved group sample sizes were too small for the results to be conclusive. Importantly, further exploratory analyses reveal systematic ‘natural reaching biases’ that are identical across participants. An interaction between adaptation and participants’ directional biases (also referred to as *anisotropy*) is therefore likely to have caused the difference in rotation direction. It is argued that the observed anisotropy is due to biomechanical reasons. Moreover, the observed pattern in the generalisation data replicates the finding of Diedrichsen et al. (2010) that adaptation interacts with use-dependency, namely the phenomenon that recent movements bias subsequent movements towards the original ones. Taken together, we can conclude that, even though the observed patterns provide a hint towards the assumption that uncertainty of prior knowledge impacts adaptation as well, further research is needed to conclusively answer this question. A wide range of additional exploratory analyses provides valuable insights into conceptual and methodological questions for future research in this domain.

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## Part I

# Review: Adaptation from a Bayesian Perspective

## 1 General Introduction

*What makes human thinking uniquely human?*

*Is a mouse conscious?*

*Does perception of the same object differ between different observers?*

*How do we make decisions?*

*What characteristics should a machine incorporate in order to think like a human being?*

Those questions are just an extract of the range of topics that motivate researchers in the field of cognitive science. In a broader sense, cognitive science (from the Latin word *cognoscere*: “recognise”, “experience” or “discover”) comprises everything that relates to the question of information processing in humans (Dukas, 1998; Lachman et al., 2015). Among others, this includes the abilities of perception, attention, memory, learning, as well as problem solving and creativity (Medin & Ross, 1992). Basically, the previously mentioned questions have one main question in common: How does our mind work? As the definition of cognition already indicates, cognitive scientists regard the brain as an information processing system (Geissler et al., 1992; Simon, 1981). More specifically, the underlying question would thus be: How does our brain as the biological centre of our mind represent and process information to compute the best possible output? If we consider complex cognitive abilities such as rational reasoning or theory of mind, *i.e.* the ability to put oneself in someone else’s position, as different outcomes of this information process, then it would be crucial to understand the underlying basics of how our brain generally processes information. It seems much easier to understand complex cognitive phenomena when we understand the computational basis on which everything else is built. This thesis addresses the question of what this computational basis might look like.

More specifically, we ask the question whether the Bayesian account provides an appropriate model to describe our brain’s information processing in sensorimotor learning. Previous research suggests that uncertainty in sensory information is accounted for in the integration of information (Knill & Pouget, 2004; Kording & Wolpert, 2006). In accordance with Bayesian principles, more reliable (and thus less uncertain) information has been shown to be given more weight in the integration of information from different sources. However, so far, little is known on the question of whether this also applies to prior knowledge as another source of information. If we really were to implement Bayesian principles in sensorimotor learning, not only should the uncertainty of a sensory input influence information integration but also the uncertainty of our predictions. Are predictions that are computed based on our previous knowledge also

weighted with their uncertainty?

While we directly address this question in the scope of a behavioural experiment in the second part of this thesis, the first part provides an overview of the general concepts that set the context for this field of research. The field of cognitive science is characterised by a highly interdisciplinary nature. It is less a homogeneous academical background that defines cognitive scientists but, rather, their common interest in a deeper understanding of the mind. As is always the case with collaborating heterogeneous groups, they bring the huge benefit of a wider range of perspectives, knowledge and skills which, however, make cooperation all the more challenging. Philosophers, psychologists, biologists, linguists, mathematicians, physicists, computer scientists and statisticians all enrich cognitive science with their different backgrounds, knowledge and definitions. But while it is easy for a psychologist to communicate psychological research to other psychologists, it becomes more complicated when one of them is, say, a physicist. Definitions, knowledge and concepts differ between academical backgrounds, making the establishment of a common communication basis necessary. Moreover, such a basis seems crucial, not only for scientists to communicate with other scientists but also for scientists to communicate with the non-scientific community.<sup>1</sup> The first part of the present thesis is therefore an attempt not only to bring order in the different interdisciplinary aspects that play into the research question addressed in the second part but also to provide a comprehensive overall picture for a broader public than just the scientific community. Among others, the first part addresses the following questions: Why is uncertainty a key concept for a better understanding of human information processing? Can probability theory help us to understand the human mind? How does cognitive science relate to machine learning concepts? How exactly is *learning* defined and what does a cognitive scientist mean when she talks about sensorimotor learning, adaptation or a visuomotor rotation paradigm? The first part is structured in such a way that these aspects are related to each other. The resulting bigger picture finally provides the basis for our research question in part two.

## 2 Uncertainty

*"I have a theory about the human mind. A brain is a lot like a computer. It will only take so many facts, and then it will go on overload and blow up."*

— Erma Louise Bombeck

As already mentioned, this thesis very broadly investigates the question of how fundamental human information processing works. However, when we ask this question, it is crucial to first consider the characteristics we are exposed to when our body interacts with the environment. After all, the interplay of our body with our environment sets the rules we have to follow.

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<sup>1</sup>Especially in light of the emergence of the fake news debate and the general scepticism towards science, this seems more important than ever (Waisbord, 2018, see also Allcott and Gentzkow, 2017).

In order to survive, the way we process information needs to be adapted to our body as the hardware that shapes and constrains our interactions with the environment.<sup>2</sup> One of those constraints that our body imposes is that, to us, everything is probabilistic.

The world around us is full of it. Whether we are skiing, investing in the stock market, crossing a street in the fog or just listening to someone in an everyday conversation, it is omnipresent in whatever we are doing. *Uncertainty* is part of our everyday life. That might be especially obvious when walking through fog or when trying to identify a specific person from a distance. But even under clear visibility conditions, our sensory receptors as well as the neural signals when we process the sensory input always come with noise (Faisal et al., 2008), making even simple everyday situations, such as locating a cup's position on the table or correctly identifying our name when someone is calling us in a bar, subject to uncertainty. This requires all information processing in our brain to deal with this uncertainty. Clearly, our sensors do not grasp the entire reality of our environment as it is (J. Freeman et al., 1999; W. J. Freeman, 2004). As we have seen earlier, our brain can be understood as an information processing system that constantly computes an output based on the information that comes in. However, in order for those computations to work, the amount of input that has to be processed has to be manageable. If we were to process the whole unfiltered flood of information in the environment we would feel overpowered. As a consequence, the model created by our filtering sensors is necessarily just an extract of the entirety of information that really constitutes reality. Bats, for instance, have been shown to perceive much higher frequencies as a human ever could and to use these sounds for producing echoes to orient themselves in a dark environment (*e.g.* G. Jones and Teeling, 2006). Human eyes, in contrast, are more sophisticated for colour vision (D. Wang et al., 2004). While the ability to perceive colours in high quality has proved to be a huge evolutionary benefit for us, a nocturnal bat would have no use for it. Thus, every species has its own range of sensors that are adapted to their specific needs in the sense that they map those aspects of reality that proved useful for their way of life. Accepting the fact that our sensors do not grasp everything and that they therefore provide us with an estimate about what our environment might look like rather than with reality itself, raises the question of how this estimate is computed. The data basis that constitutes our sensory input is always incomplete, noisy and to some extent unreliable, thus, uncertain. How do we deal with this uncertainty?

## 2.1 Unconscious Inference

The computation of predictions has been proposed as a promising concept to answer the question of how we deal with uncertain sensory information (see Clark, 2013 and Den Ouden et al.,

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<sup>2</sup>Even though this might change quite fast now with the development of improved bioprostheses. It might be a conceivable scenario that not only will there exist prosthetics that compensate for obvious biological deficits (such as a missing leg) but that even enhance human natural abilities (Warwick, 2005; Warwick & Ruiz, 2008).

2012 for a review).<sup>3</sup> The idea that predictions complement uncertain sensory information in perception can be traced back to the physicist and physiologist von Helmholtz (1867). According to him, perception emerges as a result of “unconscious conclusions” (von Helmholtz, 2013) and is consequently not directly determined by stimuli from the environment. Instead perception is thought to be driven by an interaction of sensory information and former experiences. Based on the observation that optical illusions work despite our awareness and knowledge on illusions, von Helmholtz (1867) concluded that, in addition to the visual sensory input, previous knowledge is used to make unconscious inferences<sup>4</sup> about the future. These predictions in turn might facilitate, if not improve perception.<sup>5</sup> In the past decades, this new concept of perception has gained increasing attention (Friston, 2005; McClelland & Rumelhart, 1981; Summerfield & de Lange, 2014).

The framework of predictive coding proposes a widely accepted theory that implements those concepts in terms of neural information processing in perception (Rao and Ballard, 1999, see Figure 1). Briefly, it states that our brain is constantly trying to generate a best fitting ‘internal model’ (Wolpert et al., 1995) of the world (Wolpert et al., 2001). Predictions deriving from this model are compared to the incoming sensory input and updated accordingly, constituting the new and more accurate model. More specifically, the process of updating is thought to be achieved by an iterative reduction of the error between prediction and sensory input until, eventually, it gets entirely “explained away” (e.g. Pearl, 2014). Hence, according to this framework, perception can be seen not only as a mere bottom up process where sensory input gets processed along the neural hierarchy of cortices but as a process of constant alternation of bottom up and top down mechanisms. Previous knowledge is used to make top down predictions which in turn are compared to the bottom up sensory input. According to predictive coding, this interplay of feedback and feedforward loops iteratively updates the prediction until it is fully consistent with the incoming sensory input. The corrected prediction is consolidated in our memory and this updated version in turn becomes the knowledge base for the next prediction (K. A. Smith et al., 2013). The framework of predictive coding thus suggests that uncertain sensory information and previous knowledge are combined for a more accurate perception. But, if so, how would we computationally integrate them to obtain a coherent representation of our environment?

## 2.2 Bayesian Integration

How do we integrate uncertain information? One conceivable option would be that our brain simply ignores all uncertainty, thereby accepting the loss of a high amount of valuable information. Consider first the hypothetical case that predictions play no role in our information

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<sup>3</sup>It should be noted that, as is the case with research in general, a scientific proposition of a solution does not mean that it is necessarily true. Instead, it rather represents the best model of reality that research identified so far.

<sup>4</sup>Unconscious because we are unable to control them consciously.

<sup>5</sup>Only in the specific case of illusions, these inferences lead to a biased perception (von Helmholtz, 1867).

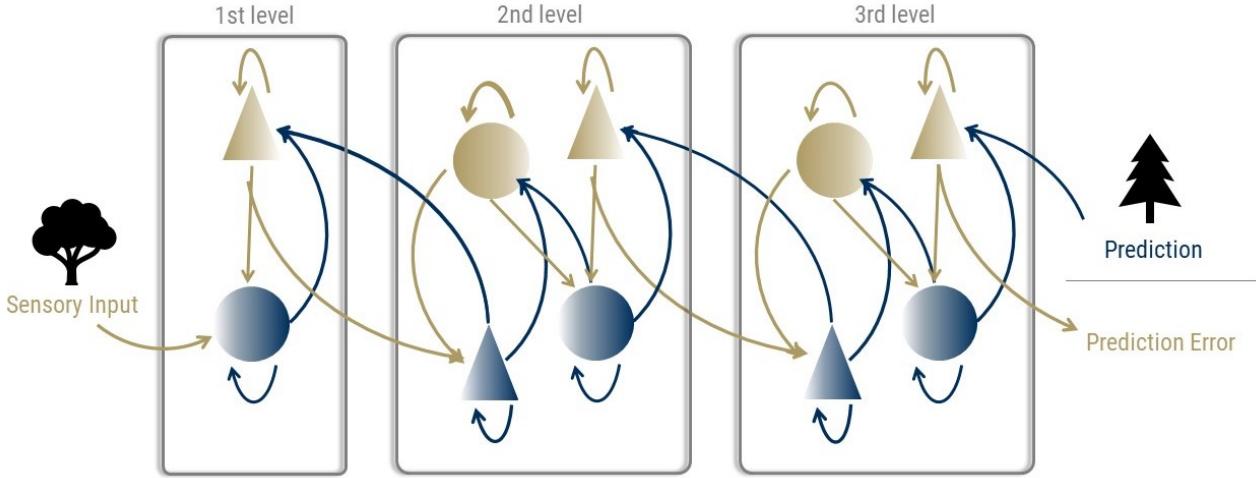


Figure 1: Illustration of the predictive coding framework. Within the hierarchical structure of the visual cortex (simplified by three levels in this example), representation units (deep pyramidal cells: *blue circles and triangles*) return the prediction (*fir tree*). At the same time, prediction error units (superficial pyramidal cells: *gold circles and triangles*) represent and feed-forward the error resulting from the comparison between prediction and incoming sensory input (*deciduous tree*). This way, only the remaining prediction error passes the hierarchical structure of the visual cortex, where the prediction is iteratively adjusted to the sensory input. This process of error minimisation is repeated until both become equal. Adapted from Feldman and Friston (2010).

processing and that we rely on sensory information only. Imagine an approaching car in the fog in an unknown environment. You might not necessarily see the car but the sound of it tells you that it is probably not far away. In this case the fog makes your vision a less certain indicator than your hearing and the question is how to best integrate the information from those two different sources. If the additional information of the uncertainty of each sensory input was to be ignored by our brain, both, your visual as well as your auditory input would be equally weighted. However, in this example combining those two sources regardless of their respective uncertainty and thus interpreting both sources as equally reliable would be devastating as it would falsely lead you to the conclusion that the car is still far away (as the fog prevents you from seeing it). The opposite assumption about how our brain deals with uncertainty would be that uncertainty is entirely accounted for. Considering the exact amount of uncertainty of a respective sensory input before coming to a conclusion would assign more weight to the more certain sensory input (in this example, the auditory one) as compared to the less certain one (visual). While you might falsely infer that you still have enough time to cross the street in the first scenario, the latter one would lead to the opposite conclusion of the car actually being quite close. In this case you would probably wait for the car to pass. Whether we account for uncertainty or not thus makes a crucial difference.

So far, the example disregarded prior knowledge and focused on the integration of two stimuli from different sensors only. Now imagine a slightly modified version of the example. It

is still foggy and you are neither able to see nor to hear any car. However, this time knowing this street quite well, your experience tells you that it is usually quite busy. In addition to the information coming in through your sensors, your previous knowledge helps you making a prediction on what is likely to happen and this prediction in turn can be used as another information source to correctly assess the situation. In this example, accounting for uncertainty would lead to the following implications: Even without seeing nor hearing any car you might still be more cautious when crossing the street because of your prediction that cars are frequent on this street being more reliable than your foggy vision. Conversely, if your prediction was only based on a single as opposed to many experiences and if it was less foggy, you would be more likely to instantly cross the street as your visual input would be more reliable than your prediction.

This latter option of weighting, both, sensory input and prior knowledge with their uncertainty – the more uncertain, the smaller the respective weight – would provide the optimal estimate (Bernardo & Smith, 2009) and is captured in the theory of **Bayesian integration** (Denève & Pouget, 2004 Jan-Jun). Bayesian integration thus provides a probabilistic description for the integration of information with varying reliability (Kersten et al., 2004; Rohe & Noppeney, 2015). According to the **Bayesian coding hypothesis**, namely the hypothesis that the brain represents information probabilistically (Knill & Pouget, 2004), the brain uses a form of **Bayesian inference** (Pouget et al., 2002), where the term Bayesian inference refers to a specific statistical inference method that is based on the **Bayes' theorem**. In this context, the theorem describes how the probability of an estimate is updated based on prior knowledge and related information. It is formalised by

$$P(E|D) = \frac{P(D|E) \times P(E)}{P(D)}, \quad P(D) \neq 0 \quad (1)$$

where  $E$  stands for any *estimate* and  $D$  for new data.  $P(E)$  refers to the prior probability (often just referred to as **prior**) which is the probability of the estimate  $E$  before the new data  $D$  has been observed.  $P(E|D)$  is the posterior probability (or just **posterior**) of the estimate  $E$  after the new data  $D$  has been observed and corresponds to the probability of the updated estimate.  $P(D|E)$  is referred to as the **likelihood**. It represents the probability of observing the data  $D$  given the estimate  $E$  and indicates the compatibility of  $D$  with  $E$ . Finally,  $P(D)$  is the probability of observing the new data  $D$  and is termed as *marginal likelihood*.

In order to understand the implications of the Bayes' theorem, it is important to appreciate that, within this framework, cognitive representations such as beliefs or expectations are modelled as probability density functions (PDF). Within these PDFs the mean can be interpreted as the main-estimate and the variance as the amount of uncertainty (noise). For instance, imagine a person estimating the size of a specific tree. Looking at this tree, the person might come to the conclusion that its height is 10 m. However, besides this main-estimate (*mean of the PDF*) the person would also assume a whole range of other possible but more or less likely

values (*variance of the PDF*). Even though your best guess might be 10 m, it could as well be 9 m or 10.5 m. In this context, the PDF indicates the persons' beliefs to which extent every possible size value is the true one. A higher uncertainty (*e.g.* your guesses ranging from 4 m to 16 m, for instance because of the tree standing far away) results in a larger variance of the PDF and vice versa.

Based on this **probabilistic** understanding of cognitive representations, Bayesian integration describes how to best combine new sensory information (captured in the likelihood) with previous knowledge (captured in the prior) in order to create the most accurate representation of the environment (captured in the posterior). A simplified illustration of Bayesian integration is provided in [Figure 2](#). Based on the assumption that the variances of the different information sources are uncorrelated, *i.e.* independent from each other, Bayes' theorem implies that those sources are combined by multiplying their PDFs. This way the resulting PDF of the posterior is precision weighted in the sense that the resulting posterior PDF is closer to the more precise information source (O'Reilly et al., [2012](#)). If for instance, the prior knowledge is not well developed yet, its amount of uncertainty (*i.e.* its variance) will be high and thus the posterior will be more driven by the more accurate sensory input. Within the optimal-Bayesian approach of modelling an information processing system every possible parameter is unexceptionally included in computation, each weighted by its own amount of uncertainty, thereby leading to highly accurate results.

Indeed, previous research provides evidence for the assumption that human perception follows Bayesian principles (*e.g.* Brown and Friston, [2012](#); Knill and Richards, [1996](#); Kok et al., [2014](#); Nour and Nour, [2015](#); Rohe and Noppeney, [2015](#); Yuille and Kersten, [2006](#)). Crucially, not only does this seem to apply to perception but also to various other cognitive abilities. Evidence suggesting that the human brain implements Bayesian principles has been found in computational neuroscience (George & Hawkins, [2009](#)), perception (Goldreich & Peterson, [2012](#)) and sensorimotor learning (Kording & Wolpert, [2004](#)). It should be noted, however, that the Bayesian framework for cognitive modelling is still under debate (see Hahn, [2014](#) for a review). One line of critique emphasises that human behaviour is often suboptimal (Bowers & Davis, [2012](#)). If the brain were to implement Bayesian principles, then why would we use heuristics as shown by a large body of research (Gigerenzer et al., [2011](#); Kahneman et al., [1982](#))? It has further been argued that Bayesian models are unfalsifiable (Bowers & Davis, [2012](#)) and that they do not provide more insights than previous mechanistic level theories (M. Jones & Love, [2011](#)). Furthermore, Elqayam and Evans ([2011](#)) state that Bayesian models reflect the idea of human thinking as a normative system and that non-normative theories would be more appropriate to formalise higher mental processing. It can therefore be concluded that, despite its popularity, the Bayesian coding hypothesis is still under debate.<sup>6</sup> In addition, it is still

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<sup>6</sup>Please note that this thesis does not address the methodological debate of Bayesian statistics and classical hypothesis testing (*e.g.* Kruschke, [2010](#); Puga et al., [2015](#)). Instead, we are interested in the conceptual question of whether our brain implements a form of Bayesian integration, that is whether the brain uses probabilities for information processing. The use of Bayesian statistics as a more appropriate method for data analysis is a

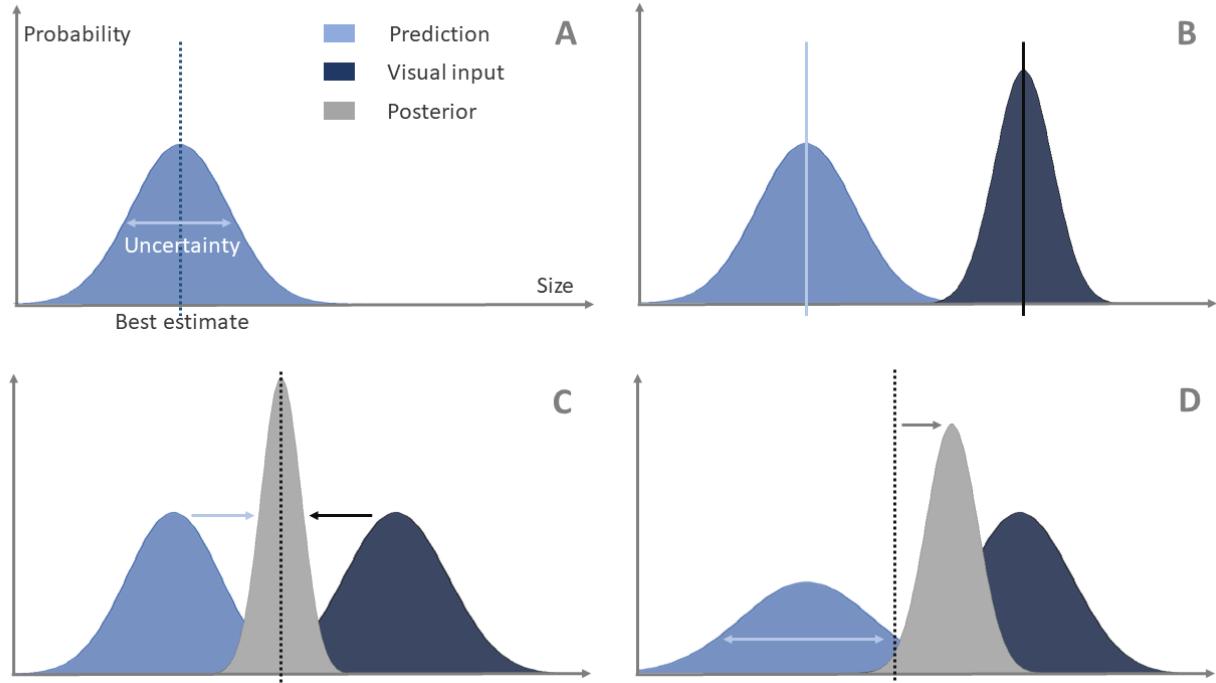


Figure 2: Bayesian inference, illustrated by the example of someone trying to estimate the height of a specific tree. (A) The prior belief, *i.e.* the prediction, is represented by a PDF (*light blue distribution*), where the mean (*dotted line*) represents the best estimate and the variance (*arrow*) the amount of uncertainty. For instance, based on previous experiences, you might expect an average height of 10 m for trees. This would be your best estimate (*mean*). However, you will also assume other heights as more or less likely and, depending on the number of these other height values, your prediction will be more or less precise (*variance*). (B) Not only a prior belief but also the likelihood of some sensory input is represented by such a PDF with again its own mean and variance (*dark blue distribution*). If prediction or likelihood were perfectly precise, their variance would be 0. In this example, the prediction is more uncertain than the sensory input. (C) Estimating the size of the tree is achieved by combining both information sources. The resulting posterior belief is again a PDF (*grey distribution*). (D) The PDF of the posterior belief is precision weighted in the sense that it is more affected by the more precise information source (in this case, the visual input). Adapted from Adams et al. (2013), O'Reilly et al. (2012).

an open question if formalising neural computation in terms of probabilistic inference is more appropriate for real-life computations than following mechanistic approaches (Pouget et al., 2013). Thus, more research in this domain is needed for further clarification.

## 2.3 The Role of Noise

At the beginning of section 2, it was argued that our sensors provide us only with an extract of the entirety of information in our environment, thereby making everything subject to uncertainty. An interesting additional finding is that, in fact, neural activity itself has been shown different debate that is not addressed within this thesis.

to be highly variable (Ermentrout et al., 2008; Faisal et al., 2008). Repeated exposure to the identical picture of a cup, for instance, would never lead to exactly the same neural firing rate (Softky & Koch, 1993). At first, this might seem a bit odd as we mostly think of noise as something disturbing that we have to deal with. However, current research indicates that noise in neural firing rates might even benefit information processing (Dhawale et al., 2017; Ermentrout et al., 2008; McDonnell & Ward, 2011; Wu et al., 2014). In the context of sensorimotor learning, one might wonder why a successful reaching movement to a specific target is never exactly repeated (Krakauer et al., 2019; Pekny et al., 2015; Vaswani et al., 2015). It seems surprising that we do not stick with a movement as soon as it proves to be useful. Why should our brain compute a slightly different solution when it already found one that works perfectly well?

Here, the Bayesian framework might provide a reasonable explanation (Krakauer et al., 2019). Allowing for a certain amount of noise implies incorporating some flexibility. Only if there is some variability in the way we conduct a specific behaviour, can we choose which one is the most appropriate one. The wider the range of options the richer the variety we can choose of. Always applying the identical movement to the same type of situation would make us unable to act in a slightly different situation. In other words, no variability in motor commands would make adaptation to changing circumstances impossible (Dhawale et al., 2017), thereby forcing us to learn every behavioural modification in a slightly changed environment as if it was a completely new behaviour. While a smaller variability for a well trained behaviour helps us selecting the best fitting action for a specific common situation (*e.g.* grabbing a cup on a table) a greater variability allows for a wider exploration in unknown settings (Wu et al., 2014).

## 2.4 Learning under Uncertainty

Based on the assumption that human information processing follows Bayesian principles, the previous section described a reasonable explanation for the phenomenon of neural noise in sensorimotor learning. But what exactly do cognitive scientists mean when they say **sensorimotor learning**? Sensorimotor learning is the cognitive ability that we focus on in part two; but before we address sensorimotor learning in more detail, we first need to take a step back to have a clear understanding of how learning in general is defined. In psychology, learning is usually understood as “a relatively permanent change in behaviour due to past experience” (Coon & Mitterer, 2012) or as “the process by which relatively permanent changes occur in behavioural potential as a result of experience” (Anderson, 1995). Within this broad definition, psychologists refer to a wide range of different concepts that represent different approaches to explain varying learning phenomena (*e.g.* habituation, social learning or classical conditioning). Similarly, in the cognitive science literature, scientists increasingly mention the terms **supervised learning**, **unsupervised learning** or **reinforcement learning** (*e.g.* Bekolay et al., 2013; Gibson et al., 2013; Jordan and Rumelhart, 1991; Rentschler et al., 1994) to categorise different types

Supervised Learning	In supervised learning, the algorithm learns a function that maps inputs to outputs based on <i>labelled training data</i> . For instance, in an input data set of fruit pictures, a label might be the correct answer “apple” to the general problem “What fruit does the picture show?”. If the system produces the output “peach” instead of the true answer “apple” the mapping function is adjusted accordingly. The goal of supervised learning is to optimise the mapping function $Y = f(X)$ to eventually correctly predict the output variables $Y$ in unlabelled novel input data $X$ . Among others, it is used for classification and regression problems and called this way because the process of training the model can be described as the system being supervised by ‘a teacher’ who knows the ‘true answers’. Among others, supervised learning algorithms are used in image recognition.
Unsupervised Learning	Among others, unsupervised learning solves clustering and association problems by finding hidden structures and patterns in the data, thus allowing us to learn more about it. Here, no labels are provided. Instead, the system learns a probabilistic model of the data. It is therefore referred to as a self-learning technique. Cluster analysis, for instance, categorises data by identifying commonalities. Semi-supervised learning can be considered as a hybrid between supervised and unsupervised learning, where a subset of the data is labelled and the rest is not. A practical application might be the clustering of customers into specific groups for unsupervised and medical anomaly detection for semi-supervised learning.
Reinforcement Learning	Similar to supervised learning, reinforcement learning also tries to find a mapping function between input and output. This time, however, feedback is not coming from predefined labels but from a reward function. Thus, the system is not learning from labels but from its own previous experiences when interacting with its environment. Its goal is to map situations to actions by maximising the reward. Among others, reinforcement learning has proved successful in learning how to solve complex games.

Table 1: Overview of the main categories of learning algorithms in machine learning that are often referred to in cognitive science.

of learning. Inspired by the classification of different learning paradigms in the computer sciences, cognitive scientists adopted and implemented those concepts to further investigate the functioning of learning mechanisms in the human brain (Dillenbourg, 1999; Jäkel et al., 2009). A rough overview of the corresponding machine learning basics is thus important for a better understanding of the categorisation of different learning types.

Similar to the psychological definition, machine learning investigates the process of automatically improved behaviour, not in humans but in computer algorithms (Mitchell, 1997). Briefly, learning algorithms are trained to build a mathematical model based on sample data in order to make predictions or decisions (Bishop, 2006). Crucially, they are not explicitly programmed to do so (Koza et al., 1996). Very broadly, three main categories of learning are distinguished in machine learning: *supervised*, *unsupervised* and *reinforcement learning*. A brief overview of those three learning types is provided in Table 1.

One might ask how this classification of learning types in machine learning might relate to human sensorimotor learning. It becomes more obvious however when we take a closer look at its definition. Sensorimotor learning is understood as “any experience-dependent improvement in performance” (Krakauer et al., 2019). It encompasses any learning process that involves movement “made by almost any animal species with any effector in any task”. It is the improvement of a specific movement based on sensory input. If we abstract this definition a little

and detach it from humans or animals as biological systems, it is very similar to the definition of machine learning in the specific context of motor outputs (*i.e.* movements). Relating sensorimotor learning to different learning concepts in machine learning can thus help us to classify and understand different learning mechanisms in humans.

In supervised learning, the human sensorimotor system (roughly consisting of sensors: *e.g.* eyes or nose, effectors: *e.g.* arms or hands and the controller: the brain) is considered to receive the feedback from its environment. It receives sensory input (seeing a cup) and produces an output (arm movement to grab the cup). The error between this output (hand position) and the target output (the actual position of the cup) acts as performance measure and is iteratively minimised (Wolpert et al., 2001). The target output can be defined either by an external teacher, such as in the case of imitation learning, or internally triggered through incoming sensory signals or ones own higher goals. Evidence that neurons in the cerebellum encode error signals that would be necessary for supervised learning, supports the idea that the brain might indeed implement supervised learning (Kitazawa et al., 1998; Shidara et al., 1993). Reinforcement learning differs from supervised learning in that the feedback consists either in reward or in punishment as opposed to a concrete target output. The sensorimotor system is thus only provided with information about success or failure but the exact information on direction and magnitude of the error is missing (Taylor et al., 2014; Wu et al., 2014). In this case the performance measure is the maximised amount of reward, where instant reward is given more weight than future reward. Here, the dopaminergic system can be seen as a neural correlate for reinforcement learning (Schultz et al., 1997). In unsupervised learning, the motor system only receives an input from its environment but no feedback on its output. One learning rule that has been shown to implement an unsupervised learning algorithm is the Hebbian rule (Oja, 1982; Wolpert et al., 2001). According to Hebbian learning, the connection between neurons gets enforced by the mere repetition of the pre-synaptic firing to the post-synapse, thereby providing an explanation for neural plasticity (Hebb, 2005). The more a post-synapse is stimulated by a pre-synapse the greater the connection between those two cells.

Taken together, these three computational learning paradigms account for differences between various types of sensorimotor learning in humans. For a better understanding, Wolpert et al. (2001) propose Bayesian learning as a powerful unifying framework: While Bayes rule can explain how a posterior model is generated in supervised and unsupervised learning by combining the prior model with new data, Bayesian decision theory<sup>7</sup> accounts for reinforcement learning, where both the model and the cost function are learned from the environment. One specific type of sensorimotor learning that plays a pervasive role in our everyday life can be classified as a form of supervised learning: **sensorimotor adaptation**. In order to modify our behaviour according to the specific requirements of the present situation, our prior (*e.g.* our prior model of how to best reach for the cup) is constantly compared to the new sensory

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<sup>7</sup>Bayesian decision theory refers to an approach to decision making, where the Bayes' theorem is used as a basis to make optimal decisions in an uncertain environment.

evidence (our vision of the cup on the table). The posterior model is generated by minimising the error between the outcome (the hand position) and the label (the cup’s position). The fact that adaptation is a simple form of learning where information from several sources is integrated to generate an easily observable output makes it suitable for the experimental investigation of underlying computational principles. Since Kording and Wolpert (2004), a growing body of research therefore became interested in sensorimotor adaptation as a promising field of research to further examine the question whether or to what extent our brain implements Bayesian principles. This also applies to the experiment described in [Part II](#). The following sections therefore provide an overview of adaptation including its characteristics, respective experimental paradigms, neural correlates, its properties and typical components, as well as a description of state space models as a useful formalisation of adaptation.

