



**A series of (un)predictable events:
Influences of somatosensory predictions and
action control on goal-directed movements**

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Abstract

Every day, we move through our environment and interact with it. After switching off the alarm clock and drinking our first coffee, our day is filled with a wide variety of activities. For all these movements, the brain must select appropriate actions, formulate motor plans and process feedback from the body's sensory systems. This entire process of executing a goal-directed movement is influenced by a multitude of factors. The aim of this dissertation is to investigate the influence sensorimotor predictions on perception and action in the context of goal-directed movements. A specific emphasis will be placed on sensorimotor predictions based on direct feedback signals, sensorimotor memories, and action control processes. The research is based on three studies and aims to elucidate the intricate interplay of sensory feedback, task relevance, and motor planning in executing precise and adaptable movements in varied contexts.

The first study explores how task-relevant feedback signals and their intensity modulate predictions based on efference copies during reaching. As a target is approached, there is a greater probability of physical contact with a surface, which in turn makes the tactile signals at the end of a movement more predictable. Feedforward prediction mechanisms can explain a resulting reduction of tactile sensitivity. However, previous research yielded contradictory findings, prompting the question of whether the relevance of feedback signals exerts a greater influence on the modulation of tactile perception than their mere predictability. My findings demonstrate that tactile suppression dynamically adjusts to the necessity of processing anticipated feedback, especially when the feedback signal is weak yet crucial for task completion. This highlights the brain's ability to selectively enhance sensory processing based on task demands.

The first study focusses on predictions based on current information, whereas my second study examines the influence of predictions derived from past sensorimotor memories on tactile perception and movement kinematics during the interaction with objects that possess uncertain properties. In the presence of uncertainty regarding object properties, humans tend to plan their movements based on their most recent experiences with that object. For example, when placing their fingers and grasping an object to prevent tilting, they usually repeat their grasping configuration in anticipation of constant object properties. In this instance, it is probable that one must compensate for errors in movement, thereby rendering incoming somatosensory signals crucial for the process of motor adjustments. My results indicate that while predictions based on sensorimotor memories significantly impact movement kinematics on a trial-by-trial basis, they do not similarly affect tactile sensitivity. This suggests that tactile perception necessitates a more stable informational foundation for sensorimotor predictions to exert an

effective influence. Moreover, explicit knowledge about the change in object properties had no effect on either kinematic behavior or tactile sensitivity.

The third study aims to gain a deeper understanding of the extent to which predictions based on past somatosensory memories influence goal-directed movements. In this study, the focus is on a cognitive approach, specifically action control and predictions made on the basis of event files. A recent approach, the Binding and Retrieval in Action Control (BRAC) framework, aims to provide an overarching theory to explain results from different action control paradigms. This is achieved by using two core principles, feature binding and retrieval. My investigation revealed that previous experiences influence sensorimotor predictions, which in turn shape current motor planning. These results support the BRAC framework and highlight the importance of past interactions in shaping future actions, even in the context of complex motor tasks. It appears that goal-directed movements may serve as an effective means of integrating features of varying task-relevance and temporally varying accessibility.

Overall, this dissertation contributes to a deeper understanding of the mechanisms underlying goal-directed movements, emphasizing the importance of sensorimotor predictions based on current and past information and their influence on motor planning and execution.

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I Synopsis

1. Introduction

Max stood in the kitchen, preparing a meal for his friends. With a knife in hand, he applied just the right amount of force and pressure, relying on the tactile feedback from his hand to control the movement of the blade. Each vegetable presented its own challenge - but Max, being an experienced cook - knew how to address them: Carrots, with their firm texture, required a more robust grip and precise cutting angle, while onions, with their layers and varying sizes, demanded adaptability in his motor plan. Even a seemingly simple tomato could vary in consistency from firm to mushy, requiring Max to constantly adjust his actions. With each cut, he learned to properly adjust his knife for the next cut. His brain was busy planning and executing goal-directed movements, making decisions about cutting trajectories, angles, and speeds. In this culinary challenge, Max balanced the importance of somatosensory feedback signals with the uncertainties presented by different vegetable properties such as texture and size. His cognitive control helped him to make proper decisions about cutting angles and speeds based on his previous cooking experience, ensuring a delicious meal for him and his friends.