### 3 Sensorimotor Adaptation

The previous chapter covered the definition of sensorimotor learning and discussed how computational learning paradigms might relate to it. We have seen that different paradigms are well suited to describe various types of sensorimotor learning. It was further mentioned that sensorimotor adaptation can be classified as a form of error-based and, more specifically, as supervised learning. Adaptation is defined as an adjustment in already well practised behaviour as a reaction to a change in the environment or in our body. Its aim is to maintain the same performance level for a specific task under new circumstances. According to Krakauer et al. (2019) it differs from [de novo learning](#) in the sense that the latter describes a mechanism of acquiring a completely new skill such as learning to ride a bike for the first time (see Krakauer et al. (2019) for a detailed review on the distinction between adaptation and de novo learning). Adaptation, in contrast, is used to adjust a behaviour we are already quite familiar with to new circumstances. For instance, imagine grabbing a cup laying on a table in front of you. As this is probably not the first time you are grabbing a cup, your previous experience provides you with a clear concept and motor plan, *i.e.* a plan on how to conduct a movement given sensory input and a higher goal, on how to move your arm, hand and fingers to eventually hold the cup in your hand. However, it is highly unlikely that the exact movement for grabbing a cup is always identical. For instance, the size of the cup may change or its position on the table. This requires your motor system to flexibly adjust the well known basic movement for ‘cup grabbing’ to the specificities of the respective situation defined by your environment and your body. The whole process of using sensory input to adapt your general motor plan to this specific situation is referred to as *sensorimotor adaptation*.

### 3.1 Adaptation Paradigms

Research established several paradigms to investigate visuomotor adaptation in laboratory tasks. The first one to systematically study adaptation was von Helmholtz (1867). Using *prism goggles* that shifted the participants visual field either laterally or vertically, he observed that participants adapted to their shifted environment. For instance, a participant being engaged in the perceptual motor task of pointing to a visual target while wearing goggles will initially perceive himself to point off-target. However, as he continues pointing, he accounts for the shift and the error gets iteratively reduced. It usually takes less than 10 trials for participants to fully adapt and to successfully point to the target (Rossetti et al., 1993). Importantly, adaptation is initially maintained after removing the goggles. This result is known as the adaptation **after-effect** and fades away over time until the behavioural performance completely recovers to the baseline level.

Recently, a more common paradigm largely replaced prism goggle experiments. In a *force field paradigm*, participants have to grab a robotic arm to reach for specific targets in space while compensating for an applied force into another direction (Shadmehr & Mussa-Ivaldi, 1994). The way the force is applied to the task can vary across experiments. For instance, one common way of implementing force is by using a *viscous curl field*, where the applied force is proportional to the velocity and the direction orthogonal to the direction of the participants reaching movement (Hwang et al., 2003; Melendez-Calderon et al., 2011).

Another common paradigm is referred to as *visuomotor adaptation*. It can be seen as the modern version of the prism goggle paradigm as it also aims to change the mapping between the movement of an effector and the respective visual feedback (FB). Here, participants perform reaching movements with a robotic arm, allowing for a much more controlled setting. In contrast to the force field paradigm, the perturbation is not an imposed force but a perturbation of the visual FB. A common type of visuomotor adaptation is changing the visuomotor gain, *e.g.* by manipulating the speed of a cursor for a given hand movement (Hegele & Heuer, 2010; Ingram et al., 2000; Pearson et al., 2010). Probably the most common manipulation type in visuomotor adaptation is referred to as **visuomotor rotation** (VMR). In such a paradigm, the FB is not altered in speed but in position. Importantly, participants cannot see their true hand position while performing the reaching task. Instead, they have to rely on visual FB.<sup>8</sup> Participants are told that a cursor represents their occluded hand position while performing a reaching task to outward targets. However, instead of representing the actual hand position the cursor position is a function of their real hand position and a lateral rotation (see Figure 3 for an illustration). Visuomotor rotation is the paradigm we focus on in Part II.

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<sup>8</sup>Note that, strictly speaking, such an experimental paradigm that manipulates visual information to investigate movement outcomes would also need to account for proprioception, *i.e.* perception and awareness about the current position of our body in space. However, the possibilities for excluding or controlling proprioceptive effects are very limited. It is therefore important to bear in mind that, even in controlled paradigms, reaching movements do always rely on proprioception to some extent.

### 3.2 Neural Correlates

Neural evidence supports the idea of adaptation as an error-based learning mechanism (Krakauer et al., 2019; Tan et al., 2014) where the cerebellum is assigned an important role (Cullen & Brooks, 2015). A wide range of evidence reveals deficits in adaptation, both, in VMR (Contreras-Vidal & Buch, 2003; Kerr et al., 1993; Werner et al., 2010) as well as in force field adaptation paradigms (Donchin et al., 2011; Maschke et al., 2004; Rabe et al., 2009) when cerebellar functions are impaired. By comparing subjects with cerebellar lesions to healthy controls Taylor et al. (2010) found that while both groups were able to adapt to a rotation adaptation task using explicit strategies, only the healthy control group showed additional implicit adaptation patterns. Butcher et al. (2017) replicated this finding of impairments in implicit learning. However, unlike Taylor et al. (2010), they describe an additional difficulty to compensate the deficit in implicit adaptation with explicit aiming strategies. This unexpected finding led to assume that the cerebellum might form a part of a wider network involved in learning and maintaining action-outcome associations. In general, the idea of the cerebellum encoding a feedforward model which predicts the output of a motor command is widely supported by numerous studies (Bastian, 2006; Ebner & Pasalar, 2008; Pisotta & Molinari, 2014; Wulff et al., 2009). In line with this idea of the cerebellum being involved in prediction, several studies concluded that the cerebellar *Purkinje cells* might encode the motor output such as the final arm movement rather than the motor command to conduct this movement (Bastian, 2006; Ebner & Pasalar, 2008; Herzfeld et al., 2015). In sum, the cerebellum is widely accepted as a crucial structure for adaptation as it probably encodes the prediction of the motor outcome. While lesions of the cerebellum lead to a significant impairment of adaptation, the basal ganglia do not seem to directly affect implicit adaptation (Gutierrez-Garralda et al., 2013; M. A. Smith & Shadmehr, 2005). However, a few studies found that after-effects and retention seem to be impaired, suggesting that basal ganglia might play a more cognitive role of long-term memory in adaptation (Bédard & Sanes, 2011; Leow et al., 2012). Although a few studies investigated the role of the cortex in motor adaptation (*e.g.* Baraduc et al., 2004; Della-Maggiore et al., 2004; Mathis et al., 2017) the overall picture of how the cortex affects behaviour in adaptation paradigms remains unclear (see Krakauer et al. (2019) for a review).

### 3.3 Properties

Numerous studies (Kitago et al., 2013; J. Wang & Sainburg, 2006; Woolley et al., 2011) have shown that visuomotor adaptation comes with characteristic properties (see subsection 3.3). As already described for the prism goggles in the first paragraph of subsection 3.1, subjects quickly adapt to their manipulated environment. In addition to this improvement in behavioural

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<sup>9</sup>Previous literature is not consistent in terminology. Often the error, as it is defined here, is also referred to as **hand angle** (HA). Conversely, others refer to the error as the angle between aiming target and cursor position.

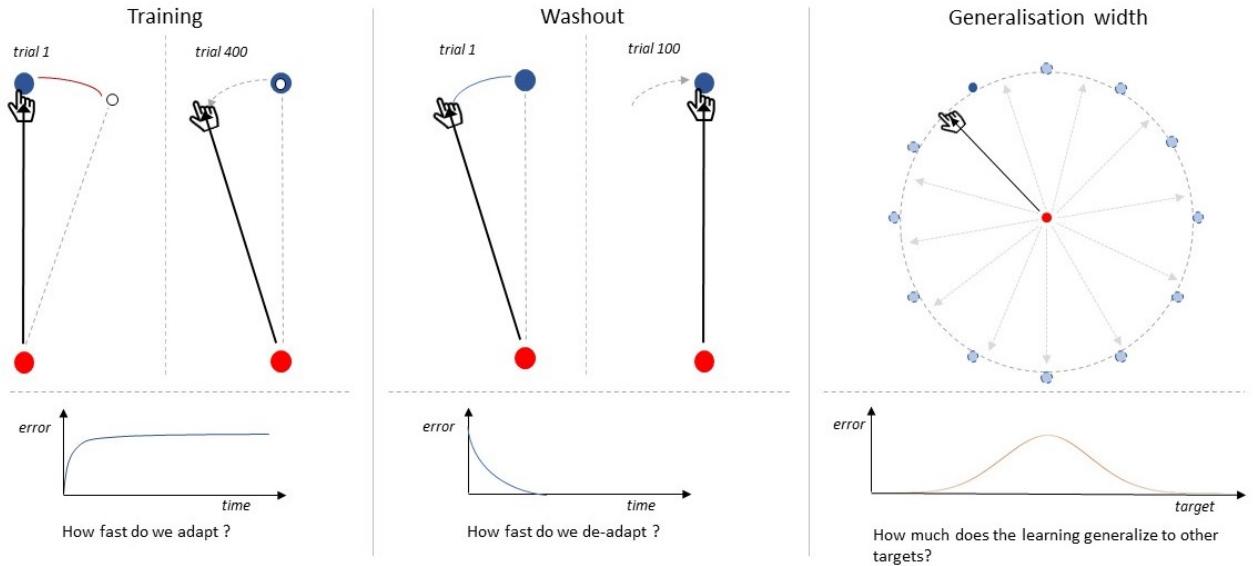


Figure 3: Illustration of the properties of adaptation in a VMR paradigm. *Left:* Participants are instructed to perform reaching movements from a start target (red) to an aiming target (blue). During *training*, participants learn to adapt to visually shifted FB (white cursor) and reach counterclockwise (CCW) in order to make the cursor appear on the aiming target when vision of their hand position is prevented. Note that the error depicted on the  $y$ -axes is defined as the angle between final hand position and aiming target location.<sup>9</sup> *Middle:* In *washout*, participants slowly de-adapt and reaches normalise back to baseline level when no perturbation is applied. Washout is accelerated when veridical FB is provided. *Right:* After adapting to a perturbation, participants have been shown to *generalise* the learned shift to new targets. Targets that are located close to the learning target typically reveal a greater amount of generalisation.

performance, it was further mentioned that due to after-effects this process of learning affects behaviour even after removing the respective manipulation, a phenomenon known as *washout* (Huang et al., 2011; Kitago et al., 2013). The duration of washout is shorter when subjects are provided with veridical FB. However, even if slightly more time consuming, no FB is necessary to de-adapt. Passing time alone is sufficient to return to baseline (Kitago et al., 2013). Another property of adaptation is *generalisation*. Not only does adaptation to a new environment apply to the target that the adapted behaviour was learned for but also to other targets. This phenomenon, referred to as *intralimb generalisation*, is a robust finding (Berniker & Kording, 2008; Malfait & Ostry, 2004; Zhou et al., 2017). In addition, (Hewitson et al., 2018) found evidence for *interlimb generalisation*, thereby showing that adapted behaviour further generalises across limbs. Both, washout and generalisation are caused by after-effects. Crucially, those after-effects still persist even when a subject is fully aware of it, indicating that adaptation cannot be entirely under explicit control.

### 3.4 Components

Originally, adaptation was referred to as one single process of implicit recalibration. However, a growing body of research indicates that the total amount of adaptation is rather the result of several processes that work in parallel (Huberdeau et al., 2015). The predominant distinction is the one between implicit and explicit processes (Taylor et al., 2010). Both, **implicit learning** as well as the use of **explicit aiming strategies** have been shown to contribute to adaptation. While implicit learning is usually characterised as an automatic and subconscious process, explicit aiming strategies refer to a conscious and cognitively driven form of compensation (Redding & Wallace, 1993). Importantly, the typical shape of the adaptation learning curve, characterised by an initial fast learning and a subsequent slower learning phase, can be achieved by decomposing it into a *fast* and a *slow* learning process, where the fast component has a high learning rate and low retention, and vice versa for the slow system (M. A. Smith et al., 2006). Results from Taylor et al. (2010) relate explicit strategies to the fast and implicit learning to the slow component. Moreover, participants who are either instructed on how to deal with a perturbation or who report being aware of the imposed perturbation show better or faster learning (Benson et al., 2011; Malone & Bastian, 2010; Werner & Bock, 2007). In order to investigate the question to what extent adaptation follows Bayesian principles, implicit learning is of primary relevance to the empirical part of this thesis.

A qualitatively different but also very common dissociation in the literature of motor adaptation is the distinction of two mechanisms: **feedback adaptation** and **feedforward adaptation** (Botzer & Karniel, 2013; Lam et al., 2006; Wagner & Smith, 2008). For a better understanding of those two processes, consider again the example of someone conducting an arm movement to reach for a cup. Visual input on the cups location is used to optimally compute the best fitting reaching movement for eventually holding the cup in our hand. We thus use the visual input to make a prediction on where we will end up when conducting a specific movement. In the sensorimotor adaptation literature, this process of conducting a movement based only on the first estimate is called a *feedforward process*. Here, only *top-down* knowledge is used to compute the best estimate. For instance, you would rely on feedforward processes only when you reach for the cup with closed eyes after memorising its position on the table. However, you would probably reach more accurately with your eyes being open. Only relying on the feedforward process would imply that the reaching movement always needs to be completed, no matter if it is appropriate or not. When your eyes are closed, you will only know if your reach was successful once you completed the reach. Hence, if the prediction and the respective motor plan turned out to be off, no **online correction**, *i.e.* the process of correcting the reach while conducting it, is possible in mere feedforward adaptation. In contrast, you will probably use visual information to adjust your movement while reaching when your eyes are open. Those *feedback processes* help us to integrate visual information with our motor goal while conducting the reaching movement, thereby allowing for an online adaptation of our reach. As we have seen

earlier, a growing body of research suggests that visuomotor adaptation works as an interplay of both feedback and feedforward processes (Botzer & Karniel, 2013; Grafton et al., 2008; Hinder et al., 2008). Bayesian integration formalises how feedback is integrated with the feedforward prediction. Mere feedforward adaptation would rely on the prediction, hence, prior knowledge only.

### 3.5 State-Space Models

When it comes to modelling the process of adaptation, **state-space models** prove to be a useful and predictively highly accurate formalisation (Cheng & Sabes, 2006; Thoroughman & Shadmehr, 2000). They provide a valuable description of the properties described in **subsection 3.3** and help us predicting adapted behaviour on a trial by trial basis (Donchin et al., 2003). The basic state-space model describing a simple visuomotor rotation adaptation paradigm would be formalised as follows:

$$x_t = \beta x_{t-1} - \alpha \delta_{t-1}, \quad (2)$$

$$\delta_t = x_t - r_t \quad (3)$$

where the *hand angle*  $x_t$  on the current trial  $t$  is obtained by subtracting the product of the *learning rate*  $\alpha$  and the error  $\delta_{t-1}$  experienced in the previous trial  $t-1$  from the product of *washout rate*  $\beta^{10}$  and the hand angle value of the previous trial  $x_{t-1}$ . The experienced error  $\delta_t$  on trial  $t$  is formalised as the difference between the hand angle  $x_t$  and the imposed rotation  $r_t$ , *i.e.* the cursor position, on the current trial  $t$ . Learning and retention rate are scalar parameters capturing how quickly learning occurs when updating to another state (*i.e.* the next trial) in response to the error and how much is retained from the hand angle value from the previous state, respectively. They have both been estimated from previous data by numerous studies with the learning rate  $\alpha$  typically ranging from 0.1 to 0.3 (Gonzalez Castro et al., 2014; M. A. Smith et al., 2006) and the retention rate  $\beta$  being around 0.9 (Zarahn et al., 2008). Retention rate accounts for the observation that adaptation, though getting close, never reaches full compensation (Vaswani et al., 2015) and second for the slower washout when no veridical FB is provided (Kitago et al., 2013).

Be aware that, despite the high usefulness in terms of description and prediction of behaviour in an adaptation paradigm, the class of state-space models cannot provide any mechanistic explanations of adaptation and its properties. They do not provide an explanation as to why adaptation has those properties (*e.g.* why do we learn at this rate?). According to Krakauer et al. (2019), the Bayesian perspective of learning might provide a possible explanation on the success of state-space models in providing an accurate description of those properties. Under the assumption that the variability of prior estimate and sensory FB is Gaussian, the

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<sup>10</sup>Note that retention rate is the counterpart of the forgetting or washout rate  $1 - \beta$ .

Bayesian framework becomes identical with the *Kalman filter* or *linear quadratic estimation (LQE)* (Kalman, 1960) which describes an algorithm that produces optimal estimates under uncertainty in partial trial by trial learning. This algorithm in turn is very similar to a state-space model, thereby formalising that the learning rate from one trial to the next would be the result of uncertainty about the best possible compensation in the next trial (Korenberg & Ghahramani, 2002). In addition, the Bayesian framework would predict that adaptation to a perturbation would be less the more the sensory input is uncertain. Empirical evidence provides support for this assumption (*e.g.* Burge et al., 2008; Kording and Wolpert, 2004; Krakauer et al., 2006; Wei and Körding, 2009).

Given the fact that the implication of sensory uncertainty has been studied so extensively, it seems surprising that little literature exists on the influence of uncertainty in predictions. Previous research in sensorimotor adaptation provided valuable insights in support of the idea that we might indeed implement a form of Bayesian learning. However, further implications of the framework of Bayesian integration need to be accounted for as well. Not only is it important to consider the influence of uncertain sensory input but also of uncertain predictions. Just as Bayesian integration predicts that higher uncertainty of sensory input leads to lower learning rates, it does the same for uncertainty of our prior estimate. A comprehensive validation of the Bayesian account in human information processing cannot rely on support for one prediction only. Further research is needed that additionally investigates whether uncertainty of prior knowledge leads to less adaptation as well. Part II of the thesis describes an experiment that investigates this question by means of a behavioural VMR study.

## Part II

# Study: Impact of Uncertain Prior Knowledge on Adaptation

## 4 Theoretical Background

Part one of this thesis gave an overview on visuomotor adaptation by outlining the main concepts from different research backgrounds. It was emphasized that adaptation can be characterised as a specific form of supervised learning, different from de novo learning in the sense that adaptation relates to well trained behaviour that needs to be adjusted to the specificities of the current setting. Generalisation and washout have been characterised as two significant properties of adaptation. Moreover, sensorimotor adaptation has been shown to consist of the two components implicit learning and explicit aiming. Finally, the state space models were introduced as a useful description of adaptation and its properties. However, it was also em-

phasized that they provide no mechanistic explanation. In contrast, the Bayesian framework might be a useful approach to find answers to the question of why adaptation has those properties. It was outlined that if our brain was following Bayesian principles all information was to be weighted with its respective uncertainty when being integrated. Not only would this apply to sensory input but also to previous knowledge which is integrated and updated in the form of predictions. Those predictions are believed to get updated by a piecewise reduction of the error between prediction and actual outcome. It was elucidated that this updating mechanism probably works based on an interplay of feedback and feedforward processes. In line with this concept, the cerebellum has been identified as a crucial area for adaptation as it seems to generate predictions for a motor output.

The second part of this thesis attempts to provide further insights in the question whether our brain implements Bayesian principles in sensorimotor learning, more precisely in visuomotor adaptation. Over the past few years a growing body of research supports the idea of a Bayesian implementation in human information processing (Kersten et al., 2004; Nour & Nour, 2015; Pouget et al., 2002). However, controversies exist (Bowers & Davis, 2012; Pouget et al., 2013), making further research necessary to definitely answer the question and to gain more detailed insights on the exact implementation in our brain. As stated above, following Bayesian principles would imply that our brain somehow weights the different information sources with their respective uncertainty, hence, their variance. In their seminal paper, Kording and Wolpert (2004) showed for the first time that participants seem to account for uncertainty of visual input in a VMR task, thereby being a pioneer in using a classical sensorimotor paradigm to investigate whether integration in sensorimotor learning behaves according to Bayesian principles. In their paradigm, participants were required to reach for a target with their right index finger. The use of a virtual-reality set-up enabled them to apply a lateral shift to the participants' trajectories. The participants' hands were never visible and, instead of showing them FB during the whole reach, participants were only provided with brief FB once they were halfway to reaching the target. Importantly, the quality of the FB varied between four levels of reliability: from highly reliable to completely uncertain. Since then, numerous studies used this paradigm to further investigate the role of a visual input's uncertainty in visuomotor adaptation (*e.g.* Fernandes et al., 2014; Hewitson et al., 2018), thereby mixing feedback and feedforward components of motor control. This stands in contrast to many investigations of visuomotor adaptation, which purport to study the feedforward component in isolation (*e.g.* de Rugy and Carroll, 2010; Tseng et al., 2010).

## 4.1 Aim of the Present Study

Numerous studies replicated the finding of Kording and Wolpert (2004) which supports the Bayesian assumption that uncertainty of sensory input is involved in human information processing. However, if our brain was to implement Bayesian principles in visuomotor adaptation,

not only would the variance of a sensory input be taken into account but also the uncertainty of prior knowledge. If we have reliable knowledge about the present situation and the movement we plan to conduct, our prediction would be reliable and, thus, it would be given more weight when integrating it with sensory information. Interestingly, to our knowledge, only two studies used a pure feedforward design to investigate the influence of uncertainty in predictions. While Fernandes et al. (2012) found no group difference in generalisation but an influence of uncertainty on learning, Canaveral et al. (2017) were not able to replicate the effect on learning. However, they reported an effect of uncertainty on retention. The fact that the findings of those two studies are at odds with each other leaves the impact of a prediction’s uncertainty in visuomotor adaptation still an empirical open question and, hence, further research is needed. The purpose of the present study is to add to this literature and to clarify the apparent conflict.

In order to do so, we investigated learning, generalisation and washout in a behavioural feedforward VMR paradigm. Findings of studies investigating the impact of uncertainty of sensory information support the Bayesian coding hypothesis (Knill & Pouget, 2004). As we have elaborated earlier, we expect this to apply not only to sensory input but also to prior knowledge. We therefore predict that, if feedforward visuomotor adaptation follows Bayesian principles, then high variance perturbations and, thus, noisy predictions should be adapted to more slowly than more certain predictions. For generalisation width and washout rate, the theoretical Bayesian account does not seem to make direct predictions. Neither does the existing literature provide a solid basis. In the case of washout, Canaveral et al. (2017) weakly suggest that training under a more variable perturbation leads to faster washout as compared to a less variable perturbation. In what concerns the generalisation width, Fernandes et al. (2012) report no significant differences in feedforward adaptation after manipulating the perturbation variance. To our knowledge, no other existing empirical studies addressed these questions. As such, also given the significant methodological differences between our proposed study and the existing literature, there is no solid basis on which to make strong predictions regarding the effect of perturbation variance on generalisation and retention.

## 5 Methods

### 5.1 Ethics

The experimental designed was approved by the Macquarie University Human Research Ethics Committee. The respective Human Ethics Committee Approval Code is 52019339910155. All participants gave in informed consent before participating (see [Appendix B](#)) and were extensively debriefed after the experiment.

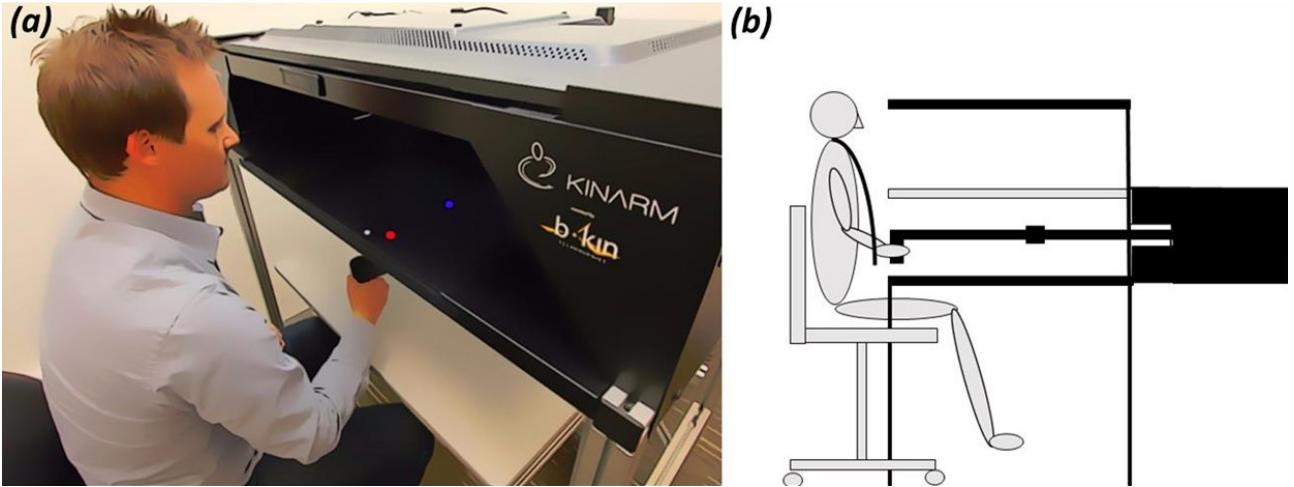


Figure 4: *Left:* A unimanual KINARM robot was used to impose perturbations on participants’ reaching movements. *Right:* Schematics of the KINARM apparatus. Copied from Hewitson et al., 2017.

## 5.2 Participants

As predefined in the [OSF preregistration<sup>11</sup>](#), the target sample size consisted of 48 participants, with 3 groups of 16 participants each. The sample size was chosen based on the existing literature (Brayanov et al., 2012; Fernandes et al., 2012; Schween & Hegele, 2017). 5 participants had to be excluded, two of them due to too many missing values, one because of a technical problem leading to incomplete data and another two because they were not naive to the purpose of the experiment. They were replaced by 5 new participants. Thus, 53 healthy undergraduate students from Macquarie University Sydney participated in the experiment, leaving us with 48 valid participants for the analysis (22 male, 24 female, 1 non-binary, aged between 18 and 59 years). Participants were recruited using the Macquarie University first year psychology [SONA Participant Pool<sup>1213</sup>](#) and were rewarded with 4 credits after completion. Following the convention in the literature (Canaveral et al., 2017; Fernandes et al., 2012; Kording & Wolpert, 2004), only right-hand dominant participants with normal or corrected to normal vision were eligible for the study.

## 5.3 Experimental Apparatus

Analogous to the experiments of Hewitson et al. (2018), a unimanual KINARM endpoint robot (BKIN Technologies, Kingston, Ontario, Canada) was utilized in the experiment for motion tracking and stimulus presentation (see [Figure 4](#)). The KINARM has a single graspable manipulandum that permits unrestricted two-dimensional arm movements in the horizontal plane. A projection-mirror system enables presentation of visual stimuli that appear in the movement

<sup>11</sup>Link: <https://osf.io/gndca>

<sup>12</sup>Link: <https://mq-psych.sona-systems.com/>

<sup>13</sup>See [Appendix A](#) for the study advertisement on the SONA platform.

plane. Participants received visual feedback about their hand position via a cursor (solid white circle, 2.5 mm in diameter) controlled in real-time by moving the manipulandum. Mirror placement and an opaque apron attached just below the participant’s chin ensured that visual FB from the real hand was not available for the duration of the experiment. Eye tracking data was collected by means of the integrated EyeLink 1000 Plus eye-tracker (SR Research, Ottawa, Ontario, Canada). The camera was fixated in the rearer left corner of the mirror plane in the KINARM robot.<sup>14</sup>

## 5.4 Pilot Study

In order to shed light on certain questions concerning the experimental design, 12 participants (7 female) were previously tested in a pilot study. Results revealed no difference of order (generalisation, re-learning, washout *vs.* washout, re-learning, generalisation). However, we found a different tendency in reaching behaviour in participants who were exposed to a clockwise (CW) and those who were exposed to a counterclockwise (CCW) rotation. We therefore decided to include rotation direction as a covariate in our main experimental design. Other questions that were addressed in the scope of the pilot study were whether 400 trials in the learning phase were enough for the participants’ learning curves to plateau and the total duration of the experiment. The design of the main experiment was adapted according to those findings. Importantly, we noted that pilot participants were able to fully compensate for the perturbation after few trials already. As this was likely to happen because of explicit aiming strategies, we further modified the main experiment insofar as measures were implemented to reduce as well as to control for explicit strategies (see [subsubsection 5.5.2](#) for more details).

## 5.5 Experimental Design

The experimental design was adapted from Hewitson et al. (2017). In a centre-out reaching task, participants were instructed to perform fast and accurate reaching movements with the dominant (right) arm using cursor FB, whenever it was available. Subjects performed reaches from a start target located at the center of the workspace (coordinates:  $x = 0$  cm,  $y = 20$  cm) to 12 different end targets arranged in a circle 10 cm away from the start target and spaced 30° apart. The start target was a solid red circle (5 mm diameter), and each reach target a solid dark blue circle (5 mm diameter). The appearance of the reach target served as the go cue. Participants were positioned in such a way that the start target was directly in front of their torso.

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<sup>14</sup>See Hewitson et al. (2017) for a detailed description of the general KINARM setup. Processing scripts for extracting the c3d files are accessible in the following GitHub repository: <https://github.com/HinrichsSa/uncertainty-goofiness-study>.

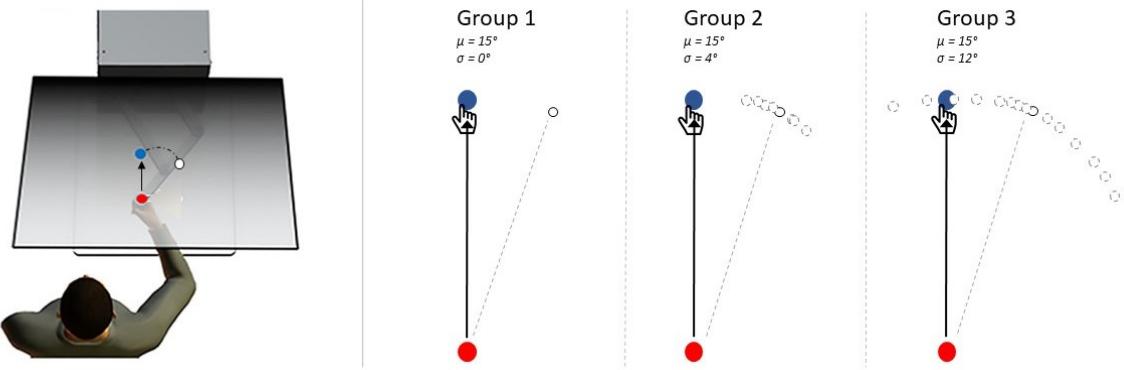


Figure 5: Illustration of the variance conditions. *Left:* Illustration of the participants view on the display during training. Hand vision is occluded and participants have to perform reaching movements from a start target (red) to an aiming target (blue). For all participants, FB on their hand position (*white cursor*) is shifted by a mean of  $15^\circ$  (*dashed line*) and only provided at the end of the reach. Adapted from Hewitson et al., 2017. *Right:* Variance of the applied perturbation was manipulated between the three groups. Group 1 was always exposed to a shift of  $\pm 15^\circ$  ( $0^\circ \sigma$ ), whereas perturbations were randomly distributed around  $\pm 15^\circ$  with a standard deviation ( $\sigma$ ) of  $4^\circ$  for group 2 and a  $\sigma$  of  $12^\circ$  for group 3. Note that half of the participants were exposed to a CW rotation and the other half to a CCW rotation.

### 5.5.1 Group Conditions

The study involved a between-subjects design with two factors. The main factor was rotation variance, *i.e.* the variance of the imposed rotation perturbation, with the three group levels  $0^\circ$ ,  $4^\circ$  and  $12^\circ$  standard deviation  $\sigma$ . The second factor, which we included as a covariate, was rotation direction with the two levels CW *vs.* CCW. For all participants, the mean perturbation was set to  $\mu = \pm 15^\circ$  (see Figure 5).<sup>15</sup>

Participants were randomly assigned to a rotation direction and a rotation variance group, respectively. In order to ensure the same number of participants per group, two vectors were created: one of 24 ones (CCW) and zeros (CW) respectively for rotation direction and another one with 16 zeros ( $0^\circ$ ), ones ( $4^\circ$ ) and twos ( $12^\circ$ ) for each of the rotation variance conditions. Subsequently, the resulting vectors were pseudo-randomised using the `sample` function in R. The vector of participant indices (representing the order of their assignment to the experiment) was then merged with those pseudo-randomised rotation direction and rotation variance vectors.

### 5.5.2 Reducing Explicit Strategies

As stated in Part I of the thesis, literature divides adaptation into two components: an explicit and an implicit component. While explicit adaptation makes use of specific aiming strategies to intentionally compensate for a perturbation, implicit adaptation refers to an unintentional and

<sup>15</sup>Mean and group variances are based on the studies of Canaveral et al. (2017), Fernandes et al. (2012). Variances were taken from Fernandes et al. (2012) because variance differences used by Canaveral et al. (2017) seemed too small to reveal clear group differences. In contrast, a mean of  $\pm 30^\circ$  seemed to enhance explicit aiming strategies in our pilot study. In line with Canaveral et al. (2017), we therefore applied a mean of  $15^\circ$ .

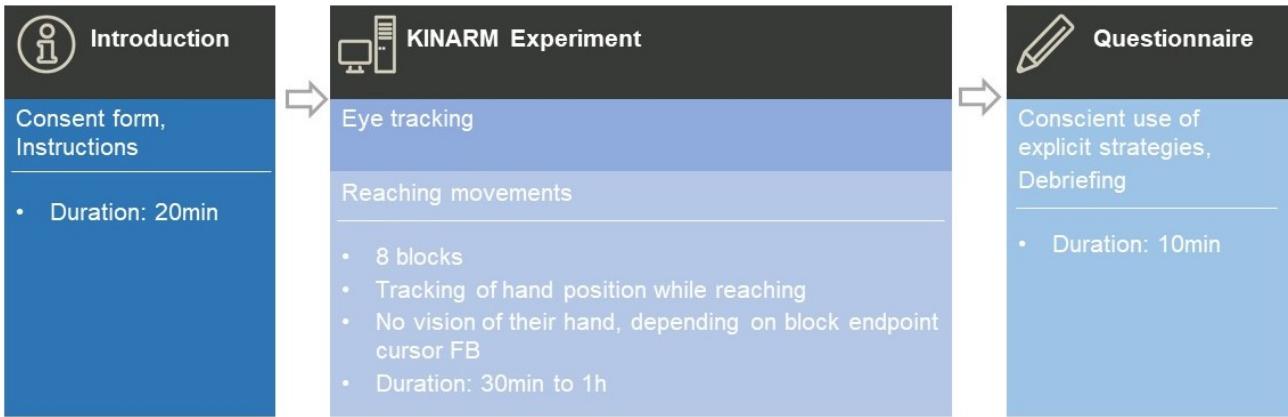


Figure 6: Overview of the general procedure of the study.

involuntary drift (Taylor et al., 2010). As the former is rather cognitively driven, the current project focused on the implicit error-based process of adaptation reflecting the updating of an internal model. Thus, several measures were implemented in order to reduce explicit strategies to a minimum. First, following (Fernandez-Ruiz et al., 2011; Haith et al., 2015; Leow et al., 2017), trial duration was limited to 600 ms. Once the hand position left the start target participants had only 600 ms to reach the radius of the end target. Participants were therefore instructed to slice through the targets as fast and accurately as possible. However, they were allowed to take their time to come back to the start target. The second measure is based on previous literature that suggests that a participant is more likely to use explicit aiming strategies with **endpoint feedback** only (rather than continuous feedback during the whole reach) and when the visuomotor perturbation is introduced abruptly rather than gradually (Taylor & Ivry, 2012). We therefore inserted a post-baseline block with a rotation distribution of  $\mu = 0^\circ$  and  $\sigma = 8^\circ$ . Basically, the idea was to accustom the participants to noisy feedback without implementing a mean perturbation before they start with the training block. The reason why we decided against the approach of a gradual shift from the smallest to the largest perturbation was that we did not want this measure to corrupt the learning rate. In addition, the qualitative questionnaire of explicit awareness by Benson et al. (2011) was implemented after completion of the experiment as a way to assess the usage of explicit aiming strategies. Research further suggested the use of verbal reports before each reaching trial (Taylor et al., 2014) as another way to measure the explicit component. In order to not only rely on verbal reports, we decided to additionally explore two implicit indicators for the use of explicit strategies that have been reported in the literature: reaction times (RT) (Haith et al., 2015) and gaze (de Brouwer et al., 2018; Rand & Rentsch, 2015).

### 5.5.3 General Procedure

Each participant was assigned to a time slot of 2 h. Although the total duration of the experiment rarely exceeded 90 min, the bigger time slot was required due to the temporal fluctuation

with the eye tracking calibration. [Figure 6](#) provides a schematic overview of the general procedure. Participants were first familiarised with the KINARM setting, the experimental procedure and the task before filling in the consent form. The KINARM experiment started after this first introduction of approximately 10 min and the subsequent eye tracking calibration. Depending on how well the calibration worked as well as on the respective participant's reaching speed, this part took between 30 min and 60 min. Afterwards, the participants completed the questionnaire on explicit strategies. Finally, the study ended with a comprehensive debriefing. The last part took about 20 min.

#### 5.5.4 Experimental Procedure

[Figure 7](#) illustrates the experimental procedure (top) as well as the applied rotation (bottom) for each of the 3 variance groups, respectively. The experimental protocol consisted of 8 blocks and a total number of 1272 trials. The first block was an exploratory pre-familiarisation phase of 120 trials (10 trials per target in pseudo-random order<sup>16</sup>) without any cursor FB. The purpose of this phase was to investigate the participants' initial reaching behaviour in an exploratory analysis in order to explore their predictions in a new environment when not provided with any FB. Subsequently, participants were exposed to a familiarisation phase, again of 120 reach trials (10 per target) with veridical visual FB provided throughout the reach (this type of FB is referred to as *online FB*). The baseline phase consisted of 240 reach trials across all 12 target directions (20 trials per target). For 50 % of the reaches (120 trials), veridical cursor FB was provided as soon as participants reached the threshold of the target distance (at 9 cm distance from the centre target). For the remaining 50 %, visual FB was withheld. During no-feedback (NFB) trials, the cursor disappeared as soon as the hand left the start target. No cursor FB was provided during the return movement. However, to help guide the participant's hand back to the start target, a dark blue ring centred over the start target appeared with a radius equal to the distance between the hand and start target (see this short <https://github.com/HinrichsSa/uncertainty-goofiness-study/blob/master/illustration-reachingtask.mp4><sup>17</sup> for an illustration). Once the participant's hand reached a distance of 1 cm from the start target, the ring was removed and cursor FB reinstated. FB and NFB trials appeared in a pseudo-randomly interleaved order. In order to reduce awareness for the applied perturbation in the training phase, we intersected a post-baseline phase of 120 trials (10 per target) with an applied perturbation rotation drawn from a normal distribution with a mean of 0° and a  $\sigma$  of 8°. The subsequent training phase consisted of 400 reaches towards a single target, positioned at 0° in the frontal plane. As the subject reached towards the target, cursor FB was rotated about the start target by on average of 15° with a  $\sigma$  of 0°, 4° or 12°, depending on the participant's respective group. Perturbations in the latter two groups were pseudo-randomised in such a way that the randomisation protocol was

<sup>16</sup>Randomisation was performed by means of the inbuilt Dexterit-E randomise function.

<sup>17</sup>Link: <https://github.com/HinrichsSa/uncertainty-goofiness-study/blob/master/illustration-reachingtask.mp4>

identical for all subjects within a group. Rotations were counterbalanced between participants, such that a participants' applied rotations were all either CW or CCW. For the cursor to move directly toward the target, hand motion would on average need to be directed 15° opposite to the direction of the cursor rotation. Visual FB was withheld for the duration of the outward reach on all trials and was only provided when the participant's hand came within 1 cm of the start target during the return movement (Brayanov et al., 2012). For all trials, visual endpoint FB was provided as soon as the invisible radius of 10 cm was crossed. The FB was shown for a duration of 100 ms. The generalisation phase consisted of 72 reaches to 1 of 12 target directions (11 untrained directions) presented in pseudo-random order without visual FB. After a re-learning phase of 100 trials (same procedure as in the adaptation phase) participants were exposed to a washout phase of 100 trials to the 0° target only where no FB was provided. Participants had a break of 1 min after each block.

## 5.6 Analysis

BKIN's Dexterit-E experimental control and data acquisition software (BKIN Technologies, Kingston, Ontario, Canada) was used to record and extract movement and gaze data from the unimanual KINARM robot. Hand position and gaze was recorded with 1000 Hz and logged-in Dexterit-E. Custom MATLAB scripts for preprocessing were adapted from Hewitson et al. (2017) and are accessible in [this GitHub repository<sup>18</sup>](https://github.com/HinrichsSa/uncertainty-goofiness-study) (this also applies to any other analysis script and output). Hand trajectories, velocity, reaction and movement time as well as gaze data were extracted from the c3d files. In order to measure the amount of learning, some type of error signal is needed. Note that even though endpoints and **initial movement vector** (IMV) were both computed, only **endpoint errors** (EE) have been defined and used as the dependent measure for the quantitative analysis (see the [OSF preregistration<sup>19</sup>](#)). The reason for additionally computing the IMV was our exploratory curiosity about which measure is more appropriate and reliable. Both measures are established in the literature (Lefumat et al., 2015; Sober & Sabes, 2005; van Sonderen & Denier van der Gon, 1991), though endpoint position seems to be more common which is why we chose this one. While IMV denotes the participant's first impulsive direction right at the beginning of a trial, endpoint is defined as the participants hand position at the end of a trial. In a mixed design, such as in Kording and Wolpert (2004), endpoints provide an appropriate measure for investigating Bayesian integration, whereas IMV captures the feedforward component only. In a pure feedforward design, however, the lack of sensory feedback during the reach forces the participant to rely on the participants prior only and, thus, the absence of online correction suggests no difference between EE and IMV error (IMVE). In the case of this study, no systematic difference between endpoint and IMV is therefore expected. Endpoints were computed using a spacial threshold of 9 cm distance from the start target, whereas IMV was based on a combined spacial- and velocity-based criterion.

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<sup>18</sup><https://github.com/HinrichsSa/uncertainty-goofiness-study>

<sup>19</sup>Link: <https://osf.io/gndca>

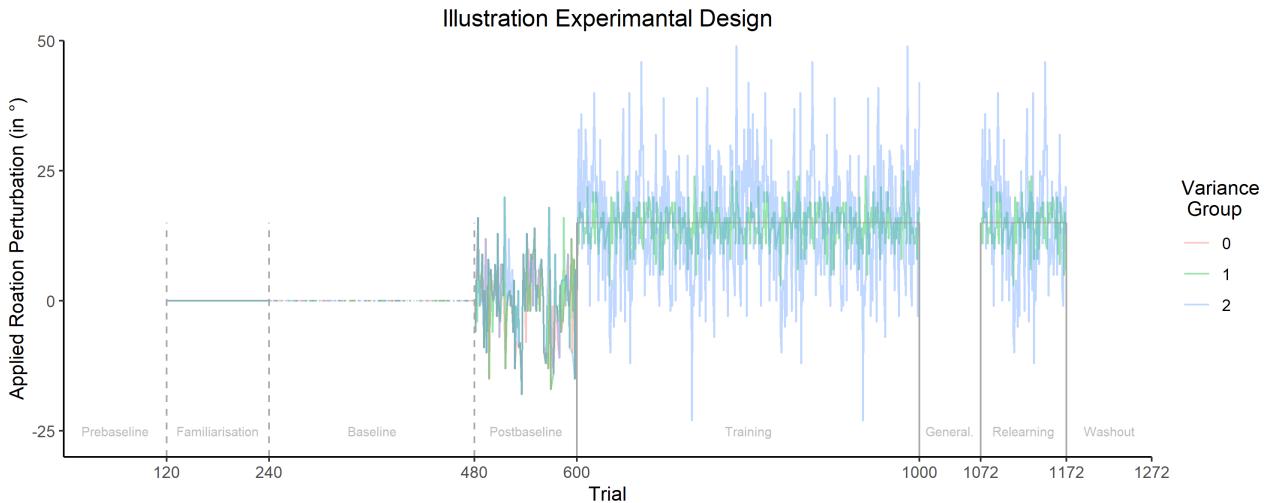
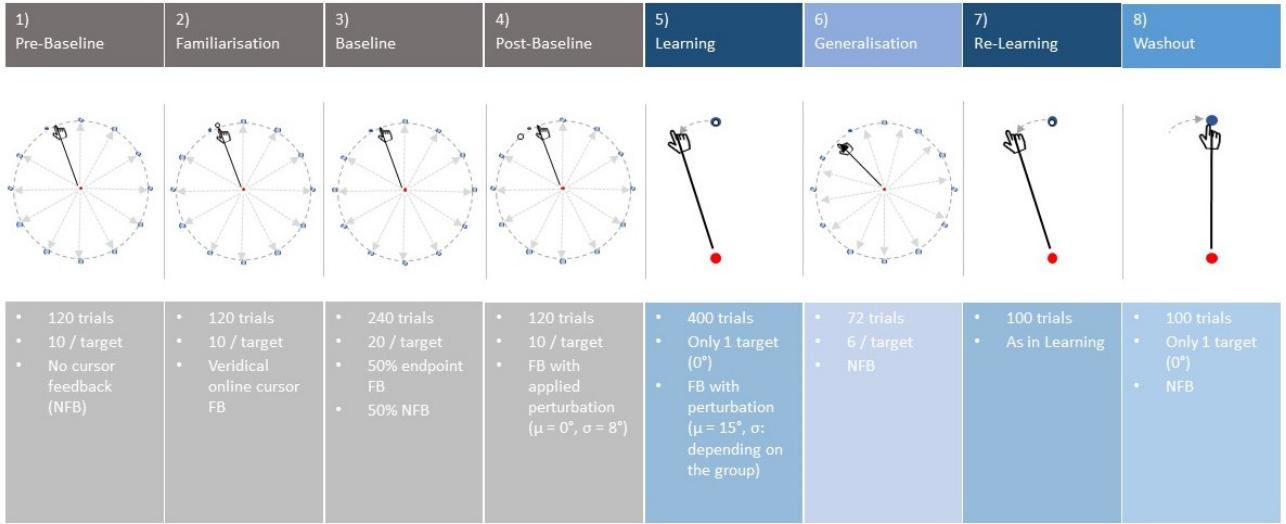


Figure 7: *Top:* Illustration of the experimental protocol. Cursor FB is represented by the white circle and the aiming target by the dark blue filled circle. *Bottom:* Applied rotation perturbation across all phases for the 3 different conditions, respectively. No FB was provided in pre-baseline, generalisation and washout, as well as in half of the baseline trials.

More specifically, IMV was quantified as the angle when the movement first exceeds 40 % of its peak velocity (Sober & Sabes, 2003, 2005) after a minimum reach length of 0.6 cm, that is when the start target region has been left. A reach was defined to start as soon as the participant left the start target region (defined by a radius of 0.6 cm centred around the start target) and ended once he passed the threshold of 9 cm distance from the start target. Reaches that took longer than 600 ms were replaced by missing values (*Nan*) and excluded from analysis. EE and IMVE were computed as the hand angle at the 9 cm end target radius, relative to the target location for EE and the IMV, relative to the training target direction for IMVE.

The preprocessing in MATLAB resulted in a csv file for the raw gaze, trajectory and velocity data as well as in a summary indices csv file for each subject and each block, respectively. Further preprocessing steps were done with the statistics programming language R (version 3.6.1). Once all 48 participants have been tested, subjects were analysed for missing values before starting the main analysis. A subject was excluded from analysis if the number of missing trials exceeded 1 per target in the generalisation phase or 10 % of the trials in at least one of the other phases (see [Appendix D](#) for an overview of the missing values of the 48 subjects who were included in the analysis).<sup>20</sup> After replacing the five subjects with corrupted EEs and IMVEs, errors were baseline corrected. Specifically, this was achieved by subtracting EE and IMVE values in post-baseline, training, generalisation, re-learning and washout from the respective mean of the NFB trials in the baseline block. Baseline correction was performed to control for participants idiosyncrasies. This is in line with previous literature (*e.g.* Fernandes et al., 2012; Hewitson et al., 2018; Schween and Hegele, 2017). In a subsequent step, we tested whether the data was systematically affected by a CW *vs.* a CCW rotation perturbation. Data was finally formatted appropriately for our main state space model analysis in python.

### 5.6.1 Two-State Space Model

As already stated in [Part I](#) of this thesis, state space models are highly useful in describing visuomotor adaptation as a mapping process between motor goals and movement execution and, thus, in predicting key parameters in adaptation such as learning rate, washout rate and the amount of generalisation. It was further elucidated that sensorimotor learning is understood as a mixture of implicit adaptation and explicit strategies. Previous research could show that simple state space models underestimate the learning rate early on after perturbation onset (J.-Y. Lee & Schweighofer, 2009; McDougle et al., 2015; M. A. Smith et al., 2006), indicating the presence of aiming strategies. For a more accurate description, we thus implemented two

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<sup>20</sup>In the [OSF preregistration](#), we further specified that we would simulate the model described in [subsubsection 5.6.1](#) with varying degrees of missing values in order to characterise the ability of our fitting routine to correctly recover simulation parameters as a function of missing values. On this basis, we planned on adjusting our 10 % threshold to be more conservative (*i.e.* smaller than 10 %) such that we only permit missing values in the domain where we are likely to still recover the correct parameter estimates. Unfortunately, we were too optimistic in our time planning and, as this additional step was not absolutely necessary for further analysis, we had to skip it.

states in the state space model: one state representing a fast system (explicit strategies) and the other one representing a slow system (implicit learning).

Such a state space model with two states is governed by the following equations:

$$\mathbf{x}_t = \mathbf{x}_{f,t} + \mathbf{x}_{s,t}, \quad (4)$$

$$\mathbf{x}_{f,t} = \beta_f \mathbf{x}_{f,t-1} - \alpha_f \delta_{t-1} \mathbf{G}_f, \quad (5)$$

$$\mathbf{x}_{s,t} = \beta_s \mathbf{x}_{s,t-1} - \alpha_s \delta_{t-1} \mathbf{G}_s, \quad (6)$$

$$\alpha_f > \alpha_s, \beta_f < \beta_s. \quad (7)$$

Here,  $\mathbf{x}_t$  is a  $12 \times 1$  dimensional vector, where each value denotes the state at the current trial  $t$  for the 12 targets, respectively. It is computed as a combination of the current state of the fast  $\mathbf{x}_{f,t}$  and the slow system  $\mathbf{x}_{s,t}$ . As already described in subsection 3.5,  $\beta$  and  $\alpha$  are scalar parameters, with the learning rate  $\alpha$  defining how much weight is given to the error and, thus, how fast the model updates based on the error signal and the retention rate  $\beta$  denoting how much is retained from the value of the state in the previous trial. Equation 7 defines the constraints on learning and retention rate for the fast and the slow system, respectively. It ensures that learning is faster and less stable in the fast system than in the slow system. The error term  $\delta_t$  refers to the difference between the value of the current state  $x_t$  for the training target and the applied rotation at trial  $r_t$ :

$$\delta_t = x_t - r_t. \quad (8)$$

Note that the reason for  $\mathbf{x}_{f,t}$  and  $\mathbf{x}_{s,t}$  both being a vector is the respective generalisation terms  $\mathbf{G}_f$  and  $\mathbf{G}_s$ . A simple state space model as described in subsection 3.5 assumes that information is learned independently for every target. Hence, according to such a model, learning a perturbation for target 1 would have no impact on the performance on another target 2. However, as we have seen in subsection 3.4, previous literature (*e.g.* Zhou et al., 2017) strongly supports the notion that, to some extent, learning is generalised from an active to other targets. We thus implemented a generalisation term for the fast and the slow system, respectively, where  $\mathbf{G}_f$  and  $\mathbf{G}_s$  are both  $12 \times 1$  dimensional vectors with each value  $g_{f,j}$  and  $g_{s,j}$  indicating how much learning is generalised to each target. This was modelled independently for the fast and the slow system:

$$\mathbf{G}_f = \begin{bmatrix} g_{f,1} \\ g_{f,2} \\ \vdots \\ g_{f,12} \end{bmatrix}, \quad g_{f,i} = f(\theta_i), \quad \mathbf{G}_s = \begin{bmatrix} g_{s,1} \\ g_{s,2} \\ \vdots \\ g_{s,12} \end{bmatrix}, \quad g_{s,i} = f(\theta_i) \quad (9)$$

where  $\theta_i$  is the angle of a given target  $i$  in degrees. It has been shown that the closer a target is located to the training target, the higher the respective amount of generalised learning

(Fernandes et al., 2012; Woolley et al., 2011). We therefore modelled the generalisation factors  $g_{f,j}$  and  $g_{s,j}$  as an exponential function of their position in degrees:

$$f(\theta) = e^{-\frac{(\theta - \mu_\theta)^2}{2\sigma_\theta^2}}. \quad (10)$$

As  $\mu_\theta$  represents the  $0^\circ$  target, the training target has a generalisation value of 1 while all other targets vary between 0 and 1, with the targets located closer to the training targets being assigned higher values. Note that the variance  $\sigma_\theta^2$  represents the only difference between fast ( $\sigma_{\theta,f}$ ) and slow ( $\sigma_{\theta,s}$ ) system, determining the width of the generalisation curve, *i.e.* how much learning is generalised to the other targets.

### 5.6.2 Model Fitting

This linear time-invariant two-state space model was fitted to the trial by trial EEs observed separately for each group. Such models provide excellent fits to the type of visuomotor adaptation experiment we conducted here and yield reliable estimates for learning rate, washout rate, and generalisation width. Each of these corresponded to a free parameter in the model. There were no additional free parameters.

To recap, this model assumes that an EE causes a change in direction of reach on the next trial that is proportional to the negative of the error magnitude. The constant of proportionality on this term captures the *learning rate*. Through generalisation, there is also learning to targets, even though they were not the objective of the current trial. Learning to these other targets is equal to learning to the goal target, but further scaled according the Gaussian distance from the goal target. The parameter that controls the width of this Gaussian is the estimate of **generalisation width**. Finally, the model assumes a certain amount of forgetting (*i.e.*, return to baseline levels of adaptation) on each trial. The free parameter that controls the proportion of learning that is forgotten on each trial is the estimate *washout rate*. All 3 parameters were estimated for, both, a fast and a slow system.

Model fitting to the group data was performed using the statistical bootstrapping technique with  $N = 1000$  repetitions. Mean as well as the respective 95 % confidence intervals (CI) of each parameter estimate were then computed by taking the 2.5 and 97.5 percentile values from the bootstrap estimated sampling distribution.<sup>21</sup> Group differences in the mean

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<sup>21</sup>Bootstrapping is a statistical method to estimate measures of accuracy of an estimator, in this case the CIs of learning rate, washout rate and generalisation width respectively for each group. This is achieved by  $N$  repetitions of random sampling with replacement from one empirical distribution. It is used to infer the distribution of an estimate when its theoretical distribution is unknown. The following example should make the basic idea somewhat more tangible: Let us assume that you would like to estimate the mean age of the world population and that, for this purpose, you would acquire data from a tiny representative part of say 10.000 people. This single sample only results in one mean and if we want to reason about the world population, we need some sense of the variability of this estimate. This can be achieved by randomly sampling from this 10.000 people sample where the sample size is typically identical to the original one. In the resulting sample, person 1 might be represented 5 times, whereas person 2 might not be represented at all. Repeating this procedure of computing the estimate in a new sample  $N$  times (typically 1.000 or even 10.000 of times) provides you with

parameter estimates were then tested for significance by means of bootstrapping as well. More specifically,  $p_0$  values were computed by finding the parameter differences from a bootstrapped sampled difference distribution ( $N = 1000$ ) that are greater than the observed mean parameter difference.<sup>22</sup>

$$p_0 = \frac{1 + \sum_{n=0}^N (|\mathbf{d}_{\text{boot}}| > |d_{\text{obs}}|)}{N + 1} \quad \text{with} \quad (11)$$

$$d_{\text{obs}} = \bar{x} - \bar{y}, \quad (12)$$

$$\mathbf{d}_{\text{boot}} = \mathbf{d} - \bar{\mathbf{d}} \quad \text{and} \quad (13)$$

$$\mathbf{d} = \mathbf{x}_{\text{boot}} - \mathbf{y}_{\text{boot}}. \quad (14)$$

Here,  $x_{\text{boot}}$  and  $y_{\text{boot}}$  are both samples of size  $N = 1000$  with replacement from the respective original bootstrap estimated sampling distribution. This procedure was repeated for each variance and rotation direction condition. Note that we first tested for significant differences in rotation direction to determine whether the data needs to be analysed separately for the CW and the CCW rotation condition.

### 5.6.3 Predictions

According to the argument made in subsection 4.1, we expected learning rates in the high variance groups to be smaller than the learning rates in the groups with more precise feedback. Figure 8 illustrates this prediction with exemplary learning rates of  $\alpha_{s,0} = 0.2$ ,  $\alpha_{s,1} = 0.05$  and  $\alpha_{s,2} = 0.01$  for the  $0^\circ$ ,  $4^\circ$  and the  $12^\circ\sigma$  group, respectively. We thus chose a directional one-tailed significance test for learning rates. In contrast, the fact that the Bayesian theoretical account does not make any direct prediction for retention and generalisation in a feed forward design, together with the lack of solid evidence from previous literature led us to analyse retention rate and generalisation width by means of a non-directional two-tailed significance test. The significance level  $\alpha$  was set to 0.05.

### 5.6.4 Exploratory Analyses

As mentioned earlier, we were further interested in a number of additional questions. Those questions were examined in an exploratory fashion. The statistical programming language R was used for those analyses. Most importantly, after our pilot findings suggested a tiny difference between CW and CCW rotation we wanted to further understand if there really is an effect of rotation direction on learning, generalisation and washout, and if so, where it originates from. The second broad topic we were additionally interested in was the distinction between implicit adaptation and explicit aiming strategies in our data, which might also come into question as an explanation for a possible effect in rotation direction. As mentioned in

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an idea on the range in which the true mean value is most likely to be found.

<sup>22</sup>see Efron and Tibshirani (1994) for more information on bootstrapping in hypothesis testing.

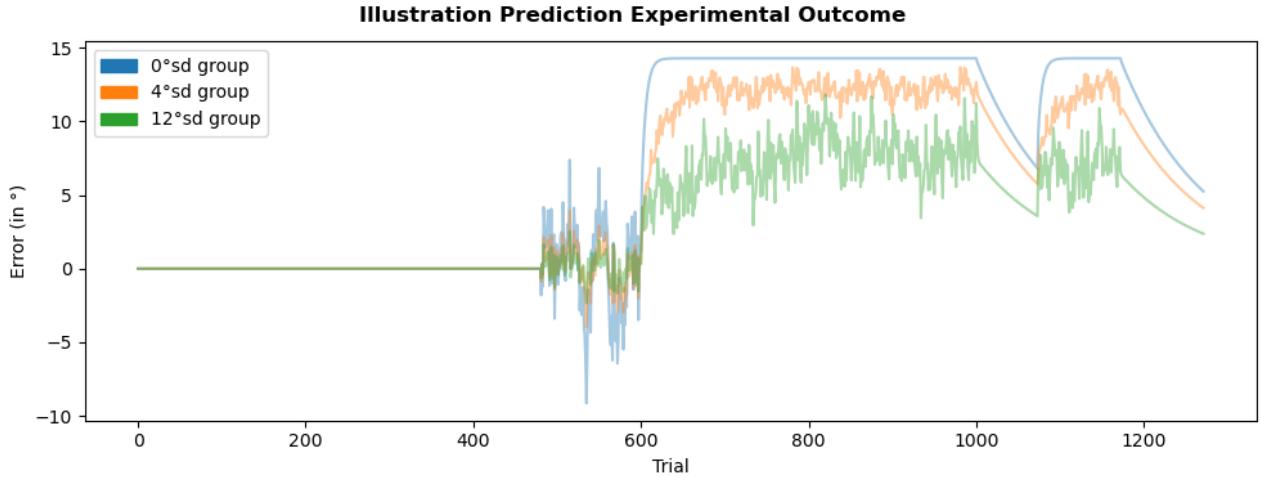


Figure 8: Illustration of group performances across all phases under the assumption that learning rates are smaller when the prediction’s variance is higher. Group performances were modelled with the two-state space model described in [subsubsection 5.6.1](#), where the applied rotation matches the respective group perturbations. Learning rate is set to  $\alpha_{s0} = 0.2$ ,  $\alpha_{s1} = 0.05$  and  $\alpha_{s2} = 0.01$  for the  $0^\circ$ ,  $4^\circ$  and the  $12^\circ\sigma$  group, respectively. All the other parameters are identical across the groups.

[subsubsection 5.5.2](#), several measures have been taken, first, to reduce and, second, to quantify the remain of aiming strategies. More specifically, we were interested whether the different measures we implemented would be predictive in explaining different learning rates. In a first step, the questionnaire for explicit awareness has qualitatively been evaluated according to Benson et al. (2011) (see [Appendix F](#) for the flow-chart of the questionnaire). The binary results of explicit *vs.* implicit have subsequently been encoded in 1 (*explicit*) and 0 (*implicit*) respectively for each subject, and used for further exploratory analyses. If participants used explicit aiming strategies more than others we should be able to observe a steeper learning curve for them as opposed to the other participants. RTs were examined as another measure to infer the use of explicit strategies. RT, *i.e.* the preparation time a participant needs at the beginning of a trial, was defined as the point in time when the participant has reached 5% of her peak velocity. According to Haith et al. (2015), shorter preparation times prohibit the use of cognitive strategies. Longer RTs might therefore be an indicator for the use of explicit strategies. Gaze data was analysed as another indirect measure of explicit strategies. Following de Brouwer et al. (2018) whose findings support the use of gaze as an indicator for aiming, we descriptively related gaze to the respective trajectories. Specifically, this was achieved by graphically overlaying the mean learning trajectories of explicitly aware participants with the respective gaze data in a time series and by comparing those with the respective figures of implicitly learning participants. Basically, gaze has been shown to be strongly related to motor planning in the sense that the location we are aiming for is previously focused on with our eyes (Johansson et al., 2001; Land & Furneaux, 1997). Accordingly, we expected the following outcome: Implicit participants will look at the aiming target while being off with their reach to

compensate for the applied perturbation, whereas aiming participants will focus the location they explicitly aim for (*i.e.* the shifted location) with their gaze before reaching exactly there.

Another exploratory question we investigated with our experimental design was the question of what participants' reaches would look like in a novel environment when no visual FB is provided. Therefore, no FB and thus no prediction was induced in the very first block, the pre-baseline phase. Inter- as well as intra-individual commonalities in participants' pre-baseline trajectories were examined in order to explore the participants' 'natural predictions'.

Finally, we were interested in the difference between EE and IMVE as two possible dependent measures in a feedforward VMR paradigm. Due to the lack of **online feedback**, we expected those two measures not to differ systematically from each other. Nevertheless, it would be interesting to compare the two measures in terms of suitability for future feedforward paradigms.

In addition to the previously mentioned exploratory analyses that were planned in advance, we spontaneously decided to conduct an exploratory post-hoc **Bayes factor** (BF) analysis<sup>23</sup> in order to assess the conclusiveness of our main analysis results. This exploratory BF analysis was performed using the open source software Jasp (Version 0.11.1.0). Taken together, the following questions were examined in the scope of our exploratory analyses:

- Does the direction of the applied rotation have an impact on adaptation?
- Do we find inter-individual differences in the use of explicit strategies?
- How do participants behave in a new environment when no prediction is induced?
- Which of the two measures, IMVE or EE, is more suitable in a feedforward VMR adaptation paradigm?
- Are our main analysis results conclusive?