Goal-directed movements

This everyday example of preparing a homecooked meal illustrates a sequence of actions comprising a number of steps that collectively contribute to the achievement of a single overarching goal. In order to achieve the desired outcome, it is essential to select the most appropriate movement from the available range of goal-directed movements for each step of the action sequence. Goal-directed movements can range from very simple actions, such as reaching for a glass, to very complex sequences of actions, such as driving in heavy traffic. In such a scenario, a driver must constantly adjust their speed, change lanes, navigate, and respond to unexpected situations while maintaining awareness of their surroundings. Humans perform goal-directed movements in everyday life to communicate and interact with a wide variety of objects. Executing a goal-directed movement begins with perceiving and processing multisensory information (Desmurget, 1998). Together with memories derived from previous experiences, this information is used to build predictions about the potential trajectory of a movement and associated somatosensory feedback (Desmurget & Grafton, 2000; Flanagan et al., 2006). These predictions serve as the foundation for the formulation of a motor plan that outlines the sequence of muscle activations necessary to perform movements (Adams et al., 2013; Kawato, 1999). During the execution of a movement, the brain persistently receives feedback

from the body's proprioceptive, somatosensory, and visual systems. This allows for real-time adjustments to sensorimotor predictions, which in turn guarantee precise and efficient goal achievement. To control goal-directed movements, it is fundamental for the brain to select relevant aspects of incoming sensory information and separate them from somatosensory noise (Williams et al., 1998; Williams & Chapman, 2000, 2002). All the aforementioned processes are influenced by a multitude of factors and interact in the planning and execution of goal-directed movements.

The objective of my dissertation was to investigate different factors – in particular current information, past sensorimotor memories, and action control - upon which sensorimotor predictions can be based and their impact on tactile perception and the execution of goal-directed movements. The first study focused on the impact of current information, including task-relevant feedback signals and their intensity, on predictions based on efference copies during a reaching task. The second study sought to determine whether predictions derived from past sensorimotor memories associated with prior object interactions exert a similar influence on both kinematic behavior and tactile perception when interacting with an object characterized by uncertain properties. The third study aimed to investigate how central principles from cognitive action control approaches can explain the building of predictions made on the basis of event files within the context of executing complex sequences of goal-directed actions. The combined aim of my studies was to gain a deeper insight into the intricate mechanisms underlying sensorimotor predictions by examining how current information, past sensorimotor memories, and cognitive action control principles influence tactile perception and the execution of goal-directed movements.

Influences of current information on somatosensory predictions

Sensorimotor predictions refer to the brain's ability to anticipate the sensory outcomes of an action or event before they occur. This process enables individuals to prepare and adjust their movements and perceptions in advance, ensuring smooth and accurate interactions with the environment. These predictions are crucial for overcoming sensory processing delays and for coordinating well-timed responses, whether in everyday tasks, complex motor activities, or even in maintaining a sense of agency over one's actions (for a review see Fiehler et al., 2019). Predictions are also used to distinguish relevant somatosensory feedback signals from noise that occur during goal-directed movements. Sensorimotor noise refers to the inherent variability and uncertainty in sensory and motor systems during movement execution and can compromise the detectability of somatosensory feedback (Faisal et al., 2008; Miall & Wolpert, 1996). A predictive anticipation of somatosensory consequences of movements can help to control and coordinate

goal-directed movements. Somatosensory predictions are thought to be formed based on forward model mechanisms (Voss et al., 2008; Wolpert & Flanagan, 2001). By using the efference copy of the motor command, the brain predicts the somatosensory outcome of a movement and continuously compares it with the actual sensory input produced by the movement (Shadmehr & Krakauer, 2008). Tactile sensitivity decreases as a result of precise predictions, potentially to free capacities to make information processing more efficient (Bays et al., 2006; Blakemore et al., 1998; Chapman & Beauchamp, 2006; Desmurget & Grafton, 2000; Fuehrer et al., 2022; Williams & Chapman, 2002). This mechanism, also referred to as tactile suppression, has been studied from various perspectives. It occurs during self-touch (Bays et al., 2005; Blakemore et al., 1998; Kilteni & Ehrsson, 2017; Walsh et al., 2011) and explains why self-tickling is impossible (Blakemore et al., 2000). However, tactile suppression is not solely dependent on predictions based on the efference copy, it can also be observed for externally generated stimuli when applied to a moving limb, compared to a resting one (Chapman et al., 1987; Fraser & Fiehler, 2018; Gertz et al., 2018; Manzone et al., 2018; Voudouris & Fiehler, 2017, 2021). The suppression of external signals is not merely a consequence of the movement; it is, above all, dependent upon the predictability of these signals (Fuehrer et al., 2022; Voudouris et al., 2019). It has been shown for different movements like simple finger movements (Voss et al., 2006, 2008; Williams & Chapman, 2002), or reaching (Buckingham et al., 2010; Voudouris & Fiehler, 2017) and grasping (Colino & Binsted, 2016; Voudouris et al., 2019). Previous research has demonstrated that tactile suppression is a behavioral measure of the strength of somatosensory predictions and reflects how these predictions are used by the brain to efficiently process somatosensory signals to guide goal-directed movements (Fiehler et al., 2019).