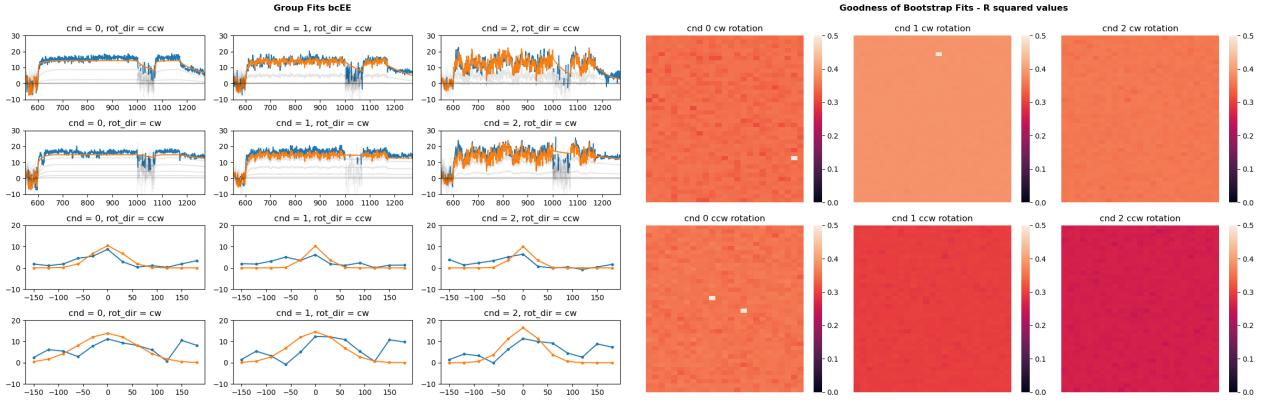
## 6 Results

### 6.1 Main Analysis

Group mean parameter values for learning rate  $\alpha_s$  and  $\alpha_f$ , retention rate  $\beta_s$  and  $\beta_f$  and generalisation width  $\sigma_{\theta,s}$  and  $\sigma_{\theta,f}$  were estimated using bootstrapping techniques. The resulting group mean parameter values are listed in [Appendix E](#) and fits are depicted in [Figure 9](#) (left panel). To measure the goodness of the resulting fits,  $R^2$  was computed for every bootstrapped model. [Figure 9](#) (right panel) depicts the  $R^2$  values from every bootstrapped model, shown separately

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<sup>23</sup>Bayes factor analyses are an alternative to classical hypothesis testing. While the  $p$ -value in a classical hypothesis test quantifies the extent to which the data speaks for the  $H_0$ , the Bayes factor quantifies the relative support for one model over another. It thus provides a measure for the weight of the evidence in favour of a given hypothesis.



**Figure 9: Left penal:** Mean fits of the bootstrap distribution (orange) plotted against the observed means (blue) for each variance and rotation direction group, respectively. The  $y$ -axis displays baseline corrected endpoint errors (bcEE) and the  $x$ -axis the trial number. Grey lines in the upper plots represent the hypothetical amount of generalisation expected for each target. **Right penal:** Heatmap of determination coefficients  $R^2$  for each bootstrapped model, grouped by rotation direction and variance condition. Homogeneous colours within a group indicate that  $R^2$  values are close to each other. The 4 values that are coded in white indicate that the estimated parameters of the respective models did not fulfil at least one of the following conditions:  $\alpha_s \geq \alpha_f$  or  $\beta_s \leq \beta_f$ .

for the six different groups (CW  $0^\circ\sigma$ , CW  $4^\circ\sigma$ , CW  $12^\circ\sigma$ , CCW  $0^\circ\sigma$ , CCW  $4^\circ\sigma$ , CCW  $12^\circ\sigma$ ). The fact that the colours within each group are very similar illustrates that the bootstrapping resulted in a small within-group variability of  $R^2$ . Thus, fits computed on the basis of different bootstrap samples resulted roughly in an equally good group fit. Mean  $R^2$  values across all bootstrap samples for each group ranged from 0.26 to 0.39 (all  $R^2$  group means and CIs are listed in [Appendix E](#)).

Before testing for parameter differences in the variance conditions, we tested whether there was a significant difference between the participants with CW and the participants with CCW rotations for every variance group, respectively. The bootstrapping statistical analysis with a significance-level of 0.05 revealed no significant differences for all fast system parameters  $\alpha_f$  [ $p_0 > 0.65$ ],  $\beta_f$  [ $p_0 > 0.38$ ] and  $\sigma_{\theta,f}$  [ $p_0 > 0.50$ ] between the CW and the CCW rotation subjects. Neither was the rotation direction difference in  $\alpha_s$  in both the  $0^\circ\sigma$  and the  $4^\circ\sigma$  group significant [ $p_0 > 0.62$ ]. However, differences between CW and CCW participants were significant for  $\alpha_s$  in the  $12^\circ\sigma$  [ $p_0 = 0.02$ ] as well as for all  $\beta_s$  [ $p_0 < 0.03$ ] and all  $\sigma_{\theta,s}$  [ $p_0 < 0.04$ ] conditions (see [Table 2](#) for an overview of all  $p$ -values). Thus, further analysis was conducted separately for CW and CCW participants.

Results are depicted in [Figure 10](#). While the graph makes it difficult to identify systematic patterns for the fast system, the slow system shows a somewhat less noisy and more systematic picture with a small trend of higher learning rates and generalisation widths for participants with smaller variances. However, errorbars are still huge which makes a clear interpretation difficult. In contrast, bootstrap retention rate estimates have small error bars while being highly

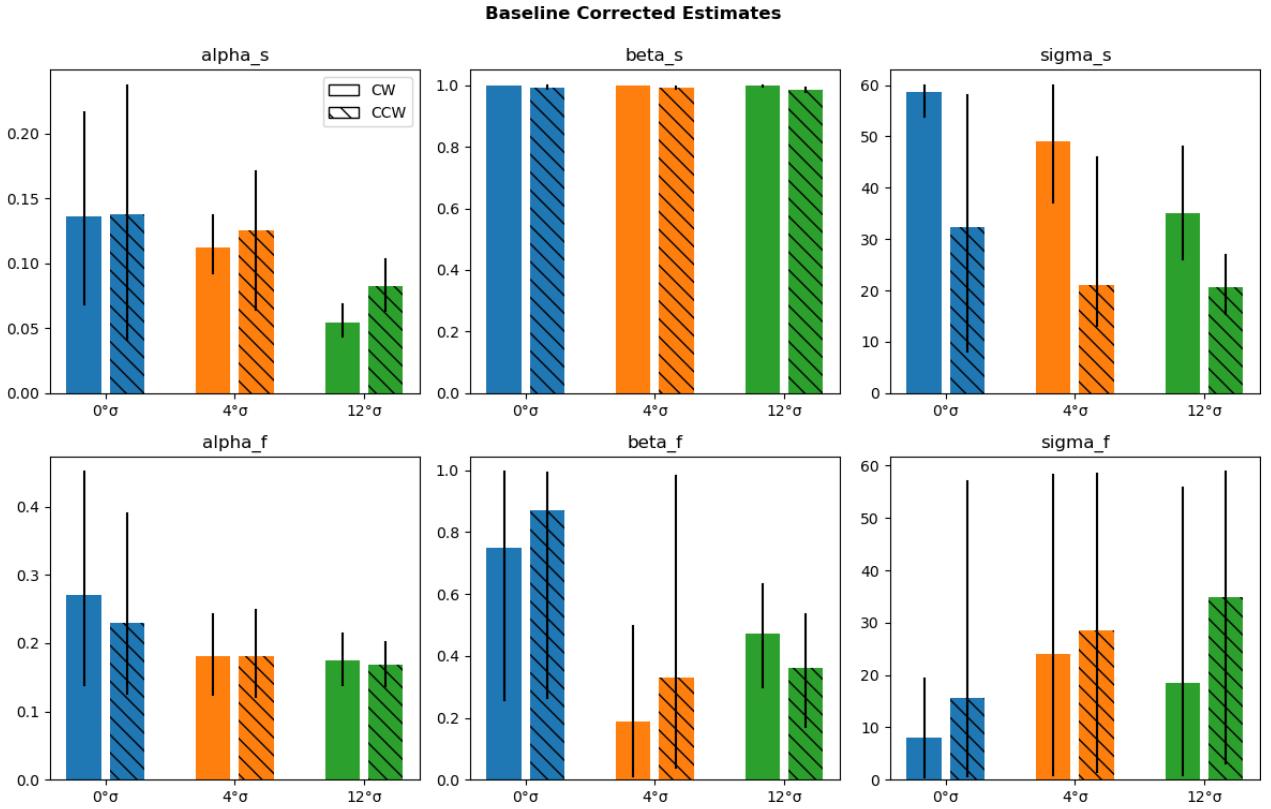


Figure 10: Results main analysis: Bootstrapped mean parameter estimates were computed based on the baseline corrected endpoint errors (bcEE) and are depicted for each rotation direction and variance group, respectively. Errorbars represent the 95 % confidence intervals.

Comparison	$\alpha_s$	$\alpha_f$	$\beta_s$	$\beta_f$	$\sigma_{\theta,s}$	$\sigma_{\theta,f}$
CW vs. CCW						
$0^\circ\sigma$	0.98	0.66	0.03*	0.68	0.04*	0.50
$4^\circ\sigma$	0.58	1.00	0.00*	0.50	0.02*	0.85
$12^\circ\sigma$	0.02*	0.77	0.00*	0.34	0.03*	0.50
CW						
$0^\circ$ vs. $4^\circ\sigma$	0.55	0.27	0.04	0.03	0.24	0.50
$0^\circ$ vs. $12^\circ\sigma$	0.02*	0.19	0.89	0.26	0.01*	0.48
$4^\circ$ vs. $12^\circ\sigma$	0.01*	0.89	0.26	0.06	0.10	0.80
CCW						
$0^\circ$ vs. $4^\circ\sigma$	0.83	0.49	0.72	0.07	0.38	0.60
$0^\circ$ vs. $12^\circ\sigma$	0.28	0.33	0.05	0.05	0.40	0.43
$4^\circ$ vs. $12^\circ\sigma$	0.11	0.74	0.10	0.89	0.94	0.81

Table 2:  $p_0$ -values of the boostrapping significance tests. Asterisks indicate that a difference is significant.

similar to each other. Bootstrapping statistical analysis with the significance level set to 0.05 for the  $\alpha$  parameter values (one-sided tests) and to 0.025 for the  $\beta$  and  $\sigma_\theta$  parameter values

(two-sided tests) revealed significant differences for  $\alpha_s$  between the  $0^\circ\sigma$  and the  $12^\circ\sigma$  as well as between the  $4^\circ\sigma$  [ $p_0 < 0.01$ ] and the  $12^\circ\sigma$  [ $p_0 < 0.03$ ] group in the case of CW rotation. It further showed a significant difference for the  $\sigma_{\theta,s}$  comparison between the  $0^\circ\sigma$  and the  $12^\circ\sigma$  group, again for participants who were exposed to a CW rotation [ $p_0 < 0.01$ ]. No other variance group differences were significant [ $p_0 > 0.05$ ].

Taken together, results indicate that, for participants exposed to a CW perturbation, there is indeed a slow system difference in learning rate for the two  $12^\circ\sigma$  group comparisons as well as a difference in generalisation width in the comparison between the  $0^\circ\sigma$  and the  $12^\circ\sigma$  group. However, all the other parameters did not show any significant difference and the small group sample sizes raise the question as to whether those findings are robust. Do those predominantly not significant results enable us to firmly reject the alternative hypothesis for all non-significant cases? This question is strongly tied to the unexpected finding of rotation direction. Analysing the data separately for the CW and the CCW applied rotation group halves the original group size of 16 participants. It is quite conceivable that the resulting group size after the split would be too small to come to a clear conclusion. The mere fact that we found this effect of rotation direction is interesting, though. Previous studies in the field of Bayesian integration in visuomotor adaptation never reported any difference in the performance of CW and CCW rotations (Fernandes et al., 2012; Turnham et al., 2011). To our knowledge, even if both rotation directions were implemented in the experimental design, data was always collapsed over rotation direction of the applied perturbation. This originally led us to believe that there is no difference between the reaching behaviour resulting from a CCW and the reaching behaviour resulting from a CW rotation perturbation in right-hand dominant participants. Why else should the data have been collapsed? As, to our knowledge, previous literature in the field did not provide further information on the influence of rotation direction in visuomotor rotation paradigms we investigated this question in further exploratory analyses.

## 6.2 Overview Performance

We started the exploratory analysis by getting a feeling for the participants' overall performance. [Figure 11](#) (top) depicts the reaching behaviour over trial in the phases *training*, *generalisation*, *re-learning*, and *washout*, separately for each group. The baseline corrected divergence from the  $0^\circ$  learning target (bcEE) is plotted on the y-axis, where a bcEE of  $15^\circ$  represents full adaptation to the applied perturbation. Note that the originally negatively coded subjects who were exposed to a CW rotation perturbation were positively recoded for the purpose of better comparability. Leaving aside the fact that the figure suggests larger perturbation variances to lead to higher variances in behaviour, it is difficult to identify an effect of variance condition on the learning rate. However, comparing the upper row of the CCW subjects to the second row of CW subjects, it seems as though CCW subjects plateaued normally at  $15^\circ$  in all three perturbation variance conditions, both, in learning and re-learning, whereas the plateau is even

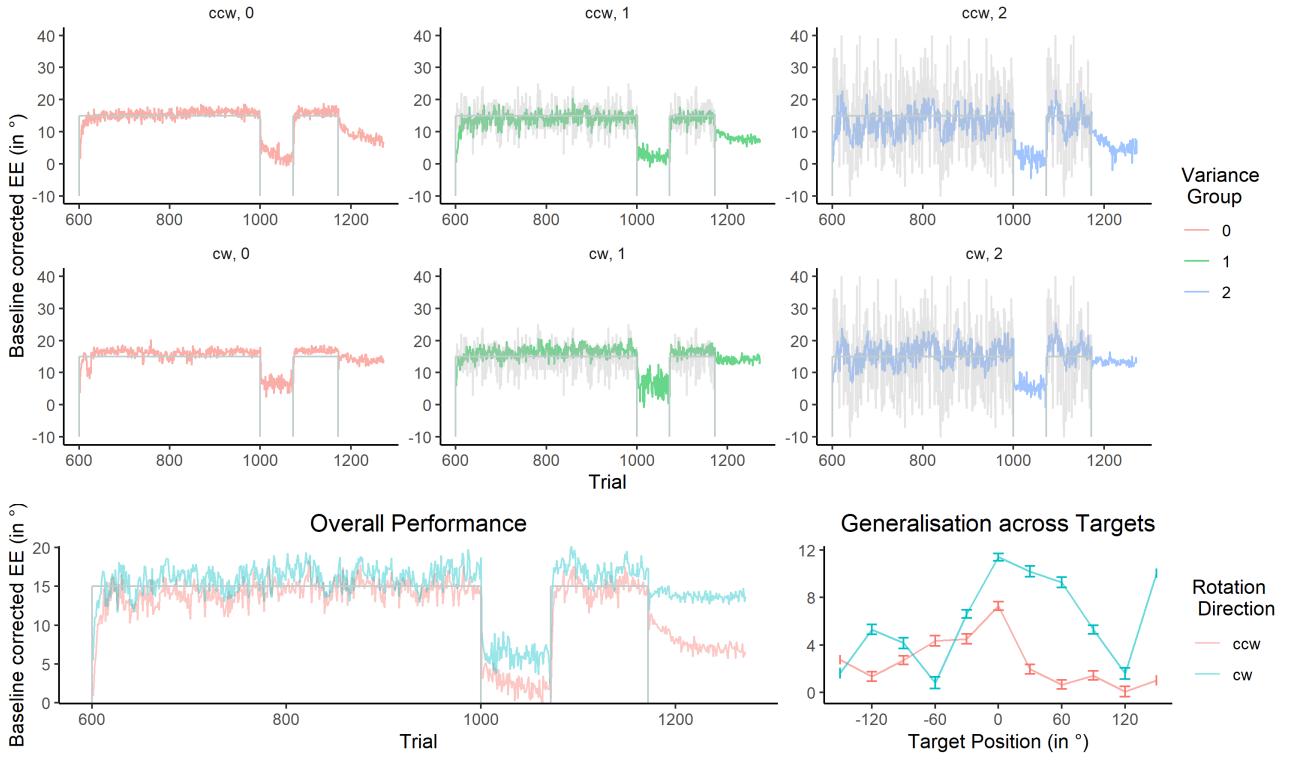


Figure 11: *Top:* Baseline corrected endpoint errors (bcEE) during training, generalisation, re-learning and washout respectively for each variance group. Group 0 refers to the  $0^\circ\sigma$ , group 1 to the  $4^\circ\sigma$  and group 2 to the  $12^\circ\sigma$  condition. Performance is plotted against the respectively imposed rotation (*light grey*). Vertical grey lines indicate the phases, presented in the same order as mentioned above. *Bottom:* bcEE during training, generalisation, re-learning and washout respectively for each rotation direction group.

slightly higher for the CW participants. Another striking observation is that, even though CCW participants show the classical washout pattern at the end of the experiment (*i.e.* the pattern of slowly falling back to the normal pre-adaptation reaching behaviour), CW participants do not. After an initial small drop they rather seem to stay at a level of about  $10^\circ$ . These observations become even more obvious when performance is plotted collapsed over variance condition and separately for rotation direction (see Figure 11 (bottom)).

A separate inspection of the CCW and the CW generalisation curves, depicted in Figure 12 yields another interesting insight. Here, the *x*-axis represents the 12 different generalisation targets and the *y*-axis the extent to which the adapted perturbation from the learning phase is generalised to the other targets, both, in absolute degree values and in percent from the total  $15^\circ$  adaptation. Even though the curves do not show a systematic pattern in variance group differences, it seems as if they are slightly left-skewed for participants exposed to a CCW perturbation and right-skewed for CW participants.

Taken together, those plots visually support the notion that exposing participants either to a CW or to a CCW rotation perturbation might have a systematic influence on learning, generalisation and washout. This further raises the question of what causes this difference.

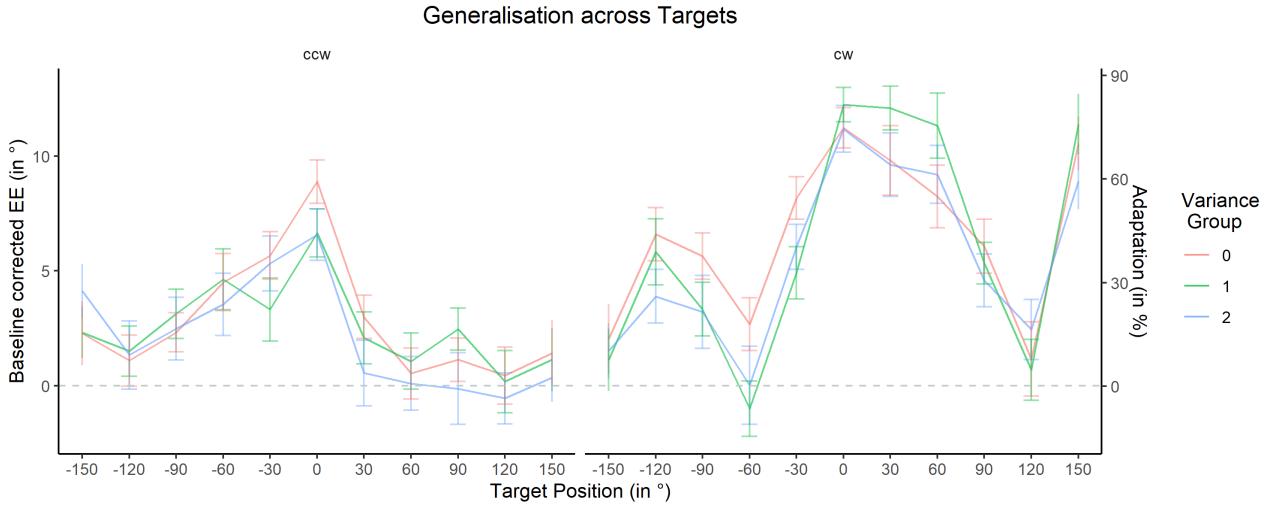


Figure 12: Generalisation across targets, separately for CW and CCW participants. Results are depicted in degree (*left y-axis*) and in % (*right y-axis*), where 100 % corresponds to the perturbation mean of 15°. The *x*-axis indicates the positions of the respective generalisation targets in degrees. Negative values represent targets on the left semicircle, positive values targets on the right semicircle and the 0° target represents the training target right in front of the participants torso. Group 0 refers to the 0 ° $\sigma$ , group 1 to the 4 ° $\sigma$  and group 2 to the 12 ° $\sigma$  condition.

One conceivable mediating factor that might explain some of the differences between CW and CCW participants might be that one of those two groups used more explicit strategies.

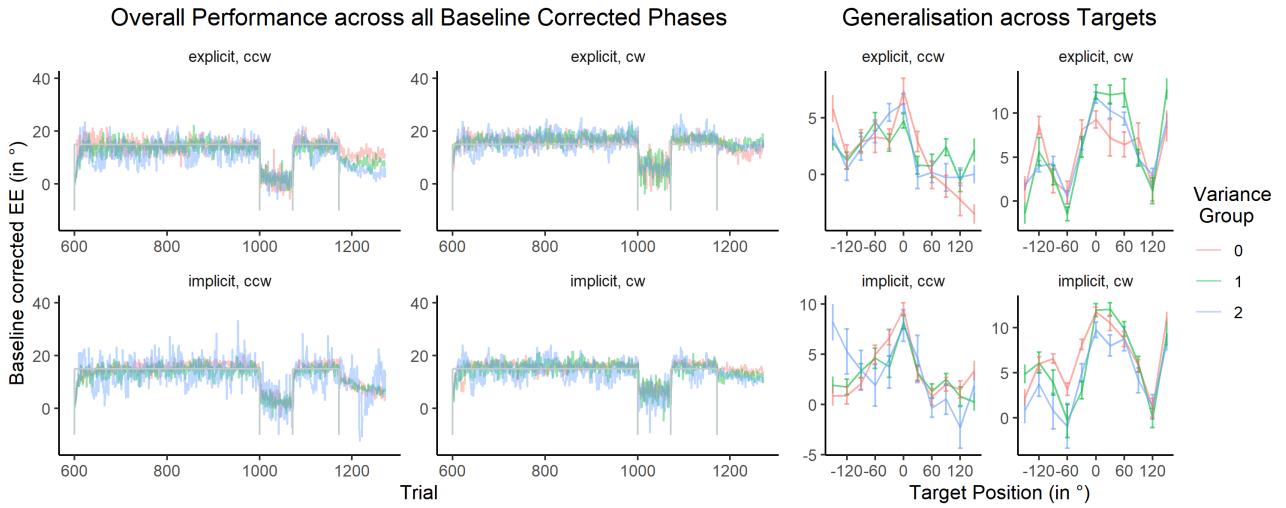
### 6.3 Explicit Strategies

As stated in [subsubsection 5.5.2](#), we implemented the qualitative questionnaire of explicit awareness by Benson et al. (2011) as an indicator for a participant's conscious use of explicit strategies. Based on the outcome of this questionnaire, participants were categorised as those who were aware of the perturbation and, thus, implemented explicit strategies and those who learned implicitly. An explicitness indicator column was added to the participants' data and used to relate differences in the use of explicit strategies to differences in rotation direction. [Figure 13](#) illustrates the the learning and washout as well as the generalisation curves, separately for explicit *vs.* implicit learning and CW *vs.* CCW rotation. Except for a different washout pattern between the rotation variance groups for explicit CCW participants, no other systematic pattern is apparent from the figure. The lack of any explanatory power of this measure might be due to various methodological reasons. First, the questionnaire relies on self-reporting, and suggestive questions as well as the well reported tendency to answer conform to the investigator's expectation (Nichols & Maner, 2008; Orne, 1962) may have biased the results, especially as the answers were given orally. In addition, awareness does not necessarily imply the use of explicit strategies or vice versa. For instance, many participants reported to have noticed that the training phase was more difficult but were not able to tell why. They also reported,

however, that they had the feeling to reach too far to the left (for participants exposed to the CW rotation) or to the right (CCW participants). Conversely, others reported no specific compensation strategy while being aware of the fact that the cursor was not providing veridical feedback of their hand position (see [Appendix F](#) for the procedure as well as the qualitative evaluation of the awareness questionnaire). Furthermore, it is important to notice that this subdivision in explicitly and implicitly learning subject was not manipulated in advance and thus not a controlled variable. As a result, the number of participants in each group were not counterbalanced, thereby maybe biasing the explanatory power. This is especially the case as each group consisted only of an average of 4 participants, respectively.

In order to further examine whether the lack of any noticeable influence of the use of explicit strategies is due to methodological reasons of such a post-hoc questionnaire, we additionally analysed the reaction times (RT). As stated in [subsubsection 5.6.4](#), previous literature identified RT as a useful indicator for the use of explicit strategies. Briefly, Haith et al. (2015) found that one component of learning needs longer preparation times than the other. The basic rational is that shorter preparation times prohibit the use of cognitive strategies, thereby proving useful to disentangle the implicit from the explicit component of learning. [Figure 14](#) depicts the RTs over trial for CW and CCW participants, respectively. Similar to the explicit measure, no effect is visible in RTs as a more implicit indicator for explicit strategies either. Accordingly, a linear regression of the residuals of RT (to eliminate a possible effect of variance condition) on rotation direction revealed no significant difference between the CW and the CCW group in training [ $p_0 = 0.09$ ], generalisation [ $p_0 = 0.46$ ] and washout [ $p_0 = 0.17$ ].

Another indicator for the use of explicit strategies that has recently been suggested in the



[Figure 13](#): Differences in awareness: Plots show the overall performance during training, generalisation, re-learning and washout (left-hand plots), as well as the amount of generalisation across targets (right-hand plots), separately for explicitly and implicitly learning participants. The distinction between implicit and explicit participants was assessed post-hoc by means of the qualitative questionnaire of explicit awareness from Benson et al. (2011). Group 0 refers to the  $0^\circ\sigma$ , group 1 to the  $4^\circ\sigma$  and group 2 to the  $12^\circ\sigma$  condition.

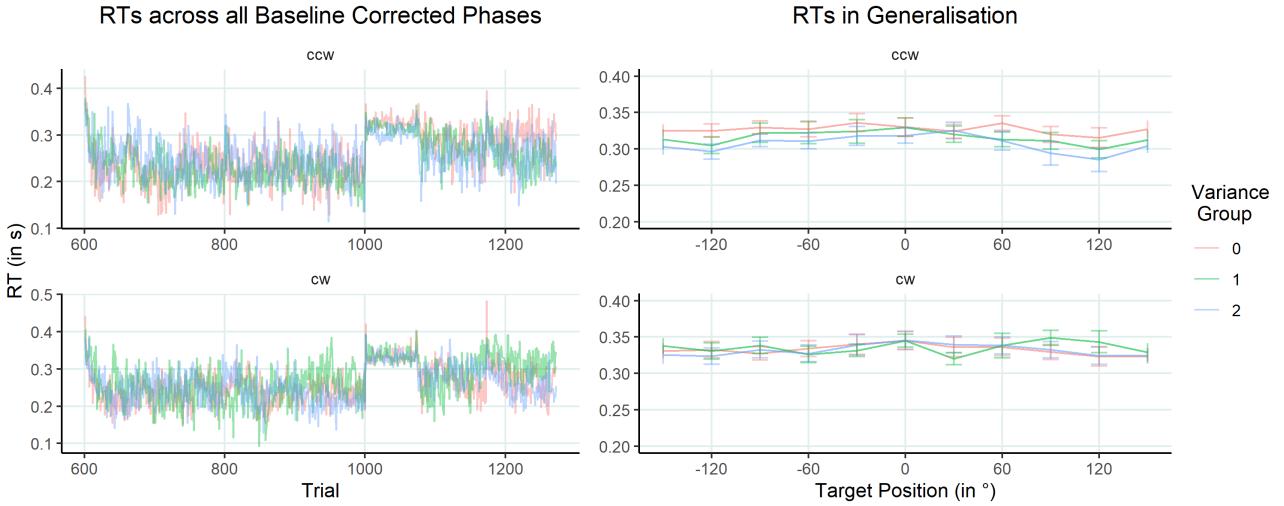


Figure 14: Comparison of reaction times (RT) in training, generalisation, re-learning and washout (left-hand plots) and across generalisation targets (right-hand plots), separately for CW and CCW participants. Group 0 refers to the  $0^\circ\sigma$ , group 1 to the  $4^\circ\sigma$  and group 2 to the  $12^\circ\sigma$  condition.

literature is gaze. As mentioned in [subsubsection 5.6.4](#) it has widely been appreciated that gaze precedes planned actions. For instance, if someone is planning to reach for a cup on a table in front of her, she will turn her gaze towards it before initiating the required arm movement. The same should apply to the use of cognitively driven explicit strategies. More specifically, someone being aware of an applied perturbation and using explicit strategies to compensate for it will aim a bit off, say to the right of the target. An implicitly learning person in contrast would not plan to reach anywhere else than to the respective target. Thus, while the subjects would be expected to look at the target itself before conducting the movement in the latter case, we expected the explicitly learning subjects to fixate the aiming location before they initiate the reach. In [Figure 15](#) we contrasted CW and CCW subjects in their reaching and gaze behaviour. Proceeding from the two assumptions that, first, the use of explicit strategies is reflected in a different gaze pattern and, second, the effect in rotation direction is explained by a different use of explicit strategies in those two groups, the gaze patterns in the two rotation direction conditions should differ from each other. However, participants always seem to fixate the target, regardless of the applied rotation direction. While the trajectory data emphasises the difference between CW and CCW participants, gaze data seems to be identical. To rule out the possibility that the effect might only be noticeable within a certain time frame we further plotted gaze and trajectories for the first 50, 200, 400, and 600 ms, not only separately for rotation direction but also for explicitly *vs.* implicitly learning subjects (according to our categorisation from the awareness questionnaire). While [Figure 15](#) confirms the assumption from previous literature that gaze precedes movement it does not show any difference in gaze. Moreover, this seems to apply not only to later but also to earlier points in time. We were thus not able to replicate the finding of de Brouwer et al. (2018), according to which gaze could be

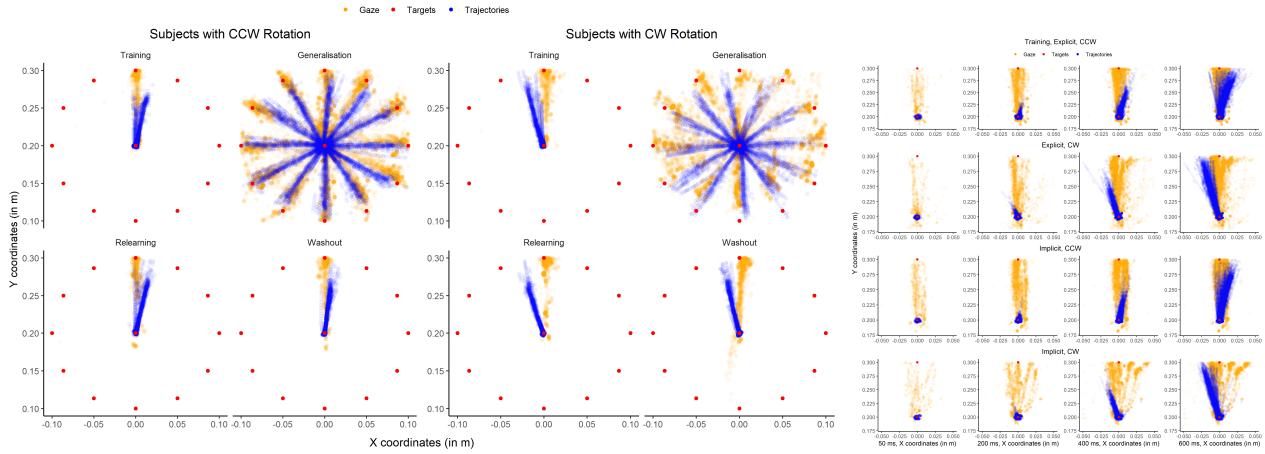


Figure 15: *Left panels:* Reaching trajectories (*blue points*) against gaze (*yellow points*) for training, generalisation, re-learning and washout, plotted separately for CW and CCW participants. Red points represent the different target locations. Please note, that although all targets are depicted in all phases, subjects did only see the  $0^\circ$  target during training, re-learning and washout. *Right panel:* Reaching trajectories (*blue points*) against gaze (*yellow points*) for training, plotted over time and separately for CW and CCW and explicitly and implicitly learning (according to the questionnaire of Benson et al. (2011)) participants.

used to identify the use of explicit strategies.

It can be summarised that three different indicators for the use of explicit strategies have been inspected and that all three provided no evidence for explicit strategies as a mediator for the unexpected effect of rotation direction. As already stated earlier, this might be due to various methodological reasons<sup>24</sup>. It nevertheless seems significant that the pattern of no systematic difference in explicitness runs across all three indicators. Many measures were taken to reduce the use of explicit strategies (see [subsubsection 5.5.2](#)). The lack of any difference might just be an indicator that those measures were indeed successful, or at least equally successful for CW and CCW participants. In this case we would reject the idea of explicit strategies being responsible for the difference between CW and CCW rotation direction participants and assume that its cause lies somewhere else.

Diedrichsen et al. (2010), for instance, reported that repeated movements bias interaction, an effect termed as **use-dependent behaviour**. Adapting our two-state space model to account for such a use-dependent term, indeed seems to reveal a generalisation pattern that is closer to the observed skewed curve (see the skewed generalisation curve for the CCW  $12^\circ\sigma$  participants in [Figure 16](#)).<sup>25</sup> This makes use-dependency a reasonable explanation for the skew. However, it does not explain the difference in peak learning.

<sup>24</sup>As this was the first time that an eye tracking study was performed in our KINARM lab, it is conceivable that gaze data was partly biased by unreliable eye tracking calibration. Calibration ratings of each participant can be found in ??.

<sup>25</sup>It is important to note that the purpose of this model adaptation was to get a first impression on the plausibility of use-dependency as a cause for the skewed pattern in the generalisation curve. A better thought-out model would be necessary for further research.

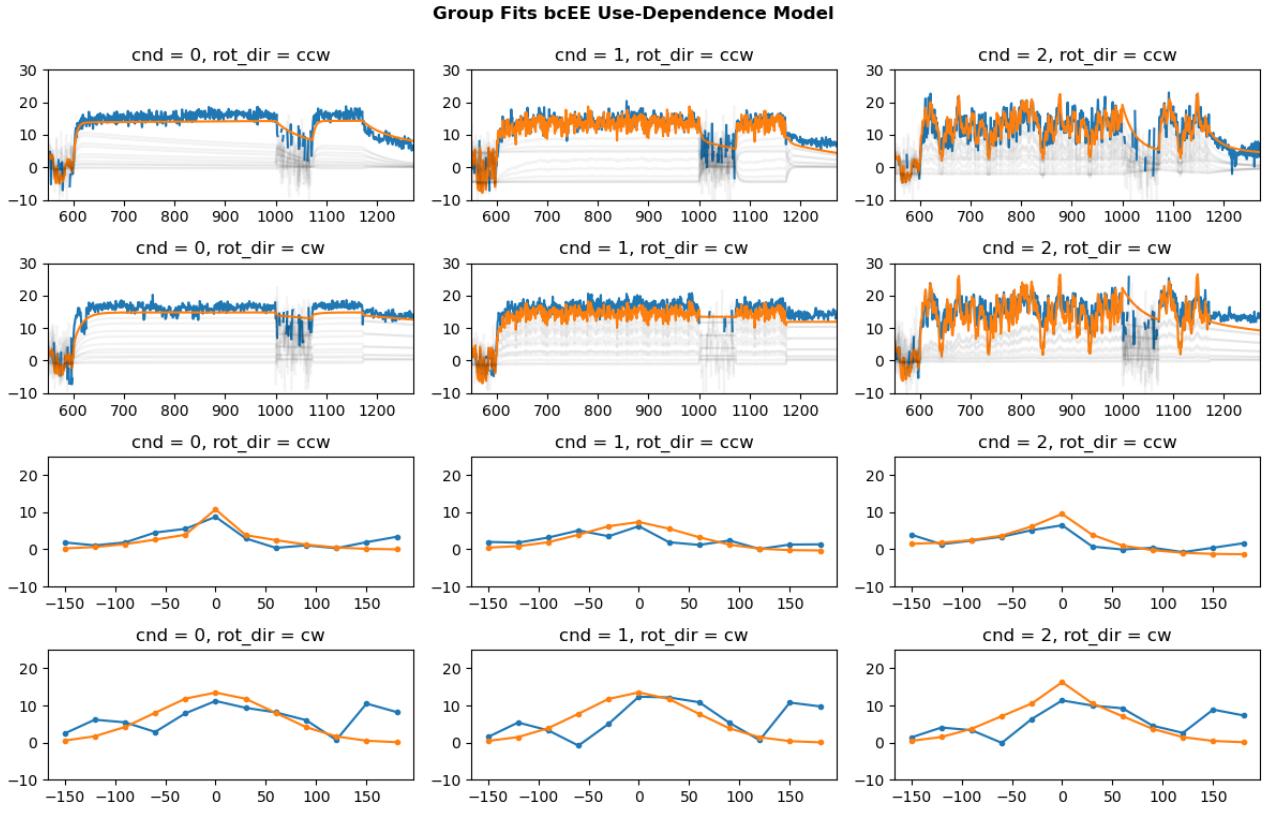


Figure 16: Use-dependency two-state space model group mean fits (*orange*) plotted against performance for each variance and rotation direction group, respectively. The *y*-axis displays baseline corrected endpoint errors (bcEE) and the *x*-axis the trial number in the upper plots and the target locations in the lower plots. Note that, due to restricted time, these fits are not bootstrapped.

## 6.4 Pre-Baseline Trajectories

So far, we have only inspected the phases that were relevant for the main analysis. Initially, we included the pre-baseline phase out of pure exploratory curiosity about what participants’ reaches would look like in this new environment before any visual feedback is given. Basically, we were interested in inspecting peoples’ behaviour when they have to ‘reach in the dark’. If we do not impose a prediction by depriving participants from feedback, would they have an initial ‘natural’ prediction? What would it be like? In addition to our initial motivation to include a pre-baseline phase, a glance at the performance across all phases in [Figure 17](#) indicates that a closer look at the pre-baseline phase might actually also be instructive in what concerns the cause of the rotation direction effect. In pre-baseline, familiarisation, baseline and post-baseline, we would expect the participants’ reaches to be distributed around an error of 0. Instead, reaches seem to be shifted CCW.

[Figure 18](#) confirms this impression. While variance group differences do not seem to follow a systematic pattern, it is striking that the error is not distributed symmetrically around an EE value of 0 but rather around  $-4$ . In order to examine whether the error is the same across all

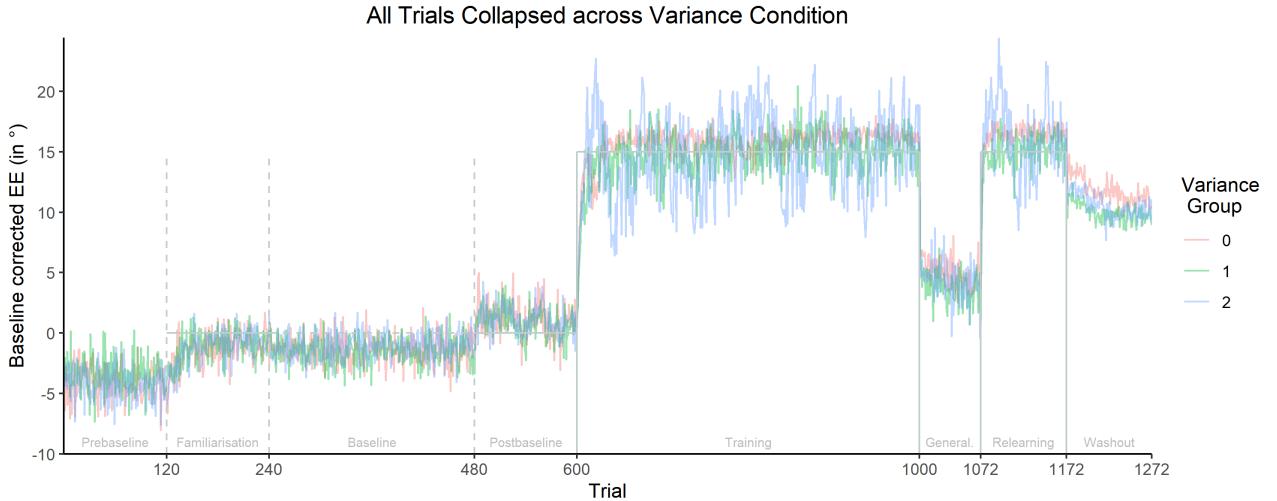


Figure 17: Baseline corrected endpoint errors (bcEE) across all trials. Phases are indicated by grey vertical lines, where the solid lines represent the phases that were relevant for the main analysis. Group 0 refers to the  $0^\circ\sigma$ , group 1 to the  $4^\circ\sigma$  and group 2 to the  $12^\circ\sigma$  condition.

targets, we further plotted bcEE against target position. Results are illustrated in Figure 18. Interestingly, it reveals a wavelike pattern for all groups, with the highest CW shifts at the  $-60^\circ$  and the  $120^\circ$  target, and the highest CCW shifts at the  $-120^\circ$ , the  $0^\circ$  and the  $150^\circ$  target. Another interesting aspect is that there seems to be an additional tiny peak around the  $30^\circ$  target, indicating that the CCW shift gets less extreme at the  $30^\circ$  target, but that it slightly falls back into extremer CCW shifts at the  $60^\circ$  target before it jumps up to the highest CW shift at the  $120^\circ$  target.

Figure 19 (left panel) depicts exemplary pre-baseline reaching trajectories to all targets for the first 4 subjects. It becomes obvious that every subject has its idiosyncrasies. Participant 1 and 2, for instance, sometimes seem to complete the trials with squiggly loops. The reaching pattern of participant 1 and 3 looks rather straight, whereas the reaches of participant 2 and 4 seem to be slightly curvy. But despite their peculiarities, all four of them have one thing in common: their reaching trajectories are all slightly shifted CCW. Figure 19 (middle panel) confirms the idea of this CCW shift in the pre-baseline phase to be a general phenomenon across subjects. What might even be more fascinating is that this pattern further endures for the familiarisation phase, where subjects were exposed to veridical FB on their hand position as illustrated in Figure 19 (right panel). Even though the participants' gaze goes to the real target location their trajectories always slightly miss the real target location by a slight CCW shift.

This tendency of a CCW shift for most of the targets might provide a plausible explanation for the rotation direction differences in the subsequent phases. If all subjects implemented a ‘natural default shift’ in a veridical task, this natural preference was likely to interfere with a rotation manipulation. Considering the preference to reach slightly CCW when participants actually aim for the  $0^\circ$  target, someone who is exposed to a CCW rotation would have to

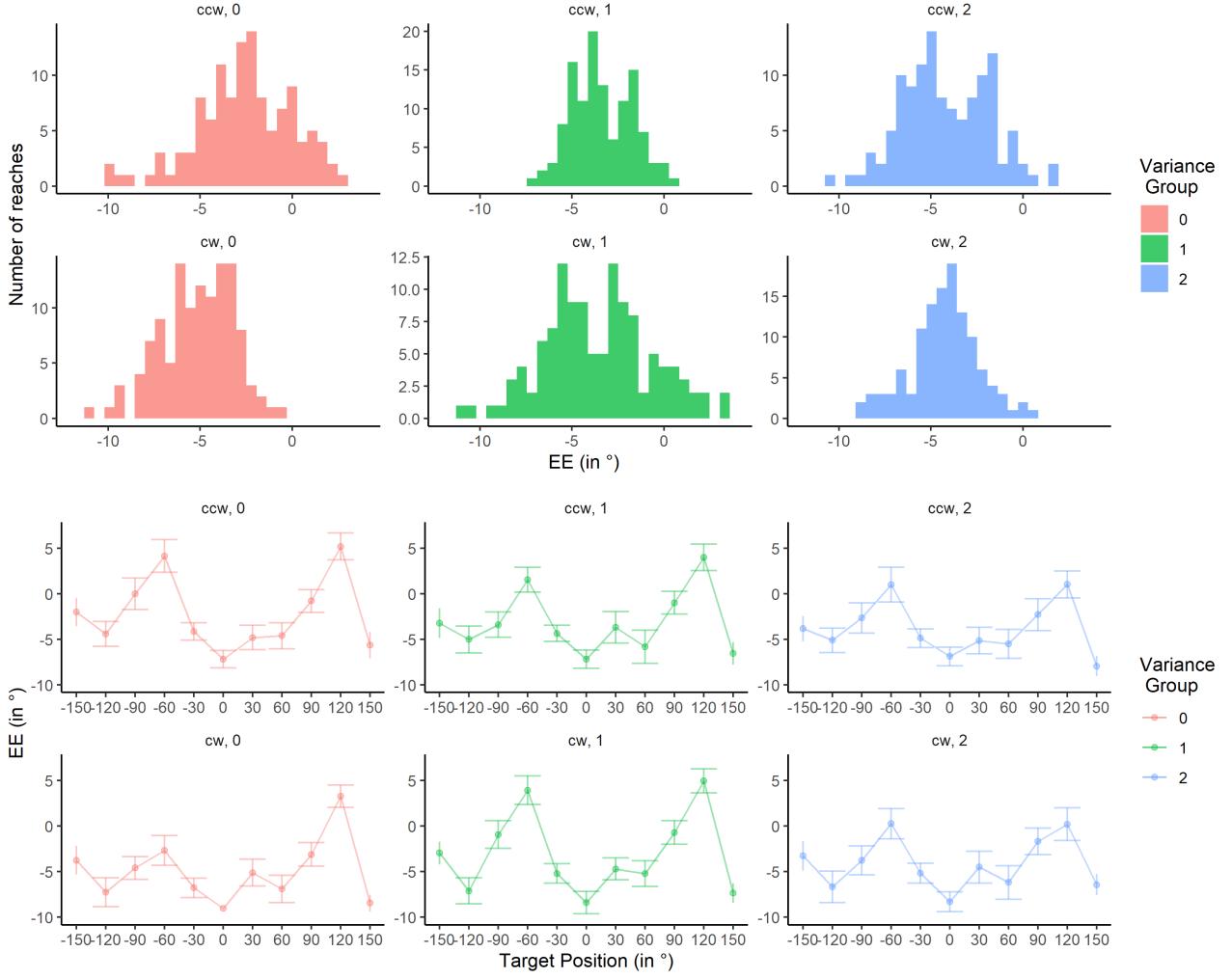


Figure 18: *Top:* Histograms depicting the distributions of endpoint errors (EE) during pre-baseline. Group 0 refers to the  $0^\circ\sigma$ , group 1 to the  $4^\circ\sigma$  and group 2 to the  $12^\circ\sigma$  condition. *Bottom:* Mean EEs per target during pre-baseline.

adapt much more than a participant who is exposed to a CW rotation. While the natural tendency to reach CW facilitates adaptation to a CCW rotation, a participant exposed to a CCW rotation would need to adapt to an even higher degree in order to additionally compensate for the natural shift. Given that the natural shift phenomenon adds up with the effect of use-dependent behaviour, it thus makes sense to assume that a participant exposed to a CW rotation, first, takes less time to reach the plateau, second, that he falls back much less in washout and, thirdly, that he generalises more to targets close to the learning target than a participant exposed to a CCW rotation. The data is consistent with this line of thought in the sense that washout is enhanced for CCW participants and that CW participants reach a higher plateau in the training and re-learning phase as well as a higher peak in their generalisation curve. It might seem odd that CW participants even surpass the full adaptation level of  $15^\circ$ . However, this might be explained by methodological effects.

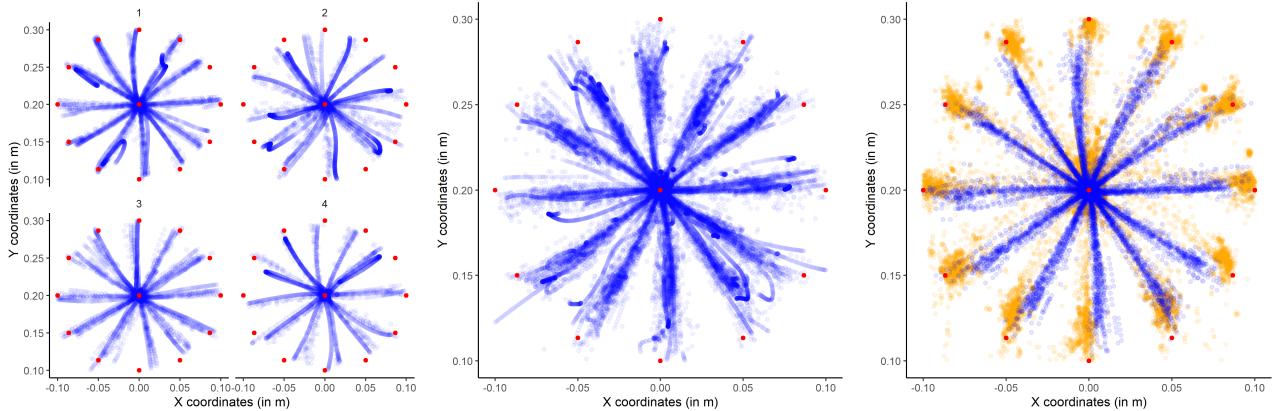


Figure 19: *Left panel:* Exemplary pre-baseline reaching trajectories (blue points) for the first 4 participants. Red points represent the different target locations. *Middle panel:* Mean pre-baseline reaching trajectories across all subjects. *Right panel:* Mean trajectories and gaze (yellow points) during familiarisation.

## 6.5 Methodological Questions

Conducting the study confronted us with a variety of methodological questions, some of which could not be answered with previous literature. For instance, we were uncertain whether to choose endpoints or IMVs as basis for our dependent error measure. Both are reported in the literature and, as we have elucidated in subsection 5.6, endpoints are used in the context of Bayesian integration, while IMVs are reported to measure the predictive feedforward component only. In this feedforward experimental design, however, endpoints and IMVs should not systematically differ from each other, leaving us with the question of which measure is the more reliable one. As can be seen in Figure 20 (top) IMVEs are much more noisy than EEs. Moreover, IMVEs result in a higher plateau than is the case for EEs. The total correlation across all phases is 0.70. However, participants' correlations defer quite a lot from each other, ranging from a minimum correlation of 0.34 to a maximum correlation of 0.85. In order to further investigate where those differences might come from, we plotted the baseline NFB trajectories of the 4 participants with the lowest correlation between EE and IMVE against those 4 participants where EE and IMVE correlated highest (see Figure 20 (bottom)). It becomes apparent that in the latter case, the reaches are mostly straight and direct, while reaches were, first, much more noisy and, second, more curvy for participants with a low correlation. The observation that almost every one of those participants reaches for the  $0^\circ\sigma$  target in a slightly curvy manner explains the higher plateau for IMVE we have seen in Figure 20. Considering this apparent tendency to form a CCW curve as well as the higher amount of noise at the beginning of a reach for some participants, we suggest endpoints as more suitable for a reliable error measure. We believe this to be an important insight for future research.

While this is also true for the question of whether baseline correction should be applied, the analysis on this specific methodological question even provided further insights regarding the effect of rotation direction. Figure 21 illustrates the difference between the baseline corrected

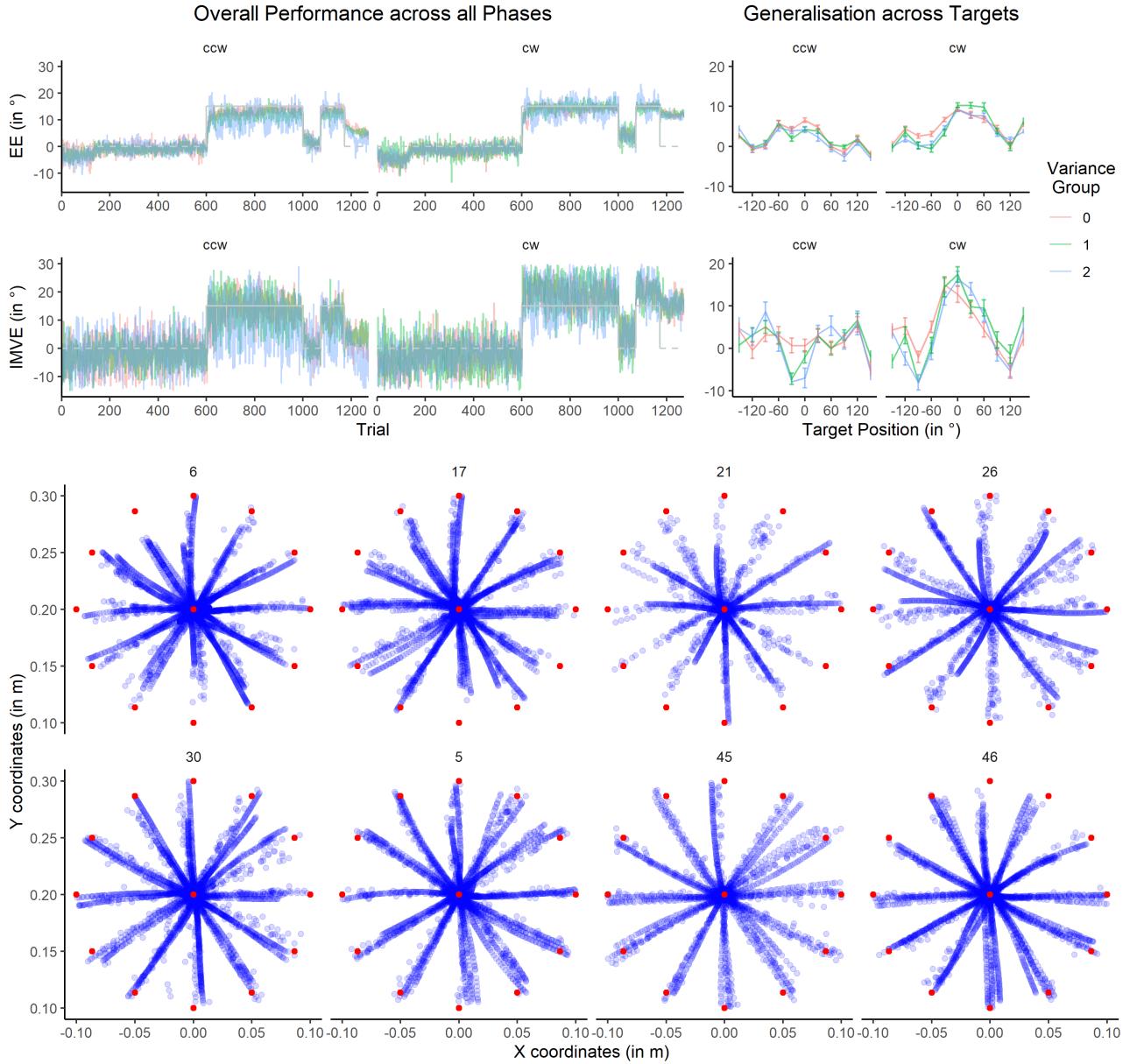


Figure 20: *Top:* Comparison of endpoint errors (EE) and initial movement vector errors (IMVE). Group 0 refers to the  $0^\circ\sigma$ , group 1 to the  $4^\circ\sigma$  and group 2 to the  $12^\circ\sigma$  condition. *Bottom:* Comparison of the reaching trajectories (*blue points*) for the 4 participants with the lowest (*upper row*) and highest correlation (*lower row*) between EE and IMVE. Trajectories are depicted for the NFB baseline trials. Red points represent the different target locations.

EE and the raw EE. Strikingly, baseline correction resulted in an upwards shift of the data. Furthermore, the shape of the CCW generalisation curve changed through baseline correction. What might seem odd at first is explained by the fact that participants apply the CCW shift for the baseline phase as well (see Figure 17). Remember that baseline correction is achieved by subtracting the mean of a participant’s NFB baseline trials per target from the participant’s respective EE values. However, as is the case for pre-baseline and familiarisation, baseline trials are shifted CCW instead of being distributed symmetrically around  $0^\circ$ . Thus, subtracting the negatively coded CCW NFB baseline mean EE from the training EEs results in an addition.

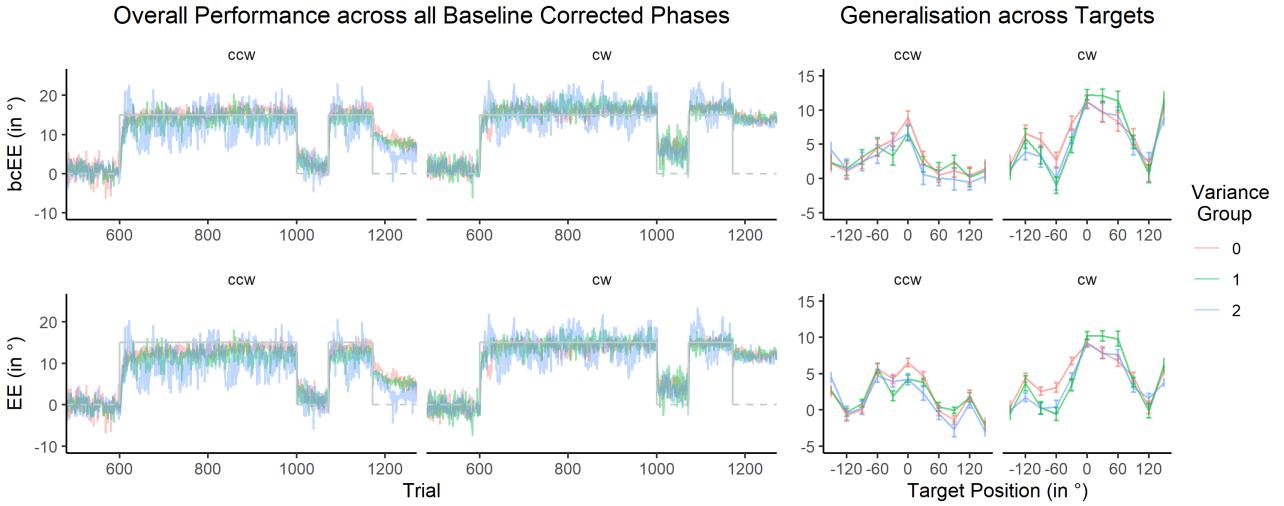


Figure 21: Comparison of endpoint errors (EE) and baseline corrected endpoint errors (bcEE). Group 0 refers to the  $0^\circ\sigma$ , group 1 to the  $4^\circ\sigma$  and group 2 to the  $12^\circ\sigma$  condition.

This in turn explains that the bcEEs surpass the mean adaptation level of  $15^\circ$ . In what concerns the generalisation curve, the difference in shape between the CCW EE and the CCW bcEE curve is probably due to the fact that different participants consistently applied different shifts to different targets. While those natural shifts interact with adaptation in the case of EEs, they are compensated for in the case of bcEEs. The resulting CCW generalisation curve has still a lower peak (probably because their natural shift impaired the learning in the previous training phase) and a left-skewed shape (probably due to use-dependent behaviour). However, baseline correction cleared out the dip of the raw EEs in the CCW generalisation curve.

The previous steps of the exploratory analysis provided valuable insights for a better understanding of the unexpected effect of rotation direction. However, as data was analysed separately for CW and CCW participants instead of collapsed, it remains unclear whether the absence of significant variance group effects can be interpreted as solid evidence against group differences. With on average only 8 subjects per group (variance  $\times$  rotation direction), it might as well be due to a lack of power. The BF analysis is characterised by its ability to quantify the relative predictive performance of the null and the alternative hypothesis<sup>26</sup>, thereby providing a measure to assess how strong the data really speaks for or against our variance group difference predictions.

<sup>26</sup>Briefly, in classical hypothesis testing, we test how likely the outcome of our data or an even extreme outcome is when we assume that a true effect (such as a systematic difference between two groups) does not exist. This assumption is referred to as the *null hypothesis*  $H_0$  and is considered the default assumption. Only when the likelihood of finding an effect at least as extreme as the one observed given the null hypothesis falls below a predefined threshold, would we reject the null in favour of the *alternative hypothesis*  $H_1$ . We then assume that it is too unlikely to find an effect of this magnitude under the null hypothesis and infer that a true effect exists. In contrast, the Bayes factor (BF) quantifies the relative predictive performance of the two rival hypotheses (null *vs.* alternative).

## 6.6 Bayes Factor Analysis

In order to get a feeling for how strong the evidence for or against the  $H_1$  is for the different parameters, respectively, we ran a BF analysis on the individual subject fits<sup>27</sup>. All BFs and the plots of the sequential analyses can be found in [Appendix G](#). In a first step, Bayesian independent samples two-sided t-tests were conducted to test for differences in the two different rotation direction groups within the three variance conditions, respectively. The prior was set to the Cauchy default with a scale of 0.707. Except for  $\beta_f$  [ $BF_{10} = 1.22$ ], BFs for all parameters were smaller than 1 [ $BF_{10} < 0.55$ ] in the  $0^\circ\sigma$  condition, thereby speaking slightly in favour of the  $H_0$  rather than for the  $H_1$ . Similarly, in the  $4^\circ\sigma$  condition, BFs for all parameters fell below 1 [ $BF_{10} < 0.83$ ]. The same applies to the test in the  $12^\circ\sigma$  condition [ $BF_{10} < 0.93$ ]. However, it is important to notice that, according to the scale of interpretation from M. D. Lee and Wagenmakers (2014) (for the original scale, see also Jeffreys, 1998), all BFs do not exceed an anecdotal to moderate level of evidence.

For the subsequent analysis of differences between variance conditions, Bayesian independent samples one-sided t-tests were used in the case of learning rate parameters ( $\alpha_s$  and  $\alpha_f$ ) and two-sided t-tests for retention rate ( $\beta_s$  and  $\beta_f$ ) and generalisation width ( $\sigma_{\theta_s}$  and  $\sigma_{\theta_f}$ ) parameters, as defined in [subsubsection 5.6.3](#). Please note that, even though almost every parameter difference between the two different rotation direction groups was not significant in the BF analysis, the subsequent tests for differences between the variance groups were conducted separately for each rotation direction condition. This was done to be consistent with the main analysis described in [subsection 6.1](#).

Except for  $\alpha_s$  in the  $4^\circ\sigma$  vs.  $12^\circ\sigma$  group comparison for CW participants [ $BF_{+0} = 3.44$ ]<sup>28</sup>, the BF was below 1 in all remaining  $\alpha_s$  and  $\alpha_f$  group comparisons for the CW [ $BF_{+0} < 0.82$ ] as well as for the CCW condition [ $BF_{+0} < 0.37$ ]. A similar pattern was found for  $\beta_s$  and  $\beta_f$ . The  $0^\circ\sigma$  vs.  $12^\circ\sigma$  group comparison for CW participants revealed a  $\beta_s$  in anecdotal favour of  $H_1$  [ $BF_{10} = 1.18$ ]. All the other BFs for  $\beta_s$  and  $\beta_f$  were below 1 for CW [ $BF_{10} < 0.55$ ] and CCW participants [ $BF_{10} < 0.68$ ]. All tests on the  $\sigma_{\theta,s}$  and the  $\sigma_{\theta,f}$  values were below 1 for, both, the CW [ $BF_{10} < 0.94$ ] and the CCW rotation condition [ $BF_{10} < 0.66$ ]. Here again, it is important to note that all of the conducted Bayesian t-tests on the parameters led to a BF that barely reached a moderate level of evidence (the sequential analysis plots in [Appendix G](#) graphically illustrate that the curves never reach the area of strong evidence).

Taken together, this BF analysis strongly indicates that the data base is too weak to make reliable conclusions for or against the alternative hypothesis of parameter differences caused by different variance levels. Considering the unexpected difference between the two rotation

<sup>27</sup>Please note that, due to lack of time, those individual fits were not estimated using bootstrapping techniques as was the case with the group fits analysed in the section above.

<sup>28</sup>The + in the notation  $BF_{+0}$  indicates that a one-sided alternative hypothesis is used as opposed to a two-sided one. Here, the BF is in favour of the alternative over the null hypothesis:  $BF_{+0}(d) = \frac{P(M_+|d)}{P(M_0|d)}$  where  $d$  refers to the observed data,  $M_0$  to the null and  $M_+$  to the alternative model. A value greater than 1 indicates an outcome in favour of  $H_1$ , while values between 0 and 1 speak in favour of the  $H_0$ .

direction groups and the resulting decision to analyse the data separately for the CW and the CCW group, it is not surprising that the average group size turns out to be too small to find robust effects.

## 7 Discussion

The field of cognitive science is a modern, interdisciplinary and fast growing field of research. Roughly speaking, it investigates human information processing. How does our brain represent our environment? Does an infant have the same level of awareness than an adult person? How does our memory work? To name but a few questions that motivate cognitive scientists all over the world. These questions can be traced back to one single question: How does our mind work? If we want to understand complex cognitive phenomena, as such as theory of mind or rational reasoning, we first need to understand the computational basis on which everything else is built. Knowing more about how our brain integrates information will help us to understand the variety of cognitive outputs, be it stretching out our arms when we threaten to fall or the answer to an intellectual question. A growing body of research has investigated the Bayesian framework as a possible model to explain information processing in our brain. Do we integrate information according to Bayesian principles, *i.e.* do we weight information according to their respective uncertainty? To ask this question, this thesis specifically focused on the field of sensorimotor learning as one of the most fundamental and vital areas of cognition. More specifically, we focused on visuomotor adaptation as the part of motor learning that ensures the performance maintenance of an already learned motor behaviour in a constantly changing environment. Lately, a growing body of research provided evidence that humans indeed seem to take the uncertainty of visual input into account in visuomotor adaptation. However, the paradigms applied in this research did not allow for a separate analysis of prior knowledge and it thus remained unclear whether predictions themselves are represented in a Bayesian manner as well. If humans were to really integrate information according to Bayesian principles, then uncertainty weighting should apply to, both, sensory input and prior information. As the two studies that focused on a prediction's uncertainty only are at odds with each other we investigated this question by using an adapted VMR paradigm.

Results predominantly emphasised our unexpected finding in the pilot study by revealing a difference between the reaching behaviour of participants who were exposed to CW rotations and those exposed to CCW rotations. This required that we had to perform the analysis separately for the two rotation direction conditions. Bootstrapping analysis results pointed in the expected direction, with significantly smaller learning rates in the two probabilistic variance groups than in the  $0^\circ\sigma$  group. However, this significant difference was only found for the CW rotation condition and, except for a different generalisation width in the slow system between the  $0^\circ\sigma$  and the  $12^\circ\sigma$  group, again for CW participants, no other group comparison led to significant effects. However, the lack of significant variance group differences for almost all

parameters does not seem surprising, considering the small average group sample size of only 8 participants. Four questions motivated our further investigation in a subsequent range of exploratory analyses:

1. Can we expect the lack of significant variance group differences to be reliable evidence against a true difference or is it rather due to the small resulting sample size?
2. What causes the different reaching patterns in CW and CCW participants?
3. What consequences do different methodological choices have on the analysis and on the interpretation of the data, and thus, what methodological choices are more suitable for future research?
4. How do participants behave in a new environment when no prediction is imposed?

While the first two questions were driven post-hoc by the surprising finding of reaching differences for the two rotation directions, the other two questions emerged during the course of the experiment. Importantly, the detailed exploratory investigation of question 2 was only possible because question 3 and 4 motivated us to adapt the experiment in order to acquire additional data for qualitative analyses. Those adaptations provided the fruitful basis for a more detailed exploration of question 2.

## 7.1 Conclusion Main Question

The statistical bootstrapping analysis on the learning rate, the retention rate and the generalisation width fitting parameters revealed significantly smaller learning rates in the two probabilistic variance groups than in the  $0^\circ\sigma$  group. However, this was only the case for the CW condition. Moreover, differences were not significant in almost every other group comparison. This result begs the question of how to interpret it. Most comparisons are not significant; Can we therefore reject the alternative hypothesis and conclude that the amount of uncertainty does not influence learning, generalisation and washout?

Statistics never provide clear yes or no answers. Instead, they provide us with probabilities that help to assess whether a certain hypothesis is more likely to be true or false. Besides the size of the effect itself, those probabilities are also influenced by the size of the sample on which the data is based in classical hypothesis testing. The greater the sample size, the greater the probability to reject the null hypothesis  $H_0$  when the alternative hypothesis  $H_1$  is true (Meehl, 1967). In other words, a true difference is more likely to be correctly identified as a significant one when the sample size is greater. Especially in the case of small effects, too small sample sizes could lead to an existing effect not being identified as statistically significant. The true effect would thus not be found. In the case of this study, the unexpected difference in reaching behaviour between participants who adapted to a CW and those who adapted to a CCW rotation led us to conduct the main analysis of variance group differences separately for

the two rotation direction conditions. This resulted in the group sample size being halved (on average 8 instead of the planned 16 participants per group). Two options are thus conceivable: One, the lack of significant differences has correctly been identified as reliable evidence for the conclusion that uncertainty of prior knowledge has indeed no influence on the parameters or, two, there is an existing effect of uncertainty on at least some of the parameters that has not turned significant because of the group sample sizes being too small. In order to explore this question, a BF analysis has been conducted. As was the case for the bootstrapping significance tests, almost no group comparison was in favour of  $H_1$ . However, almost all BFs had a value close to 0, thereby not exceeding the moderate level of evidence. It can therefore be concluded that the data base of on average 8 participants per group is indeed too small to provide us with conclusive results. Follow-up studies with bigger samples are required to provide conclusive evidence on whether the significant variance group differences, that were found for participants exposed to a CW rotation, can be replicated for both CW and CCW rotations. Further studies would also be required to answer the question of how a prediction's uncertainty influences generalisation and washout. Importantly, those future studies should account for differences in rotation direction.

## 7.2 Difference in Rotation Direction

Question 1 and 4 are related in the sense that the answer to question 4 automatically contributes to question 1, which is why they are discussed together here. Our initial assumption was that the differences between CW and CCW participants might have been mediated by a different use of explicit strategies in both groups. Our experimental design provided us with various methods for capturing explicit strategies. Those measures were used to relate differences in the use of explicit strategies to the observed differences between CW and CCW participants. However, neither the awareness questionnaire, nor the inspection of the two implicit measures of RTs and gaze provided any hint for differences in the use of explicit strategies. It was argued that this lack of any explicit strategy finding might be due to methodological issues such as the tendency to answer conform to the investigator's expectations for the questionnaire or poor calibration for eye tracking. It is significant though that all three indicators for the use of aiming strategies did not show any systematic explanatory pattern. Moreover, it was reasoned that the experiment was designed in a way that aimed to reduce the use of explicit strategies to a minimum. Briefly, trials were limited to a maximum of 600 ms and a post-baseline phase was implemented to adapt participants to noisy feedback before they start learning the mean perturbations of the 15° shift. It is conceivable that those measures were effective, even though this would not answer the question of why certain participants were explicitly aware of the perturbation whereas others were not. In any case all three measures do not seem to indicate a systematic difference between the use of explicit strategies in the CW and in the CCW rotation condition, leading us to the conclusion that the reason for this difference lies somewhere else.

Indeed, the investigation of the pre-baseline trajectories revealed an interesting pattern. Despite individual idiosyncrasies in pre-baseline reaching trajectories, all participants shared one common pattern: Reaches to the 0° target were always shifted CCW. Moreover, visualisation of the data suggested that the mean shift was not the same across all targets. How far participants reached CW or CCW, relative to the aiming target, actually depended on the respective target position. While it was clearly CCW for the 0° target, participants even reached slightly shifted CW for the -60° or the 120° target. Strikingly, this pattern even persisted in the familiarisation phase where participants received veridical FB on their hand position.

This finding suggests the presence of a ‘natural reaching tendency’ that interacts with the imposed CW or CCW rotation perturbation. More specifically, if all participants have the tendency to reach slightly CCW when they actually aim to reach straight forward towards the 0° target, adaptation to a CW rotation would be facilitated. Participants exposed to a CCW perturbation, in contrast, would need to adapt to an even higher degree. Conversely, CCW rotation participants would have a higher tendency to fall back to the 0° level, whereas CW rotation participants would only de-adapt to their natural reaching tendency which is still shifted CCW from the 0° aiming target. Thus, while this natural CCW reaching tendency facilitates learning for CW participants and impedes learning for those who are exposed to a CCW rotation, it is the opposite for washout. The same interaction applies to generalisation. However, this case even involves an additional interaction of target position. While the difference in peak hight of the two different generalisation curves (CW *vs.* CCW) can be explained by the difference in the amount of learning, the shape difference we observed in the not baseline corrected EEs is probably due to the already mentioned different reaching tendencies for different targets. This assumption is supported by the fact that the bcEE curve does not show this dip in the CCW curve, thereby indicating that baseline correction with the NFB baseline trials accounts for those target reaching differences. Interestingly, the bcEE generalisation curves are still characterised by a peculiarity: Contrary to our expectations, they are not symmetric around the 0° target. The finding that the generalisation curve is left-skewed for participants exposed to a CCW perturbation and right-skewed for those that are exposed to a CW rotation might be explained by *use-dependent behaviour*. Use-dependent behaviour (also referred to as *use-, experience- or activity-dependent plasticity*) has already been reported in previous studies and has been described as the phenomenon that “repeated movements toward a particular target bias the subsequent movements toward that target” (Mawase et al., 2017, see also Classen et al., 1998; Diedrichsen et al., 2010; Verstynen and Sabes, 2011). It has been suggested that practising movements results in plasticity<sup>29</sup> of the motor cortex and thus in improved performance such that a current movement is affected by our history of recent experiences (Bütefisch et al., 2000; Mawase et al., 2017). Basically, the phenomenon of use-dependant behaviour is

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<sup>29</sup>i.e. the capacity of the brain to remodel itself in order to optimise the brains neural networks (Duffau, 2016). The previously mentioned Hebbian rule (Hebb, 2005) is an attempt to explain plasticity on a synaptic level.

compared to a trough that has been trenched by a repeated movement, in this case the 400 (CW or CCW) shifted reaching movements to the 0° target in the training phase. In the subsequent generalisation phase, reaches to targets close to the previous movement direction (either roughly 15° CCW for the CW rotation condition, or 15° CW for the CCW rotation condition, probably a bit less in the latter case because of the interaction with the natural shift) will be attracted by this trough. The closer they located are to the centre of the trough, the more the reaches would be affected by it. Following this line of thought, we would expect a higher amount of generalisation for targets located CCW from the direction of the adaptation shift with CCW participants. As illustrated in [Figure 22](#), this is the case because the learned CW shift is even enhanced by the trough that has been trenched in the training phase for those targets located CCW from the trough centre, whereas the attraction towards the trough works against generalisation of the previously learned CW shift for targets that are located CW of the trough centre. Conversely, participants exposed to a CW rotation during training would trench a trough between the 0° and the -30° target, whose attraction enhances generalisation of the learned CCW shift for targets located CW to the trough and impairs generalisation for targets on the CCW side of the trough. This interaction between generalisation of the learned shift and use-dependent behaviour thus leads us to expect a right-skewed generalisation curve for participants who learned a CW rotation and a left-skewed curve for participants who learned a CCW rotation in the training phase. Our findings support this line of thought, thereby replicating evidence from Diedrichsen et al. ([2010](#)) that suggests that use-dependent behaviour and adaptation can occur simultaneously as two different learning mechanisms that are being integrated. The computation of a prediction thus seems to rely on, both, adaptation and use-dependent behaviour. In summary, our exploratory analyses led us to the conclusion that two phenomena are likely to explain the differences in reaching behaviour between the CW and the CCW rotation condition: Use-dependent behaviour and naturally shifted reaching tendencies, both of which seem to interact with sensorimotor adaptation.

While a solid body of research underpins the existence of use-dependent behaviour, evidence for biases based on naturally shifted reaching tendencies seems to be rather thin. The classical visuomotor adaptation literature almost seems agnostic on this issue. If perturbations were implemented for both directions, CW and CCW rotations were always collapsed in previous VMR studies, thereby suggesting no rotation direction difference in reaching behaviour. This originally led us to assume that we would be able to collapse over rotation direction as well. All the greater was our surprise when our data revealed this difference. It seems puzzling that shifted reaching tendencies did not have any impact on the data of almost every previous study. On the other hand, why should researchers decide to collapse their data if there really was a difference?

Considering the fact that, as most previous studies, this study only examined right-hand dominant participants, it is quite conceivable that left- or right-hand dominant participants who are instructed to use their left hand would show the exact opposite pattern of the one

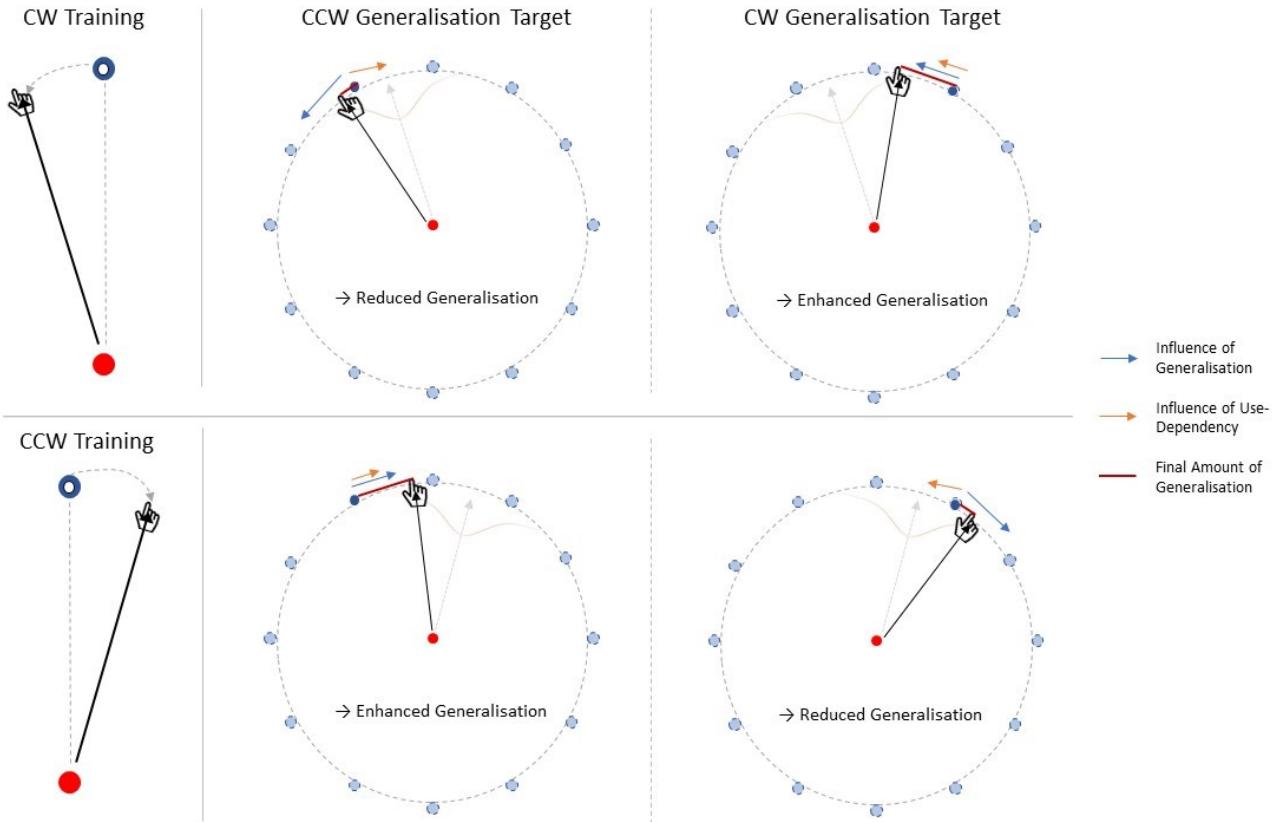


Figure 22: Illustration of the interaction between use-dependency and generalisation for, both, the CW and the CCW rotation group. Repeated reaching movements in one direction during training bias subsequent reaches towards this direction. During generalisation, use-dependency enhances the total amount of generalisation if it plays into the same direction. Otherwise, the final amount of generalisation is reduced. Note that the mechanism that describes how use-dependency interacts with adaptation is identical to the underlying mechanism for the interaction between anisotropy and generalisation. In both cases, the observed amount of generalisation is biased towards a preferred ‘default’ reach direction. The only difference is the reason of why a specific reach direction is favoured (recent movements for use-dependency or stable biomechanical reasons for anisotropy).

that was observed in this study. Unfortunately, previous literature in the field rarely reports a comparison of either right- and left-hand dominant participants or simply of used hand. Interestingly, Fernandes et al. (2011) acquired data from right- and left- hand dominant people but applied a CW rotation for right-handed and a CCW rotation for left-handed participants only. Data was then analysed collapsed across handedness groups, leaving us with the assumption that no difference was found between those two groups. However, they also report target-location dependent systematic biases in the baseline phase. Crucially, those directional biases are referred to as **anisotropy**. Earlier, Ghez et al. (1995) observed that occlusion of the hand position results in systematic biases both in extent and direction in centre-out reaching tasks. Furthermore, those biases depend on movement direction as well as on the hand position at the centre target. Gordon, Ghilardi, Cooper, et al. (1994) further observed that movements that

primarily involve forearm rotation lead to overshooting of the target, whereas targets tend to be undershot in movements involving whole-arm rotation. Evidence from Flanagan and Lolley (2001) further support this anisotropy. Importantly, the patterns reported by Flanagan and Lolley (2001), Ghez et al. (1995) are indeed very similar to the patterns observed in the present study, making the underlying mechanisms of anisotropy a quite conceivable explanation for the shifted reaching tendencies in our data. Gordon, Ghilardi, and Ghez (1994) argue that this anisotropy might be due either to biomechanical effects or to biases in perception.

In summary, the question of what causes the observed directional biases cannot be conclusively answered within the framework of this study. However, it seems very likely that they are explained by biomechanical mechanisms that bias movements in different directions when vision of the hand is prevented. More research is needed to further investigate this anisotropy in the context of feedforward visuomotor adaptation studies. Here, it would be especially interesting to model the interaction of anisotropy, use-dependency and adaptation in order to investigate to what extent they play together.

### 7.3 Methodological Conclusions

Conducting an experiment is always associated with a range of decisions. While experiences and knowledge from previous literature provide a solid basis to reliably answer some of them, others are still subject to considerable uncertainty. Just as a meaningful research question is central to a study, so too are valid methodological measurement procedures. We were thus curious to explore how those decisions we felt most uncertain about would affect data analysis. The aim was to compare the outcome of the various options we had to choose from in order to provide a guideline for future research. In this respect, two methodological questions were explored:

1. In a feedforward adaptation study, is the IMV or the endpoint the better, *i.e.* the more reliable and valid, measure to compute the dependent error term?
2. Should the dependent error variable be baseline corrected?

As mentioned earlier, little research has been conducted on the influence of uncertainty in a pure feedforward visuomotor rotation design. It is thus unclear whether IMVE or EE is the more appropriate dependent measure. Our choice of EE was based on EE being used more frequently in previous literature. However, in contrast to studies that investigate Bayesian integration, both, IMVE and EE should theoretically lead to the same outcome in a feedforward study that focuses on predictions only. To our knowledge, this has never been investigated and therefore the idea that IMVE and EE do not systematically differ from each other remains an assumption. Indeed, we observed that IMVE values were slightly higher than EE values, which is probably explained biomechanically by the slightly CCW curvy reaching trajectories across participants. Furthermore, the exploration of our data yielded a much higher degree of noise in IMVE as

was the case for EE. This observation was supported by the trajectory plots showing more noisy and squiggly reaches for subjects with a lower correlation between IMVE and EE than for subjects with high correlations. Taken together, the smaller amount of noise and the curvy reaching behaviour led us to the conclusion that endpoints prove to be the more appropriate measure.

While the high amount of noise in IMV makes the answer to the first question a relatively easy one, the choice for or against baseline correction remains an open and debatable question. In this specific case, baseline correction interfered with the participants' natural reaching tendencies – with two consequences: First, bcEE values were systematically increased and, second, the fact that different reaching tendencies for different targets were compensated for in baseline correction, changed the shape of the CCW generalisation curve. The exploratory comparison of EE and bcEE has shown how additional transformations associated with a baseline correction might interfere with other (unexpected) effects, thereby maybe masking them and impeding, if not even misleading, interpretation of the data. Applying baseline correction also raises the question of how exactly baseline correction should be performed. The lack of a single best practice of baseline correction in previous literature leaves room for a variety of more or less arbitrary decisions and thus impedes comparability between studies. On the other hand, the CCW generalisation curve has also shown that baseline correction can be useful for purifying data from undesirable effects – after all this is the whole idea behind baseline correction. This case has shown how baseline correction might impede interpretation of the data if other effects interfere with it. Here, additional analysis of the uncorrected EE data yielded valuable insights into the cause of the unexpected difference in rotation direction. Against the background of a reliable main analysis, however, it makes sense to use of a baseline corrected measure that accounts for unwanted effects. Taken together, the use of a baseline corrected measure is probably recommendable if the data is well understood. An additional exploratory inspection of the non-baseline corrected measure should be conducted in the case of unexpected effects in order to account for possible interactions. Moreover, researchers should adhere to one best practice convention of baseline correction to ensure best possible comparability between studies.

## 7.4 Future Directions

While the previous sections were devoted to answering the main questions arising from the analysis, this section focuses on the resulting implications for future research. Results of our main analysis led us to conclude that the present study is not able to reveal conclusive results on the main question of whether uncertainty of a prediction influences learning rate, washout rate or generalisation width. This, however, does not mean that we cannot learn anything from this study. On the contrary, additional exploratory analyses provided us with a wide range of useful insights and implications for future research, both in terms of methodology and content.

With respect to methodological questions, our conclusions provide a useful guideline for fu-

ture visuomotor rotation studies that aim to investigate the feedforward component in isolation. Our data indicates that IMVE is a much more noisy measure than EE. The fact that participants predominantly applied a slightly curvy reaching behaviour further leads to the IMVE values being more extreme than the EE values. Ideally, the error measure should represent the difference between the aiming target and the hand position at the time the 9 cm target radius is crossed. As, by definition, this criterion is better represented by endpoints, we recommend them as a more reliable and suitable measure to compute the error. With respect to baseline correction, this study has shown the benefits and downsides of such a transformation. While it accounts for unwanted idiosyncrasies, it might interact with unforeseen effects, thereby perhaps impeding a correct interpretation of the data. We still recommend the implementation of baseline correction. However, additional exploratory investigations should be conducted if any pattern in the data does not turn out as expected. Importantly, researchers should adhere to one convention of baseline correction to ensure comparability. Here, we suggest the use of pseudo-randomly intersected NFB baseline trials, where the mean is computed separately for each target and subtracted from the respective EE values.

In terms of content, the next steps should consist in further investigating the observed (probably biomechanical) directional biases. As a first measure, researchers from previous VMR literature should be contacted and asked if any similar pattern appeared in their data. Perhaps the difference between the reaching behaviour of participants who adapted to a CW and those who adapted to a CCW rotation was less obvious in their data as it was in ours. In this case it would be important to draw their attention to those biases. Considering that interactions with adaptation might bias or mask the research outcome, it would be crucial for researchers to be aware of them. Furthermore, future systematic research is needed in order to investigate how exactly the findings of the present study relate to the previous literature on anisotropy (*e.g.* (Flanagan & Lolley, 2001)). Based on this literature that suggests that anisotropy can be traced to biomechanical mechanisms, we predict a mirrored outcome for participants instructed to use their left hand. Here, a systematic investigation should account for, both, hand-dominance and used hand.

Another unforeseen finding was that the two generalisation curves for the CW and the CCW group, respectively, happened to be skewed in opposite directions. Based on the findings of Diedrichsen et al. (2010), we reasoned that it may have its cause in use-dependent behaviour. Indeed, our two-state space model seemed more accurate in describing the skewed generalisation curves after a use-dependent term has been implemented. A respective next step might consist in creating a model that accounts not only for use-dependency but also for directional biases in order to further examine the interplay of adaptation, anisotropy and use-dependency. Such a model could further be used, first, to determine the extent to which each of these components contributes to the outcome and, second, to predict the data of a new VMR study with right- and left-hand dominant participants.

With respect to our main question, exploratory BF analyses suggest that results from the

bootstrapping significance tests are inconclusive. The separate analysis for CW and CCW rotation participants resulted in an average group sample size of 8 participants, which was not enough to yield conclusive results. As our main question therefore still remains unanswered the obvious next step would be to conduct an improved version of this study. Crucially, the group sample size needs to be increased. Group sample sizes should be planned adequately in that the researchers should account for the fact that data has to be analysed separately for other factors such as rotation direction. Taken together, our conclusions for future research can be summarised as follows:

1. An average group sample size of 8 participants is not sufficient to conclusively answer the question of whether uncertainty of prior knowledge affects sensorimotor adaptation.
2. Instead the present study unexpectedly replicates two other findings:
  - (a) Adaptation interacts with use-dependency, as was previously observed by Diedrichsen et al. (2010).
  - (b) Adaptation further seems to interact with biomechanical directional biases (Fernandes et al., 2011).
3. Baseline corrected endpoint errors are suggested as the most suitable measure for future feedforward visuomotor adaptation studies.

## 7.5 Summary

Broadly speaking, this study was interested in the question as to whether sensorimotor learning follows Bayesian principles. More specifically, the study investigated the impact of a prediction's uncertainty on learning rate, washout rate and generalisation width. It was expected that, if sensorimotor adaptation follows Bayesian principles, not only should the amount of uncertainty of sensory information affect adaptation (as shown in the previous literature), but also the uncertainty of a prediction. To answer this question, a between-subjects visuomotor rotation study has been conducted where 3 different participant groups have been exposed to different rotation variances ( $0^\circ\sigma$ ,  $4^\circ\sigma$ ,  $12^\circ\sigma$ ). However, due to an unexpected difference between the reaching behaviour of participants exposed to a CW perturbation and those exposed to a CCW perturbation, data had to be analysed separately for those two conditions, leaving us with a too small group sample size to reveal conclusive results. Strikingly, the difference in reaching behaviour for CW and CCW participants has, to our knowledge, never been reported in the previous visuomotor adaptation literature, making this unforeseen finding even more noteworthy. Even though results of the main analysis were inconclusive, the present study still provides valuable insights; not least by virtue of the wide range of exploratory measures. It has been discussed that the differences are probably due to use-dependency and biomechanical directional biases, both of which affect adaptation. In addition, this study provides useful

methodological insights that can serve as a guidance for methodological decisions in future research. In summary, the present study was originally designed for the main purpose of contributing to the content-related question as to whether our brain follows Bayesian principles in information processing. Instead it mutated into a study that both raised and answered a range other useful and intriguing questions – just not the main one. As such, the future main direction is likely to be similar to that of a child who falls down when trying to walk. We simply have to get up again and curiously start a new attempt. Isn't this what science should be like after all?

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## List of Abbreviations

bcEE	baseline corrected endpoint error
BF	Bayes factor
CCW	counterclockwise
CW	clockwise
CI	confidence intervals
EE	endpoint error
FB	feedback
FF	force field
IMV	initial movement vector
IMVE	initial movement vector error
LQE	linear quadratic estimation
NFB	no feedback
PDF	probability density function
RT	reaction time
VMR	visuomotor rotation

## Glossary

**after-effect** The phenomenon that, for a certain amount of time, adaptation is maintained after exposure to an adaptation inducing stimulus. [16](#)

**anisotropy** Directional biases that occur when the participant's hand position is occluded. Biases are probably due to biomechanical and perceptual reasons. [57](#)

**Bayes factor** An indicator that quantifies the relative support for one model over another, thereby providing a measure for the weight of the evidence in favour of a given hypothesis. Bayes factor analysis provides an alternative to classical hypothesis testing. [36](#)

**Bayes' theorem** A theorem describing how the probability of an estimate is updated based on prior knowledge and related information. [9](#)

**Bayesian coding hypothesis** The hypothesis that the brain represents information probabilistically, *i.e.* in terms of probability distributions. [9](#)

**Bayesian inference** A specific statistical inference method that is based on the Bayes' theorem. [9](#)

**Bayesian integration** A probabilistic description for the integration of information with varying reliability. [9](#)

**de novo learning** A mechanism of acquiring a completely new skill, such as learning to ride a bike for the first time. [15](#)

**endpoint error** The predominant dependent error measure in the visuomotor rotation literature, defined as the hand angle at the end target radius relative to the aiming target location. [29](#)

**endpoint feedback** Visual feedback on a participant's reaching movement is only provided once the participant reached the end target threshold. For instance, this is done to investigate the feedforward component of adaptation only. [27](#)

**explicit aiming strategies** A component of adaptation that is characterised by a conscious and cognitively driven form of compensation for a perturbation. [19](#)

**feedback adaptation** A movement plan that integrates online sensory information to update the prior estimate in order to compute the best possible reaching movement. Here, only bottom-up sensory input is accounted for while the movement is conducted. [19](#)

**feedforward adaptation** A movement plan that was computed only based on the best estimate prior to the reaching movement. Here, only top-down knowledge is used to compute the best possible reach. [19](#)

**generalisation width** In a state-space model, a scalar parameter that controls the width of the Gaussian generalisation distribution to other targets for which a perturbation was not directly learned. [33](#)

**hand angle** The participant's hand position in space, in the context of a visuomotor rotation paradigm. Perturbations as well as target and hand position are indicated in degrees due to the radial setup of the paradigm. [17](#)

**implicit learning** A component of adaptation, characterised as an automatic and subconscious process of gradual, error-based movement adjustments in response to changes in the environment. [19](#)

**initial movement vector** A measure that captures a participant's initial impulsive direction of reach within a trial in visuomotor rotation paradigms. The error between initial movement vector and aiming target direction is therefore used to measure the feedforward component only in mixed feedback and feedforward designs. [29](#)

**learning rate** In a state-space model, a scalar parameter capturing how quickly learning occurs when updating to the next trial in response to the experienced error. [20](#)

**likelihood** In the Bayes' theorem, the likelihood captures the probability to observe some specific information given a specific prior estimate. [9](#)

**online correction** The process of correcting a movement based on incoming sensory information while the movement is being conducted. [19](#)

**online feedback** The process of providing visual feedback on a participant's hand position while the participant is performing a reach in a visuomotor rotation paradigm. Participants can thus perform online correction. [36](#)

**posterior** In the Bayes' theorem, the posterior is the probability of an estimate after information has been observed. It corresponds to the probability of the updated estimate. [9](#)

**predictive coding** A theory that implements the concept of unconscious inference in terms of neural information processing in perception. According to this framework, this is achieved by our brain constantly updating our best fitting 'internal model' of the world. [7](#)

**prior** In the Bayes' theorem, the prior refers to the probability of an estimate before new information has been observed. [9](#)

**probabilistic** Something is probabilistic when it is subject to uncertainty. The amount of uncertainty is captured in the variance. [10](#)

**reinforcement learning** A type of machine learning where the system learns from its own previous experiences when interacting with its environment. [12](#)

**sensorimotor adaptation** In sensorimotor learning, an error-based adjustment in already well practised behaviour as a reaction to a change in the environment or in our body. Its aim is to maintain the same performance level for a specific task under new circumstances. [14](#)

**sensorimotor learning** The improvement of a specific movement based on sensory input. [12](#)

**state-space models** A useful and predictively highly accurate formalisation of adaptation. They predict adapted behaviour on a trial by trial basis while accounting for typical properties of adaptation. However, they do not provide a mechanistic explanation. [20](#)

**supervised learning** A machine learning concept where the algorithm learns a function that maps inputs to outputs based on labelled training data. [12](#)

**unconscious inference** A theory in visual perception that states that previous knowledge is used to make predictions about the future. Those predictions are unconsciously integrated with sensory information to generate perception. [7](#)

**unsupervised learning** A type of machine learning where the algorithm solves clustering and association problems by finding hidden structures and patterns in unlabelled data. [12](#)

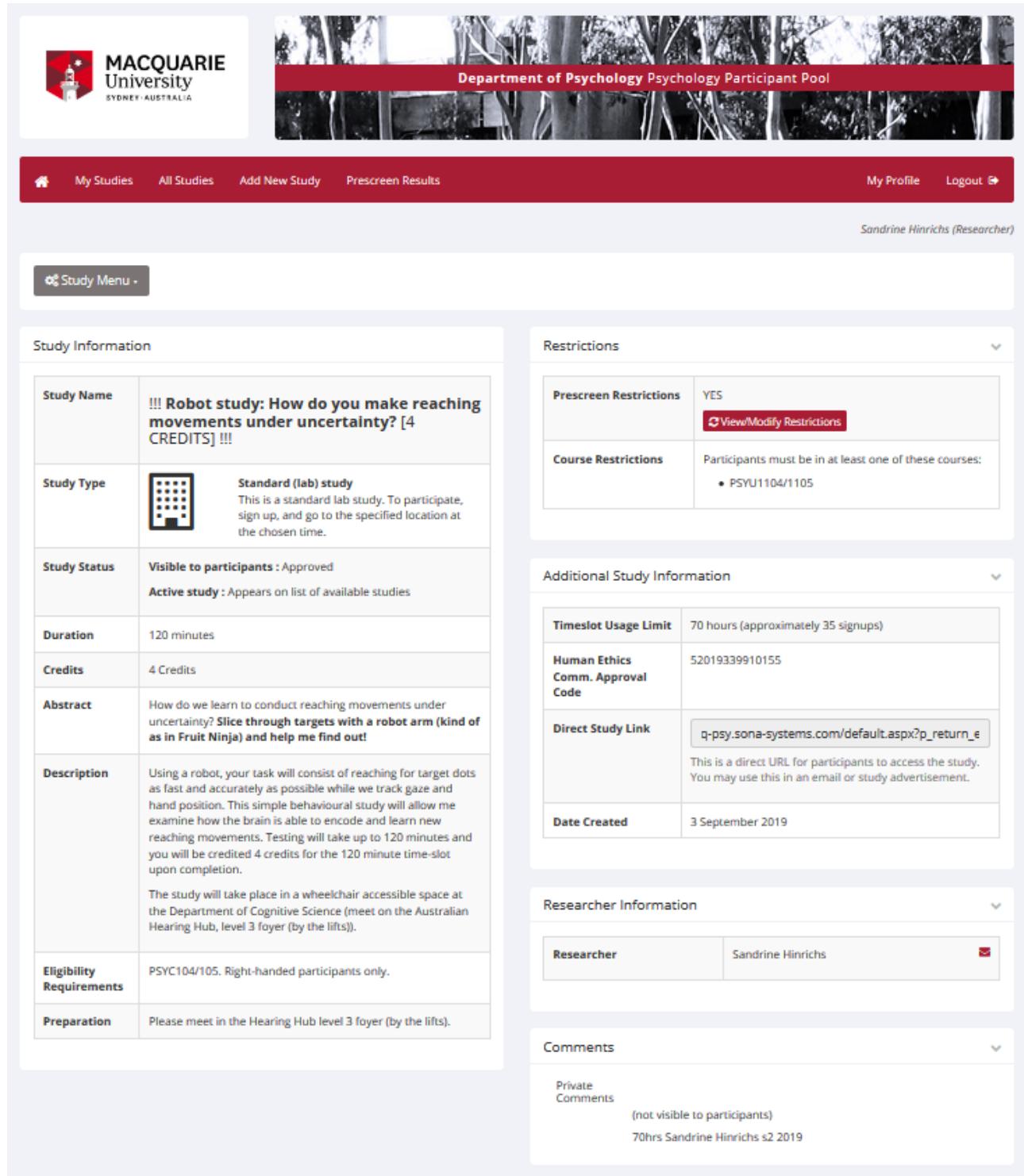
**use-dependent behaviour** The phenomenon that recent movements bias subsequent movements towards the original ones. [44](#)

**visuomotor rotation** An experimental adaptation paradigm where participants see a cursor instead of their real hand position while performing reaching movements. During a training block, the cursor feedback is rotated, thereby forcing participants to adapt to this perturbation. [16](#)

**washout rate** In a state-space model, a scalar parameter capturing how much is forgotten from the hand angle value from the previous state. It answers the question of how fast behavioural performance normalises back to baseline after the perturbation has been removed. Retention rate is the counterpart of the washout rate. [20](#)

# Appendices

## A Study Advertisement



The screenshot shows a study advertisement for a "Robot study: How do you make reaching movements under uncertainty? [4 CREDITS]".

**Study Information:**

- Study Name:** !!! Robot study: How do you make reaching movements under uncertainty? [4 CREDITS] !!!
- Study Type:** Standard (lab) study. This is a standard lab study. To participate, sign up, and go to the specified location at the chosen time.
- Study Status:** Visible to participants: Approved. Active study: Appears on list of available studies.
- Duration:** 120 minutes
- Credits:** 4 Credits
- Abstract:** How do we learn to conduct reaching movements under uncertainty? Slice through targets with a robot arm (kind of as in Fruit Ninja) and help me find out!
- Description:** Using a robot, your task will consist of reaching for target dots as fast and accurately as possible while we track gaze and hand position. This simple behavioural study will allow me examining how the brain is able to encode and learn new reaching movements. Testing will take up to 120 minutes and you will be credited 4 credits for the 120 minute time-slot upon completion.  
The study will take place in a wheelchair accessible space at the Department of Cognitive Science (meet on the Australian Hearing Hub, level 3 foyer (by the lifts)).
- Eligibility Requirements:** PSYC104/105. Right-handed participants only.
- Preparation:** Please meet in the Hearing Hub level 3 foyer (by the lifts).

**Restrictions:**

- Prescreen Restrictions:** YES. [View/Modify Restrictions](#)
- Course Restrictions:** Participants must be in at least one of these courses:  
• PSYU1104/1105

**Additional Study Information:**

- Timeslot Usage Limit:** 70 hours (approximately 35 signups)
- Human Ethics Comm. Approval Code:** 52019339910155
- Direct Study Link:** [q-psyc.sona-systems.com/default.aspx?p\\_return\\_e](http://q-psyc.sona-systems.com/default.aspx?p_return_e)  
This is a direct URL for participants to access the study. You may use this in an email or study advertisement.
- Date Created:** 3 September 2019

**Researcher Information:**

<b>Researcher:</b>	Sandrine Hinrichs <a href="#">✉</a>
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**Comments:**

Private Comments  
(not visible to participants)  
70hrs Sandrine Hinrichs s2 2019

Figure 23: Description of the study on the SONA participant pool platform.

## B Consent Form

DEPARTMENT OF  
COGNITIVE SCIENCE  
*Faculty of Human Sciences*

Macquarie University  
NSW 2109 Australia  
cogsci.mq.edu.au

ABN 90 952 801 237  
CRICOS Provider No 00002J



MACQUARIE  
University  
SYDNEY · AUSTRALIA

### Information and Consent Form (KINARM)

*Name of Project: Investigating cognitive mechanisms underlying visual, auditory, body-related information processing and sensorimotor learning.*

We are seeking healthy volunteers with normal or corrected-to-normal vision to participate in a study that investigates the cognitive mechanisms underlying visual processing, human sensorimotor learning, processing of body-related information and how such information modulates perception and action.

This research is being conducted by Ms. Sandrine Hinrichs and Mr. Chris Hewitson to meet the requirements of Masters of Research and PhD respectively under the supervision of Dr. David Kaplan [David.Kaplan@mq.edu.au] and Dr. Matthew Crossley [Matthew.Crossley@mq.edu.au] of the Department of Cognitive Science [ethics approval: 52019339910155]

In this experiment we use the KINARM End-Point Robot that can be programmed to create highly complex mechanical environments. A suite of position sensors and force/torque sensors embedded in the handle provide real time information about limb motion and forces. A visual display positioned at eye level will be used to present 2D targets that appear in the workspace plane.

If you decide to participate, you will be asked to view and respond to visual stimuli. You may be asked to provide reaching responses during the session. The responses you make and the timing associated with your responses will be collected. The experimental session may take up to 60 minutes to complete, and no risks are expected to result from participation.

If you are participating for course credit you will receive one credit for each half-hour of your participation. Alternatively, you will receive \$15 per hour (or pro rata) for your participation.

Any information or personal details (e.g. age, gender) gathered in the course of the study are kept confidential, except as required by law. No individual will be identified in any publication of the results. Access to the data is limited to persons directly involved in the research. Your individual de-identified (anonymised) data obtained through this research may be used in future research publications and be made available to journals/reviewers to support publications. At no time will you be identifiable in the publication or by the journal/reviewers. Any publication information will be provided in such a way that you cannot be identified.

A summary of the results of the data can be made available on request, please give an email address if you would like to receive this.

**Participation in this study is voluntary and you are free to withdraw from further participation in the research at any time without having to give a reason and without consequence. Macquarie University students who are participating as part of their course requirements will not forfeit their course credits if they choose to withdraw from the research.**

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# Impact of Uncertainty in Prior Knowledge on Adaptation

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DEPARTMENT OF  
COGNITIVE SCIENCE  
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ABN 90 952 801 237  
CRICOS Provider No 00002J



MACQUARIE  
University  
SYDNEY · AUSTRALIA

I, \_\_\_\_\_ have read (*or, where appropriate, have had read to me*) and understand the information above and any questions I have asked have been answered to my satisfaction. I agree to participate in this research, knowing that I can withdraw from further participation in the research at any time without consequence. I have been given a copy of this form to keep.

Participant's Name: \_\_\_\_\_

(Block letters)

Participant's Signature: \_\_\_\_\_ Date: \_\_\_\_\_

Investigator's Name: \_\_\_\_\_

(Block letters)

Investigator's Signature: \_\_\_\_\_ Date: \_\_\_\_\_

The ethical aspects of this study have been approved by the Macquarie University Human Research Ethics Committee. If you have any complaints or reservations about any ethical aspect of your participation in this research, you may contact the Committee through the Director, Research Ethics & Integrity (telephone (02) 9850 7854; email [ethics@mq.edu.au](mailto:ethics@mq.edu.au)). Any complaint you make will be treated in confidence and investigated, and you will be informed of the outcome.

**(INVESTIGATOR'S [OR PARTICIPANT'S] COPY)**



## C Eye Tracking Calibration

Sub	Min Error	Max Error	Grading
1	0.5	1.6	fair
2	1	2.6	poor
3	0.5	1.1	good
4	0.7	1.1	good
5	0.6	1.4	good
6	1.2	4.5	poor
7	0.7	1.4	good
8	-	-	Calibration not possible (dark eyes)
9	0.8	2	poor
10	1.8	5.5	poor
11	0.5	0.9	good
12	0.7	1.6	fair
13	1.4	3.1	poor
14	0.6	1.2	good
15	0.9	1.2	good
16	0.8	1.4	good
17	0.7	2.2	poor
18	-	-	Calibration not possible (glasses)
19	0.6	1.1	good
20	1	4.1	poor
21	0.4	1.2	good
22	0.8	1.3	good
23	0.6	1.4	good
24	0.8	1.4	good
25	-	-	Calibration not possible (errors greater than 50)
26	0.6	1	good
27	0.6	1.5	good
28	0.8	1.5	fair
29	0.6	1.2	good
30	0.9	1.3	good
31	0.5	1.1	good
32	0.7	1.5	good
33	1	2.3	poor
34	0.7	1.1	good
35	0.6	1	good
36	1.7	3.7	poor
37	0.8	1.3	good
38	0.5	1.1	good
39	0.6	1.2	good
40	1.2	4.2	poor
41	0.8	1.4	good
42	-	-	Calibration not possible (almost closed eyes)
43	0.7	1.4	good

44	0.9	1.8	fair
45	0.8	1.2	good
46	0.6	1.1	good
47	0.7	1.4	good
48	-	-	Calibration not possible (glasses)

---

Table 4: Eye tracking calibration errors and ratings for all 48 participants included in the analysis.

## D Overview Missing Values

Sub	Prebase	Famil	Base	BaseNFB	Postbase	Train	Relearn	Washout
1	1 (1%)	3 (2%)	0 (0%)	1 (0%)	2 (2%)	9 (2%)	1 (1%)	0 (0%)
2	6 (5%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	19 (5%)	10 (10%)	1 (1%)
3	4 (3%)	1 (1%)	0 (0%)	5 (2%)	1 (1%)	3 (1%)	1 (1%)	0 (0%)
4	4 (3%)	0 (0%)	0 (0%)	4 (2%)	1 (1%)	1 (0%)	0 (0%)	0 (0%)
5	3 (2%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	2 (0%)	0 (0%)	0 (0%)
6	3 (2%)	4 (3%)	0 (0%)	4 (2%)	2 (2%)	14 (4%)	2 (2%)	0 (0%)
7	1 (1%)	1 (1%)	0 (0%)	1 (0%)	1 (1%)	2 (0%)	0 (0%)	0 (0%)
8	3 (2%)	0 (0%)	0 (0%)	3 (1%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
9	4 (3%)	4 (3%)	0 (0%)	0 (0%)	0 (0%)	8 (2%)	0 (0%)	0 (0%)
10	4 (3%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
11	1 (1%)	0 (0%)	0 (0%)	2 (1%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
12	3 (2%)	1 (1%)	0 (0%)	0 (0%)	0 (0%)	6 (2%)	1 (1%)	0 (0%)
13	4 (3%)	3 (2%)	0 (0%)	1 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
14	2 (2%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	2 (0%)	0 (0%)	0 (0%)
15	10 (8%)	1 (1%)	0 (0%)	0 (0%)	0 (0%)	5 (1%)	3 (3%)	3 (3%)
16	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (1%)	21 (5%)	0 (0%)	0 (0%)
17	4 (3%)	1 (1%)	0 (0%)	2 (1%)	2 (2%)	2 (0%)	0 (0%)	0 (0%)
18	1 (1%)	0 (0%)	0 (0%)	2 (1%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
19	7 (6%)	0 (0%)	0 (0%)	0 (0%)	2 (2%)	14 (4%)	2 (2%)	0 (0%)
20	2 (2%)	0 (0%)	0 (0%)	1 (0%)	0 (0%)	3 (1%)	2 (2%)	0 (0%)
21	2 (2%)	0 (0%)	0 (0%)	3 (1%)	0 (0%)	12 (3%)	0 (0%)	0 (0%)
22	2 (2%)	2 (2%)	0 (0%)	0 (0%)	3 (2%)	8 (2%)	0 (0%)	0 (0%)
23	6 (5%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	3 (1%)	0 (0%)	0 (0%)
24	6 (5%)	3 (2%)	0 (0%)	2 (1%)	2 (2%)	28 (7%)	0 (0%)	0 (0%)
25	0 (0%)	0 (0%)	0 (0%)	0 (0%)	3 (2%)	4 (1%)	0 (0%)	0 (0%)
26	1 (1%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	2 (0%)	0 (0%)	1 (1%)
27	4 (3%)	7 (6%)	0 (0%)	2 (1%)	2 (2%)	4 (1%)	1 (1%)	0 (0%)
28	1 (1%)	2 (2%)	0 (0%)	1 (0%)	1 (1%)	0 (0%)	0 (0%)	2 (2%)
29	2 (2%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	2 (0%)	0 (0%)	0 (0%)
30	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	2 (0%)	0 (0%)	0 (0%)
31	1 (1%)	3 (2%)	0 (0%)	0 (0%)	0 (0%)	3 (1%)	0 (0%)	0 (0%)
32	3 (2%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (0%)	0 (0%)	3 (3%)
33	1 (1%)	3 (2%)	0 (0%)	6 (2%)	10 (8%)	22 (6%)	2 (2%)	0 (0%)
34	8 (7%)	1 (1%)	0 (0%)	4 (2%)	4 (3%)	2 (0%)	1 (1%)	0 (0%)
35	3 (2%)	0 (0%)	0 (0%)	1 (0%)	4 (3%)	3 (1%)	0 (0%)	1 (1%)
36	1 (1%)	1 (1%)	0 (0%)	1 (0%)	1 (1%)	6 (2%)	0 (0%)	1 (1%)
37	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
38	7 (6%)	1 (1%)	0 (0%)	1 (0%)	2 (2%)	12 (3%)	0 (0%)	2 (2%)
39	4 (3%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
40	3 (2%)	1 (1%)	0 (0%)	1 (0%)	2 (2%)	20 (5%)	3 (3%)	1 (1%)
41	3 (2%)	2 (2%)	0 (0%)	1 (0%)	0 (0%)	6 (2%)	0 (0%)	0 (0%)
42	1 (1%)	2 (2%)	0 (0%)	1 (0%)	1 (1%)	5 (1%)	0 (0%)	0 (0%)
43	2 (2%)	0 (0%)	0 (0%)	2 (1%)	0 (0%)	1 (0%)	0 (0%)	0 (0%)
44	0 (0%)	1 (1%)	0 (0%)	1 (0%)	3 (2%)	15 (4%)	2 (2%)	2 (2%)

## Impact of Uncertainty in Prior Knowledge on Adaptation

<b>Sub</b>	<b>Prebase</b>	<b>Famil</b>	<b>Base</b>	<b>BaseNFB</b>	<b>Postbase</b>	<b>Train</b>	<b>Relearn</b>	<b>Washout</b>
45	1 (1%)	0 (0%)	0 (0%)	1 (0%)	1 (1%)	0 (0%)	0 (0%)	1 (1%)
46	3 (2%)	0 (0%)	0 (0%)	0 (0%)	4 (3%)	2 (0%)	0 (0%)	1 (1%)
47	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
48	0 (0%)	2 (2%)	0 (0%)	0 (0%)	1 (1%)	0 (0%)	0 (0%)	0 (0%)

Table 5: Number of missing values per phase for all phases, except generalisation. Participants were excluded if missing values exceeded a value of 10% in at least one phase.

<b>Sub</b>	<b>-150</b>	<b>-120</b>	<b>-90</b>	<b>-60</b>	<b>-30</b>	<b>0</b>	<b>30</b>	<b>60</b>	<b>90</b>	<b>120</b>	<b>150</b>
1	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0
3	0	1	0	1	0	1	0	0	0	0	0
4	0	0	0	0	0	0	0	0	1	0	0
5	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	1	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0
19	1	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	1	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0

32	0	0	0	0	0	0	0	0	0	0	1
33	0	0	0	0	0	0	0	0	0	0	0
34	1	1	0	0	0	0	1	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	1	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0
44	0	0	1	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0

Table 6: Number of missing values per target during generalisation. In contrast to the other phases, a more restrictive tolerance threshold of 1 missing value per target was chosen for the generalisation phase. This was due to the small number of trials per target.

## E Two-State Space Model Parameters

Group	$\alpha_s$	$\alpha_f$	$\beta_s$	$\beta_f$	$\sigma_{\theta,s}$	$\sigma_{\theta,f}$
CW, $0^\circ\sigma$	0.14 [0.07, 0.22]	0.27 [0.14, 0.45]	1.00 [1.00, 1.00]	0.75 [0.26, 1.00]	58.58 [53.79, 59.97]	8.11 [0.54, 19.32]
CW, $4^\circ\sigma$	0.11 [0.09, 0.14]	0.18 [0.13, 0.24]	1.00 [1.00, 1.00]	0.19 [0.01, 0.50]	49.07 [37.04, 59.81]	23.95 [0.94, 58.29]
CW, $12^\circ\sigma$	0.05 [0.04, 0.07]	0.18 [0.14, 0.21]	1.00 [1.00, 1.00]	0.47 [0.30, 0.63]	35.04 [26.10, 47.95]	18.44 [0.92, 55.71]
CCW, $0^\circ\sigma$	0.14 [0.04, 0.24]	0.23 [0.13, 0.39]	0.99 [0.99, 1.00]	0.87 [0.26, 0.99]	32.40 [8.14, 57.98]	15.57 [0.76, 57.05]
CCW, $4^\circ\sigma$	0.13 [0.06, 0.17]	0.18 [0.12, 0.25]	0.99 [0.99, 1.00]	0.33 [0.04, 0.98]	20.97 [13.05, 45.93]	28.59 [1.53, 58.51]
CCW, $12^\circ\sigma$	0.08 [0.06, 0.10]	0.17 [0.14, 0.20]	0.99 [0.98, 0.99]	0.36 [0.17, 0.54]	20.63 [15.38, 26.81]	34.95 [3.18, 58.81]

Table 7: Means and [CIs] for each model parameter estimate, respectively. Estimates are the group mean estimates from the bootstrap estimated sampling distribution.

Group	$R^2$ [CI]
CW, $0^\circ\sigma$	0.35 [0.32, 0.35]
CW, $4^\circ\sigma$	0.39 [0.39, 0.39]
CW, $12^\circ\sigma$	0.36 [0.35, 0.36]
CCW, $0^\circ\sigma$	0.36 [0.34, 0.36]
CCW, $4^\circ\sigma$	0.30 [0.29, 0.30]
CCW, $12^\circ\sigma$	0.26 [0.25, 0.26]

Table 8:  $R^2$ -values for each group model fit, respectively.

## F Questionnaire Explicit Strategies

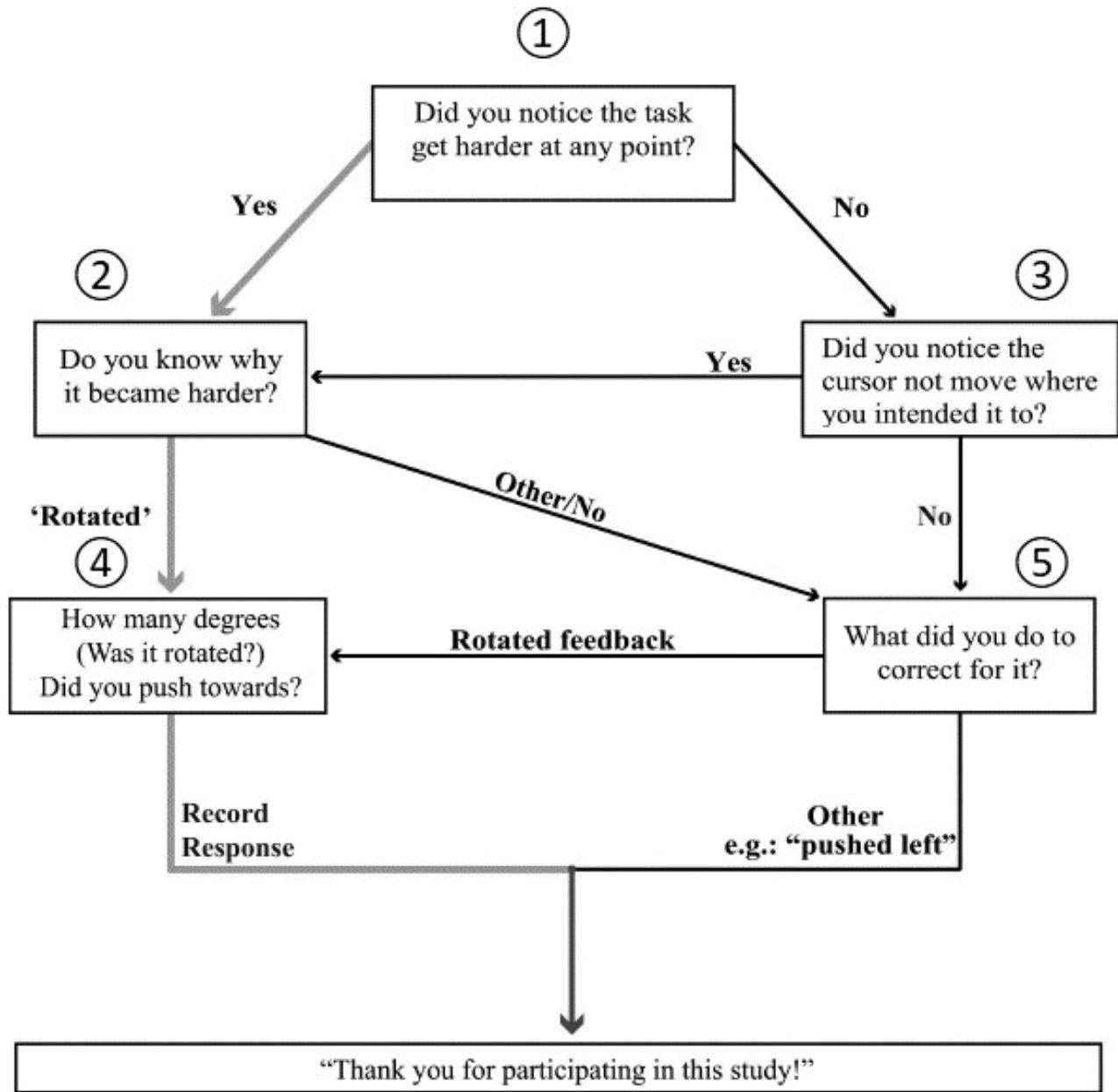


Figure 24: Awareness questionnaire to infer the use of explicit strategies. Questions and procedure followed the description of Benson et al. (2011). Adapted from Benson et al. (2011).

## Impact of Uncertainty in Prior Knowledge on Adaptation

Sub	Q1	Q2	Q3	Q4	Q5	Final
1	1	shifted	-	yes, slightly shifted move to the right 30°	-	explicit
2	1	more difficult every time, leftwards shift	-	-	-	explicit
3	1	difficult because of frequency	-	-	going right	explicit ? (wrong side)
4	1	focusing on many things, natural attention span	-	-	gather focus	implicit
5	1	right- or leftwards shift; due to perception and the paradigm	-	10-15°	pushed to the opposite side	explicit
6	0	-	slightly, but only due to perception	-	moving in a circle	implicit
7	1	-	wonky, but just due to my coordination	-	-	implicit ?
8	1	0	-	-	replicate same movement	implicit
9	1	Training, externally imposed leftwards shift	-	pushed toward the right went to the right	12° 15°	explicit
10	0	-	shifted, but that was probably just me	-	replicate same movement the way I was holding it	explicit
11	1	when I wasn't able to see the dot	-	-	only focused on dot	implicit
12	1	notice some shift	-	-	0	implicit
13	1	when exposed to fb	-	-	memorize centre	implicit
14	0	-	0	-	went to the right	explicit
15	0	-	0	-	reacting to visual input	implicit
16	0	felt as if dot went left, but assumed it was me	1	-	pushed to the left	explicit ? (wrong side)
17	1	training block was more tiring and baseline was difficult	-	-	-	explicit ?
18	1	Feedback was manipulated to the right	1	-	-	explicit
19	0	cursor randomly shifted to right or left	1	20°; change grip and shift	-	explicit
20	0	-	leftwards shift, but it was definitively me!	-	0	explicit ?
21	1	because of time and fatigue, harder when nfb, shift in training	-	-	focus on the dot, use less vision	implicit ?
22	1	feeling of loosing direction with the Training block, but dont know why	-	-	follow circle back to the center	implicit
23	1	when nfb	-	-	replicate same movement	implicit
24	1	training block, find the reaching direction	-	push right to adjust	12.25°	explicit
25	1	fatigue, no ther reason	-	-	0	implicit
26	1	when nfb, easier when moving only to one target	-	-	0	implicit
27	1	fatigue	-	-	0	implicit
28	0	cursor appeared left of target	-	5-10° shifted, push right	-	explicit
29	1	training block easy (probably because you can see where your hand is going)	1	adapt, but thought it was me	0	explicit ?
30	1	Training Block, accuracy was off, could not hit it properly	shifted fb, but it was just me	-	0	explicit ?
31	0	when nfb and also training (because it's repetetive)	felt like a leftwards shift, but not really sure	25 / 30°, push other direction	replicate same movement replicate same movement	explicit
32	0	0	-	-	replicate same movement	implicit
33	1	when nfb, got distracted by white dot, blocks with 12 targets more difficult	leftwards shift, probably due to perception	25 / 35°	push to the right	explicit
34	1	when nfb, shift in training and last two blocks (both sides)	slight shift, but think it's me, very sceptical	-	twist my arm	explicit ?
35	0	-	my judgement was off, it was in line, I was bad at it	-	not really, focusing the cursor	implicit
36	0	-	0	-	0	implicit
37	1	when blocks are longer, not noticing when there was fb / nfb	-	-	not really, loop movement	implicit
38	1	fatigue	sometimes I didn't see it move	-	push to the right because was easier than to hitting the target	implicit
39	1	blocks without nfb	0	-	0	implicit
40	1	fatigue	1	Leftwards shift, 15°	pushing to the right	explicit
41	1	when nfb, fatigue	1	Leftwards shift, push to the right, due to perception	reaching further	explicit ?
42	0	1	random shift, no specific side, due to perception	changing: 5, 10, 15°	0	implicit ?
43	1	when nfb	random shift in training, probably me	-	0	implicit ?
44	1	Training was harder, feeling of being more inacurate, but thought it was me	cursor appeared right	push to the left	0	explicit
45	1	fatigue	1	leftwards shift (20-30°) 10-45° shift	pushed to the right pushed to the left	explicit
46	1	in Training, fb was shifted to the right	-	-	-	explicit ? (wrong side)
47	1	fatigue, too much focus	in all blocks, mostly in training randomly shifted fb	10° shift	push to the opposite side	explicit
48	0	Training block, leftwards shift; due to perception	-	between 0 and 10°	push to the right	explicit ? (wrong side)

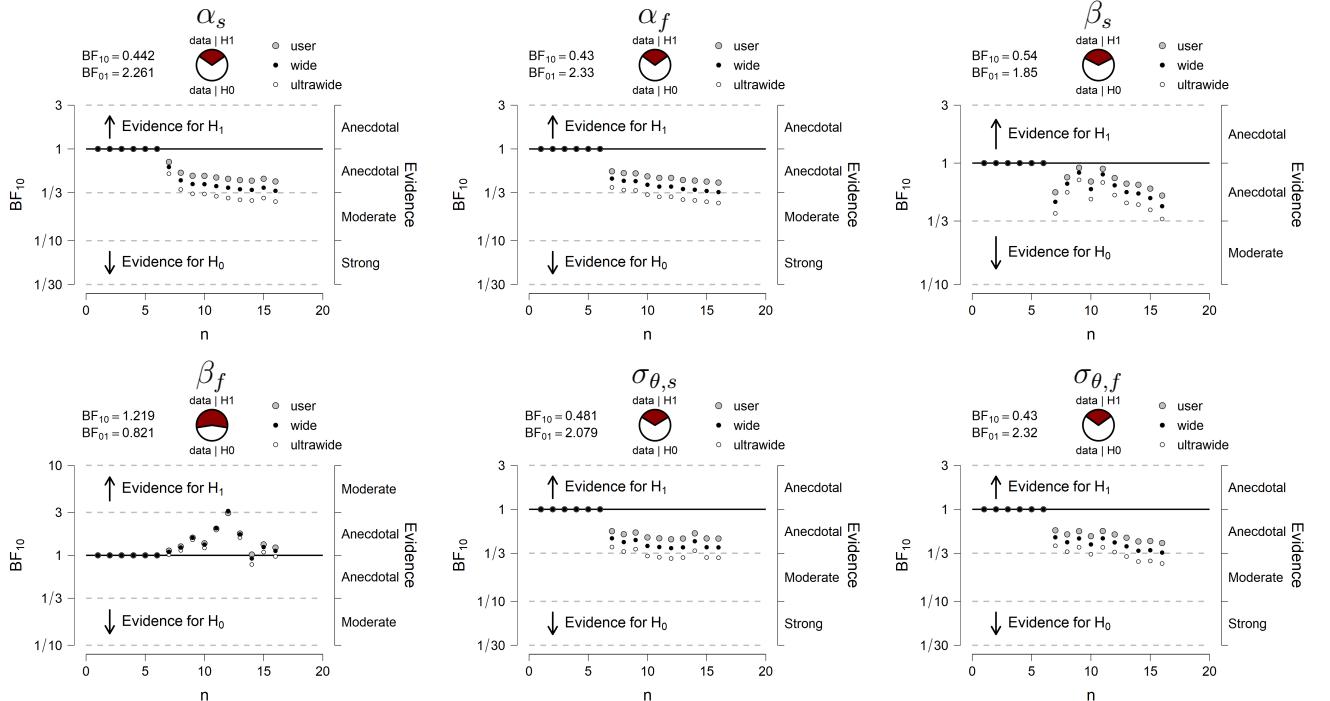
Table 9: Awareness questionnaire answers. Question numbers correspond to the numbers in the schematics from Benson et al. (2011) (see Figure 24). A participant was rated as explicit when question 1, 2 and 4 (grey) were answered similar to the answers provided in the flowchart. The answer “yes” was coded as 1 and “no” as 0. Question marks indicate that a participant’s answers were ambiguous.

## G Results Bayes Factor Analysis

### G.1 CW vs. CCW

	$0^\circ\sigma$		$4^\circ\sigma$		$12^\circ\sigma$			
	$BF_{10}$	error %	$BF_{10}$	error %	$BF_{10}$	error %		
alpha_s	0.442	2.136e-5	alpha_s	0.595	0.020	alpha_s	0.924	0.005
alpha_f	0.430	4.250e-7	alpha_f	0.456	0.011	alpha_f	0.472	3.852e-5
beta_s	0.540	0.002	beta_s	0.581	0.019	beta_s	0.693	0.001
beta_f	1.219	4.513e-4	beta_f	0.475	0.012	beta_f	0.527	0.001
g_sigma_s	0.481	9.498e-8	g_sigma_s	0.822	0.007	g_sigma_s	0.486	5.379e-6
g_sigma_f	0.430	6.572e-7	g_sigma_f	0.523	0.014	g_sigma_f	0.725	0.004

Table 10: Bayesian Independent Samples T-Test: CW vs. CCW.

Figure 25: BF sequential analysis plots for each model parameter, respectively, for the CW vs. CCW comparison in the  $0^\circ\sigma$  group.

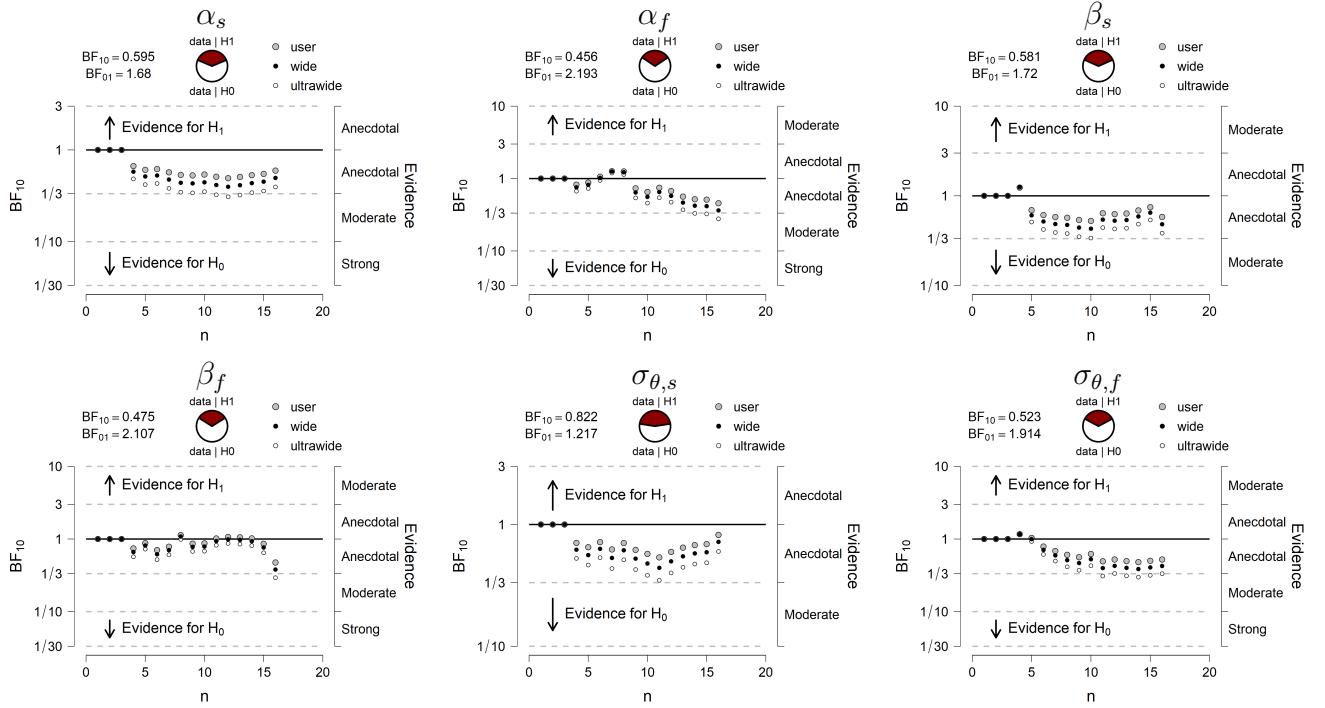


Figure 26: BF sequential analysis plots for each model parameter, respectively, for the CW vs. CCW comparison in the  $4^\circ\sigma$  group.

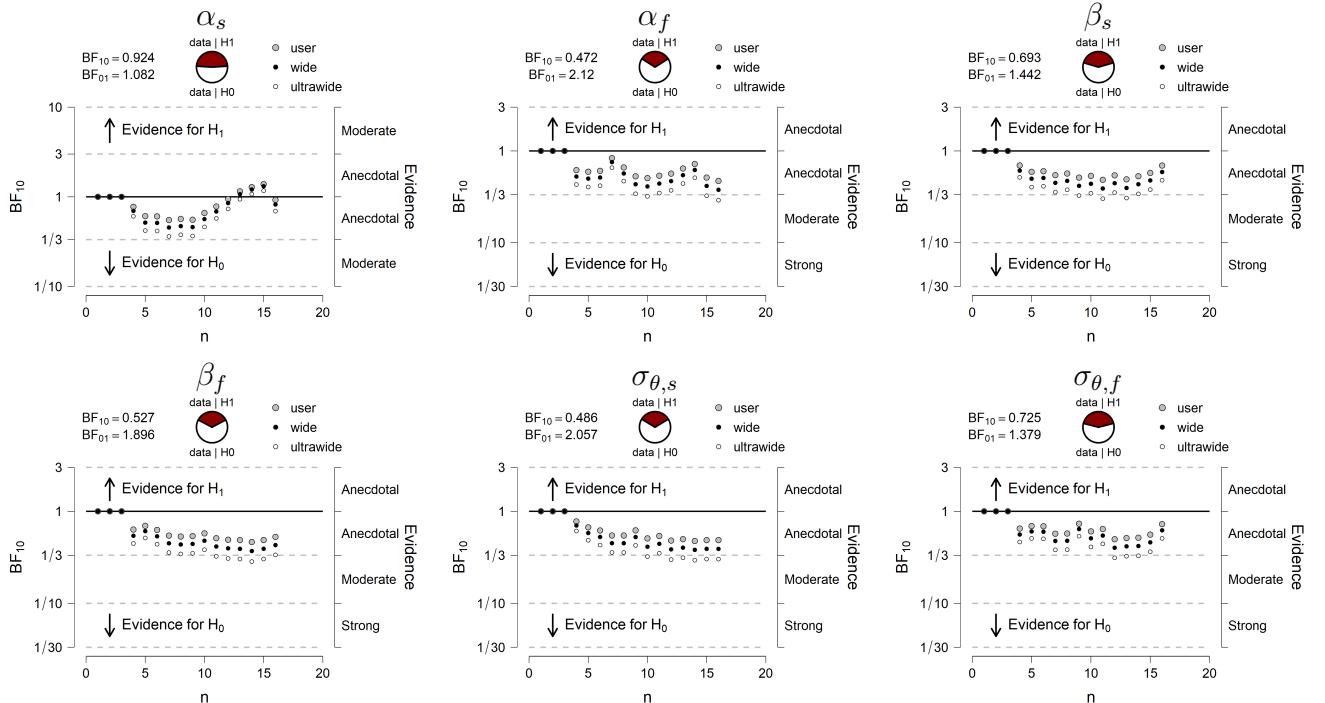


Figure 27: BF sequential analysis plots for each model parameter, respectively, for the CW vs. CCW comparison in the  $12^\circ\sigma$  group.

G.2  $0^\circ\sigma$  vs.  $4^\circ\sigma$ 

CW		CCW		
	BF <sub>+0</sub>	error %	BF <sub>+0</sub>	error %
alpha_s	0.282	0.009	alpha_s	0.349
alpha_f	0.248	0.003	alpha_f	0.239
beta_s	0.459	0.018	beta_s	0.419
g_sigma_s	0.933	1.519e-5	g_sigma_s	0.442
beta_f	0.516	0.020	beta_f	0.504
g_sigma_f	0.624	0.018	g_sigma_f	0.424

Table 11: Bayesian Independent Samples T-Test:  $0^\circ\sigma$  vs.  $4^\circ\sigma$ . Note: For  $\alpha$ , the alternative hypothesis specifies that group 0 is greater than group 1.

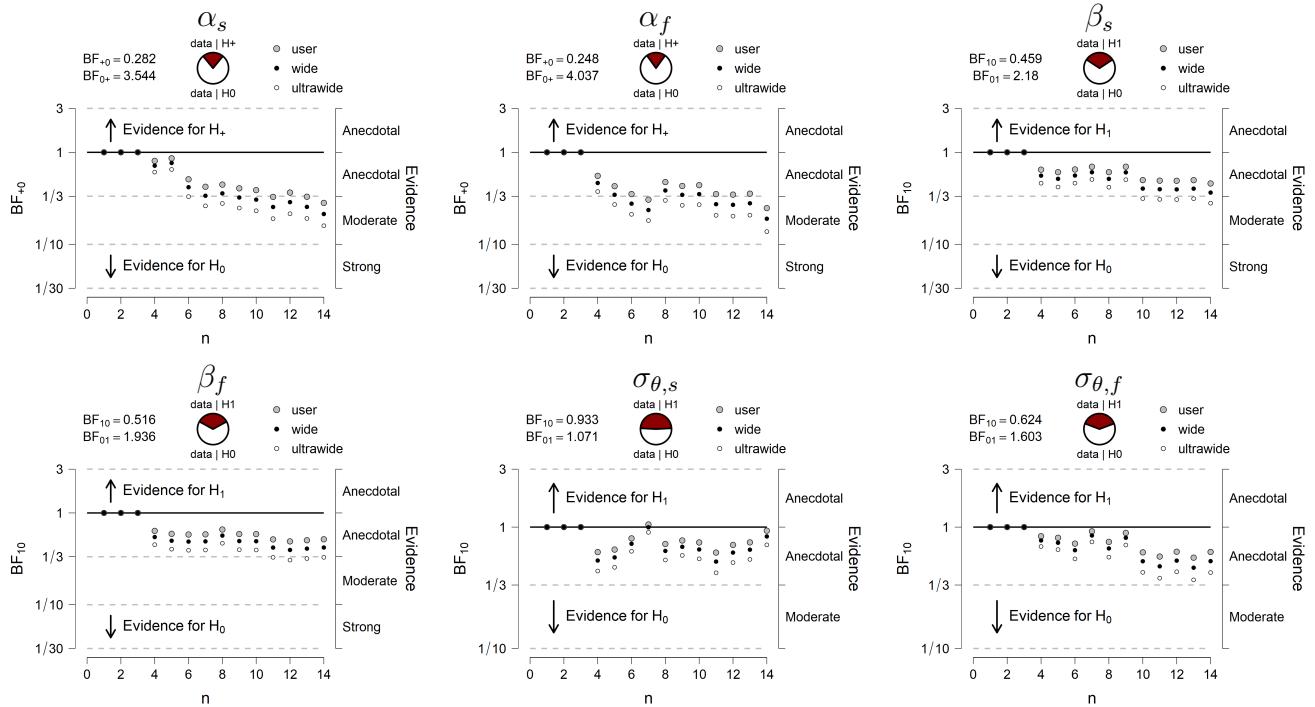


Figure 28: BF sequential analysis plots for each model parameter, respectively, for the  $0^\circ$  vs.  $4^\circ\sigma$  comparison in the CW group.

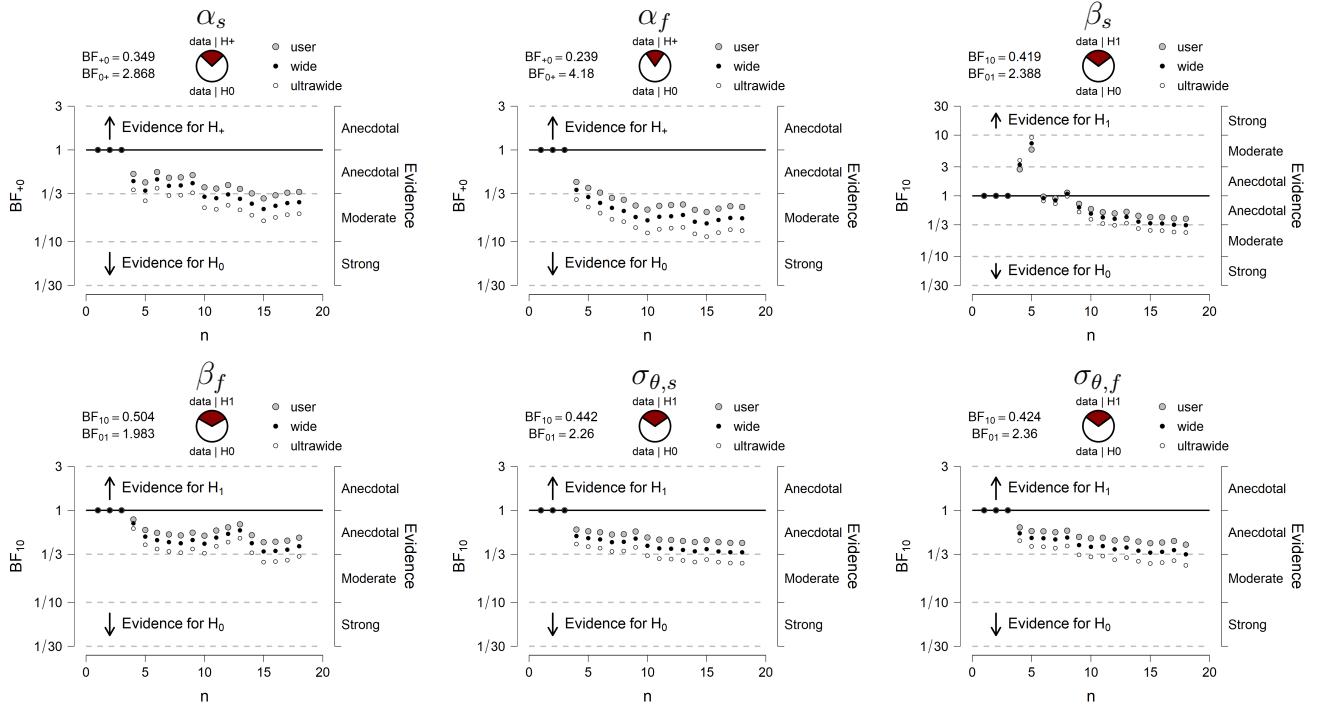


Figure 29: BF sequential analysis plots for each model parameter, respectively, for the  $0^\circ$  vs.  $4^\circ\sigma$  comparison in the CCW group.

### G.3 $0^\circ\sigma$ vs. $12^\circ\sigma$

	CW		CCW		
	BF <sub>+0</sub>	error %	BF <sub>+0</sub>	error %	
alpha_s	0.810	0.007	alpha_s	0.301	0.013
alpha_f	0.256	0.003	alpha_f	0.252	0.004
beta_s	0.453	6.372e-5	beta_s	0.534	0.018
g_sigma_s	0.405	5.183e-6	g_sigma_s	0.458	0.014
beta_f	1.178	0.004	beta_f	0.584	0.019
g_sigma_f	0.702	0.001	g_sigma_f	0.461	0.014

Table 12: Bayesian Independent Samples T-Test:  $0^\circ\sigma$  vs.  $12^\circ\sigma$ . Note: For  $\alpha$ , the alternative hypothesis specifies that group 0 is greater than group 1.

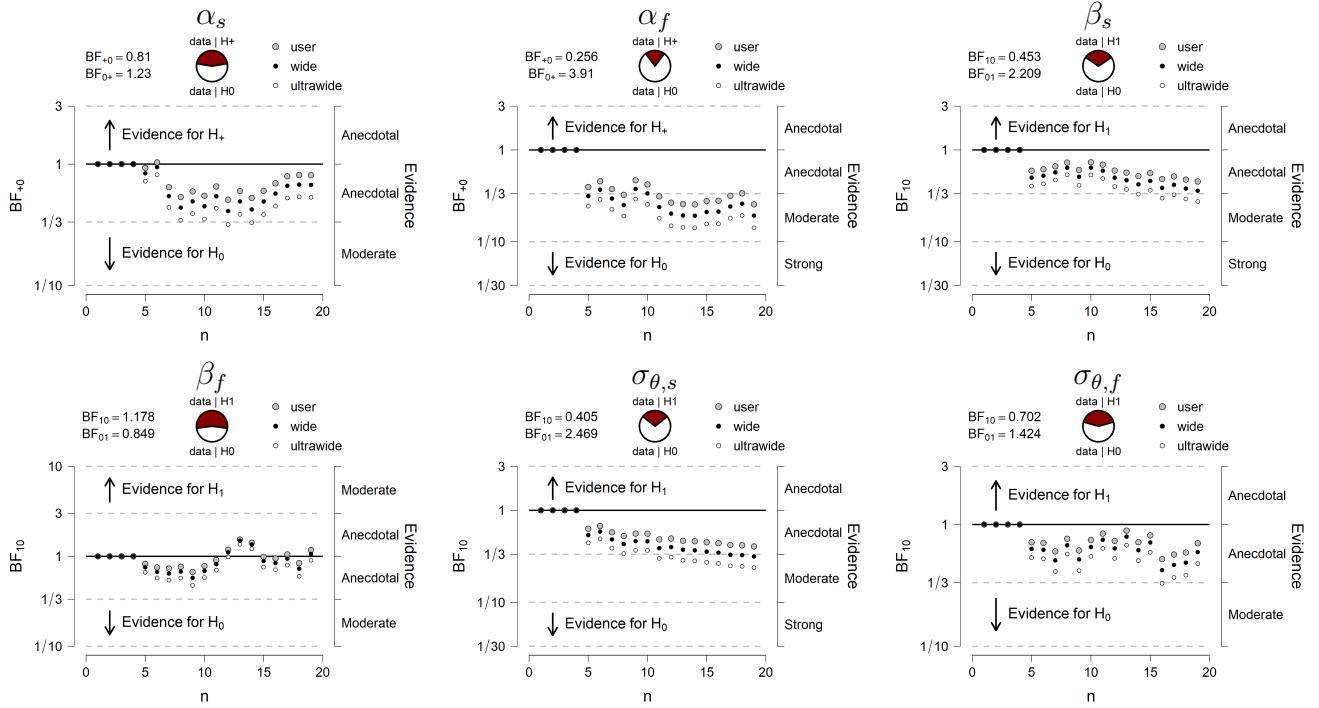


Figure 30: BF sequential analysis plots for each model parameter, respectively, for the  $0^\circ$  vs.  $12^\circ\sigma$  comparison in the CW group.

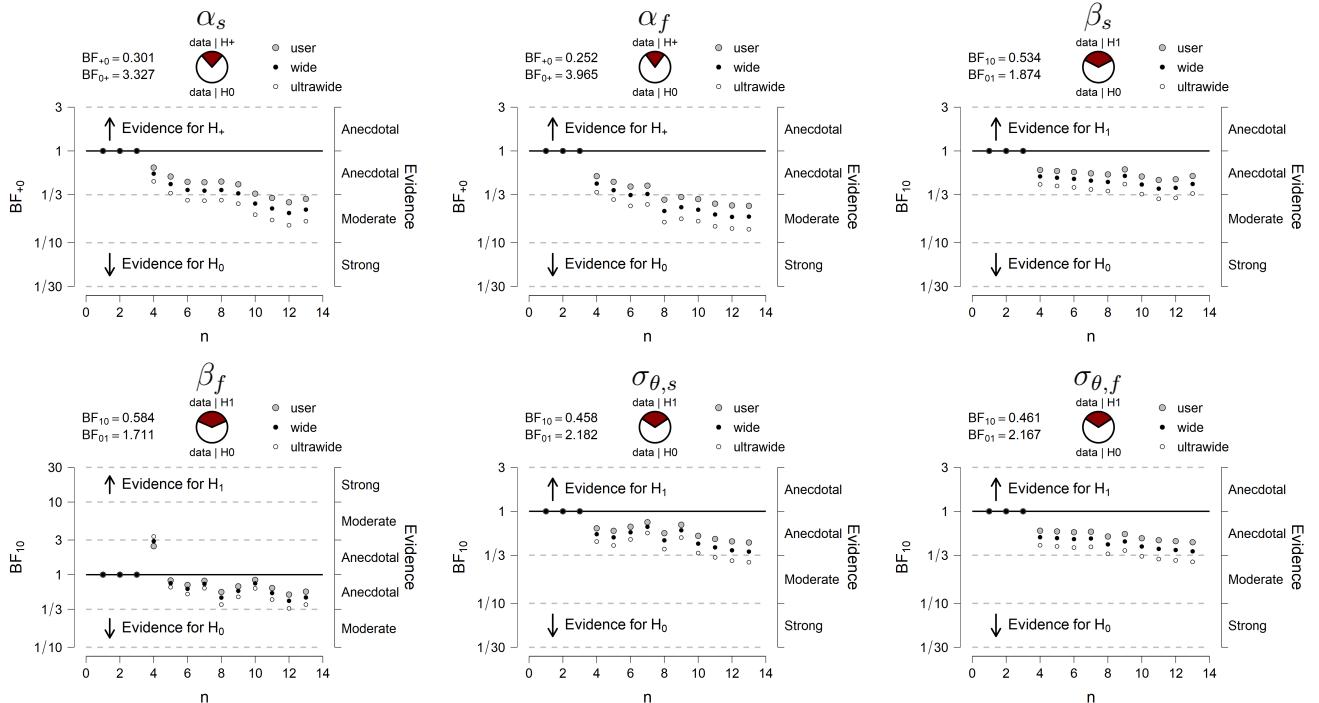


Figure 31: BF sequential analysis plots for each model parameter, respectively, for the  $0^\circ$  vs.  $12^\circ\sigma$  comparison in the CCW group.

G.4  $4^\circ\sigma$  vs.  $12^\circ\sigma$ 

CW		CCW		
	BF <sub>+0</sub>	error %	BF <sub>+0</sub>	error %
alpha_s	3.444	4.811e-4	alpha_s	0.322
alpha_f	0.608	9.521e-6	alpha_f	0.367
beta_s	0.505	1.642e-4	beta_s	0.676
g_sigma_s	0.776	0.008	g_sigma_s	0.654
beta_f	0.541	0.001	beta_f	0.488
g_sigma_f	0.453	1.466e-4	g_sigma_f	0.444

Table 13: Bayesian Independent Samples T-Test:  $4^\circ\sigma$  vs.  $12^\circ\sigma$ . Note: For  $\alpha$ , the alternative hypothesis specifies that group 0 is greater than group 1.

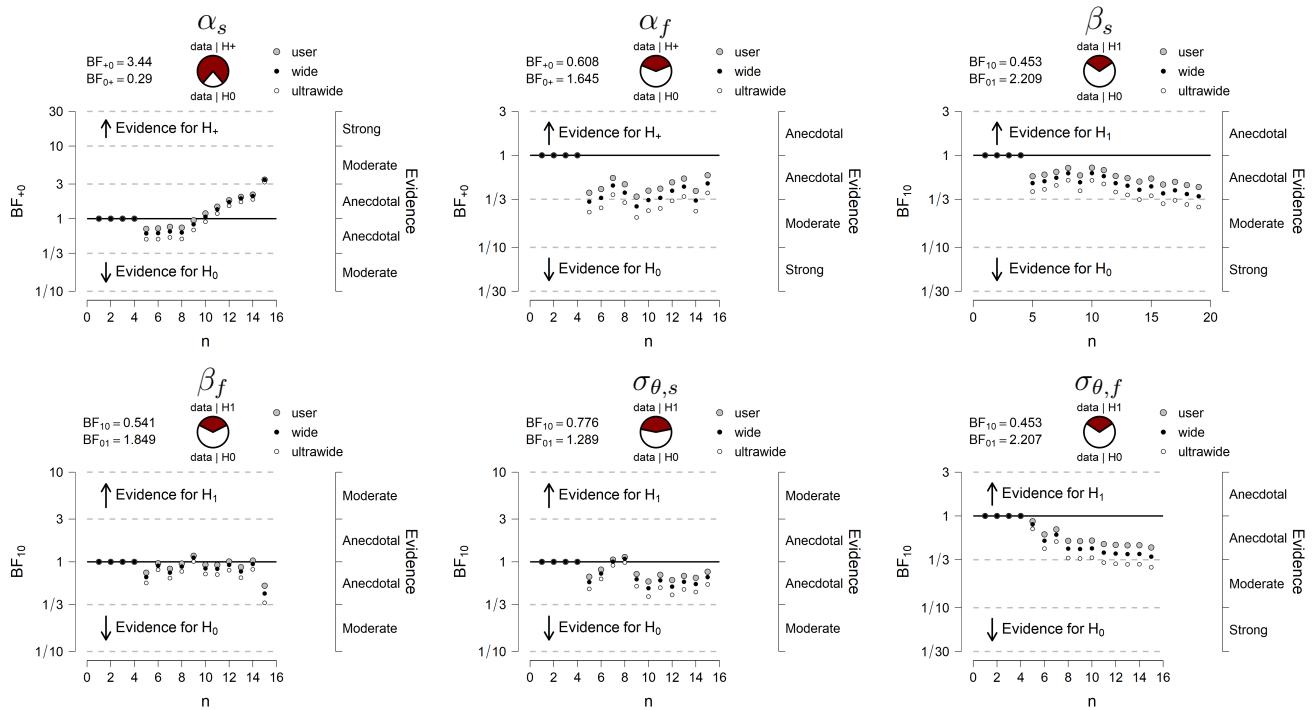


Figure 32: BF sequential analysis plots for each model parameter, respectively, for the  $0^\circ$  vs.  $12^\circ\sigma$  comparison in the CW group.

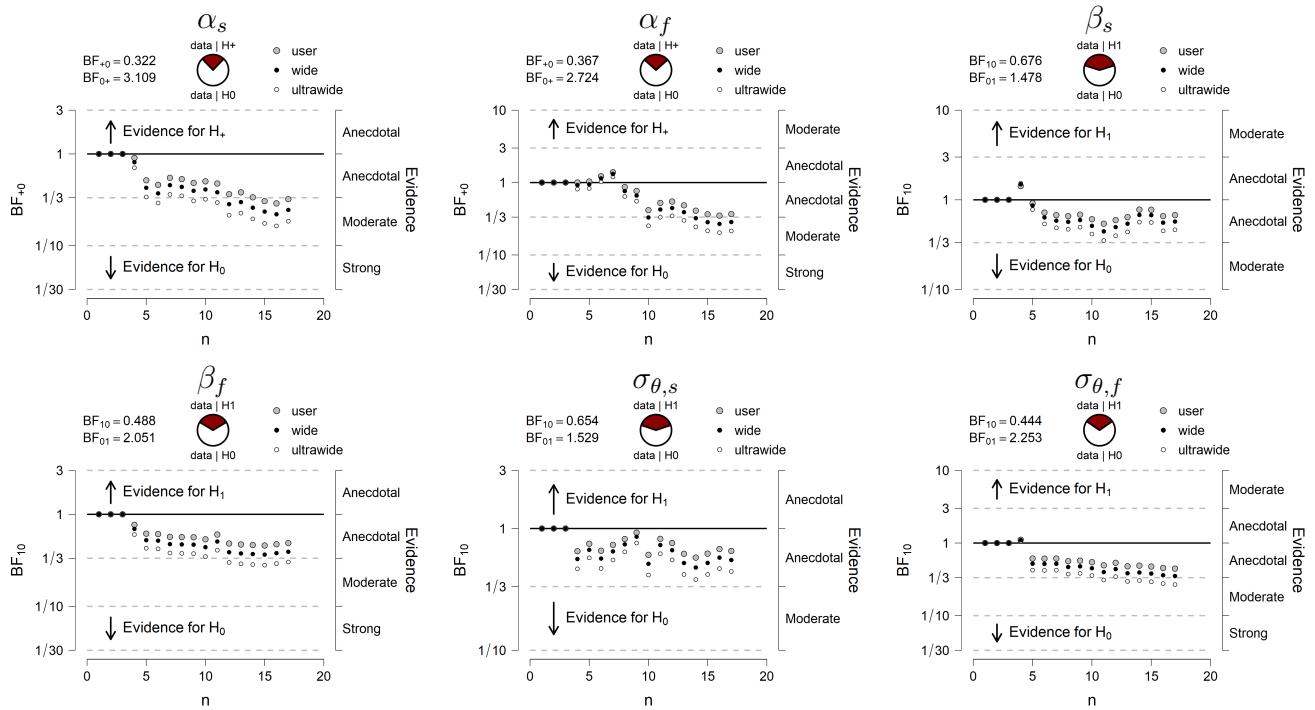


Figure 33: BF sequential analysis plots for each model parameter, respectively, for the  $0^\circ$  vs.  $12^\circ\sigma$  comparison in the CCW group.

## 8 Acknowledgements

Probably one of the most important lessons I learned from work on my master thesis on a personal level is that such a thesis is far less the result of one single person (in this case, me), but rather of a wide range of inspiring interactions with different people. Acknowledging everybody who contributed is therefore extremely important to me and, even though the list of people here is certainly not exhaustive, I try my best to be as including as possible.

Of course my first giant thank you goes to the whole team that made this research for my master thesis possible in the first place. This includes my research team in Sydney, my official supervisors in Göttingen as well as everyone involved in the organisational process who helped me making this tremendously valuable experience of a research exchange semester at the other end of the world come true. The fact that my research was conducted abroad put me in the fortunate position of having not two but five supervisors (Dr. David Kaplan, Dr. Matthew Crossley, adjunct Prof. Dr. York Hagemayer, Prof. Dr. Michael Waldmann as well as my unofficial supervisor Christopher Hewitson).

David's lab was, I believe, the closest to a perfect research environment for a young and curious Master's degree student to flourish: interdisciplinary, challenging, supportive, appreciative, full of scientific curiosity and ambition, to name but a few characteristics that I highly appreciated. In particular, I would like to thank David for welcoming me so warmly as a research student in his research empire, Matt for helping me to deal with all this goofiness in the world (especially the part of it that is hiding in code and data), Chris for being the best "kind of supervisor" with whom I spent numerous philosophical debugging nights in the KINARM lab as well as Eduardo who turned data acquisition into inspiring hours of fun. All the knowledge contained in this thesis is knowledge I acquired through the experience of studying in their lab. This thesis is therefore as much their work as it is mine. I was incredibly fortunate to be part of this team.

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I also thought about mentioning all the other amazing people whose conversations during my stay in Australia deeply inspired my way to think, and with it, my thesis. But there are simply too many of them. Where would we end up if I would start listing every single violin-playing Indian or skiing Australian? The people in question will know that they are addressed.

Finally, I would like to thank my family and my partner Felix for patiently sharing me with my thesis. Thank you for all your loving support.

## 9 Erklärung

Hiermit versichere ich, dass ich die Arbeit mit dem Titel "Does the Uncertainty of Prior Knowledge affect Sensorimotor Adaptation?" selbstständig verfasst und keine anderen als die angegebenen Hilfsmittel und Quellen benutzt habe.

Göttingen, 30.05.2020



.....  
Ort, Datum

.....  
Sandrine Hinrichs