Besides the general predictability of tactile feedback, tactile suppression is further modulated by the relevance of processing tactile information. During reaching and grasping, the processing of tactile feedback is of particular importance at the fingers involved in the grasping action (Johansson & Flanagan, 2009). In comparison to irrelevant body regions, such as the forearm, task-relevant body regions, such as the index finger of the grasping hand, demonstrate reduced tactile suppression (Colino et al., 2014; Colino & Binsted, 2016; Manzone et al., 2018). During the late phase of a reaching or grasping movement, when a target is approached and the moving hand will make contact with some kind of surface, different studies have identified either an increase in tactile suppression (Fraser & Fiehler, 2018; Juravle et al., 2010; Voudouris & Fiehler, 2021) or a reduction (Colino & Binsted, 2016; Juravle et al., 2018; Manzone et al., 2018). As the manual contact at the end of a movement is a highly predictable feedback signal, the increase in late reach suppression can be explained by a forward model, which reliably predicted this consequence of the planned movement. However, the increase in suppression could also be

explained by the fact that tactile feedback signals were not necessary to process. For example, Fraser and Fiehler (2018) demonstrated an increase in late reach suppression when participants anticipated a tactile consequence (i.e. touching a surface). Overall, it seems that tactile sensitivity is primarily adapted to the extent to which incoming signals are relevant and useful for the current task, rather than simply suppressing predictable signals.

Prominent tactile signals, such as the pressing of a button, are more likely to be reliably detected. If these intense feedback signals are not task-relevant, it is likely that they are associated with increased suppression (Fraser & Fiehler, 2018). Conversely, a lower intensity of tactile feedback may result in relevant information not being perceived. If the intensity is too low, or more precisely, if feedback signals are lower than the sensory noise associated with the processing of afferent signals, they may not be detected at all (Blakemore et al., 2000; Voss et al., 2008; Voudouris et al., 2019). Even if the signal intensity is above the detection threshold but still relatively weak, this entails a certain degree of uncertainty. If tactile suppression is too strong, it could result in the inability to detect incoming somatosensory signals. In general, predictive processes are downregulated when somatosensory input is uncertain in order to improve the processing of incoming sensory signals (Franklin et al., 2012). Research has demonstrated that tactile suppression is less pronounced when feedback is less reliable (Blakemore et al., 2000; Klever et al., 2019; Voudouris et al., 2019). When movement consequences are task-relevant, it may be advantageous to downregulate the predictive mechanisms that cause tactile suppression in order to enhance task performance. In such cases, it would be beneficial to weight the input signals higher while reducing tactile suppression.

Somatosensory processing of feedback signals becomes even more complex when movements involve interaction with objects, such as grasping, lifting or manipulating them. During object interaction, human behavior is primarily guided by prior experience and visual information. Relevant object properties, like the size (Gordon et al., 1991), orientation (Voudouris et al., 2013), shape (Kleinholdermann et al., 2007) or surface material (Klein et al., 2021), are initially extracted by vision, allowing the selection of suitable grasping points during movement planning (Roche et al., 2015; Voudouris et al., 2010). However, visual information is not always available, and the presence of varying object properties introduces another source of uncertainty (Faisal et al., 2008; Schultheis & Rothkopf, 2021). The brain may reweight the importance of different sensory inputs based on their reliability in the face of uncertainty. If visual feedback becomes less reliable due to sudden changes, the brain may rely more on proprioceptive or tactile feedback to guide the movement.

Influences of past sensorimotor memories on somatosensory predictions

The basis for predicting and executing goal-directed movements lies in sensorimotor memories, which are essential for navigating a world filled with vast sensory input and inherent sensory uncertainty. Sensorimotor memories refer to the stored representations of past sensory experiences and motor actions that the brain uses to guide future movements and perceptions (van Polanen & Davare, 2015; Witney et al., 2001). These memories are formed through repeated interactions with the environment, allowing individuals to learn and refine motor skills over time. Sensorimotor memories enable the prediction and execution of actions based on previous experiences, contributing to smooth and coordinated movements, as well as the ability to adapt to sudden changes in the environments. Predictive models can be used to anticipate potential sensory consequences and plan corrective actions when the expected feedback does not match the actual sensory signals received. For objects with unknown or changing properties, humans tend to apply a 'default' motor behavior and rely on sensorimotor memories from the most recent interaction with the object to predict the object properties and adapt their movement accordingly (Fu et al., 2010; Lukos et al., 2007; Voudouris et al., 2019). For instance, it has been demonstrated that humans select appropriate grasping points for different objects prior to initiating the grasping movement by retrieving sensorimotor memories of past interactions with a similar object, allowing them to anticipate the optimal grip based on the object's properties (Roche et al., 2015; Voudouris et al., 2010). This form of adjustment presumably occurs under the assumption that object properties do not change.

However, sudden external influences from the environment or changing object properties can increase uncertainty. In such cases, predictions based on sensorimotor memories become less reliable or can even be misleading. In this context, it would be of particular importance to attribute a higher relevance to incoming sensory signals and to consider their processing as more important for anticipatory motor adjustments (Aivar et al., 2008; Day & Lyon, 2000; Dimitriou et al., 2013; Voudouris et al., 2013). To illustrate, when a large metal mug is picked up that appears to be heavy but is in fact lightweight, the brain initially anticipates a heavy weight based on past experiences and prepares to apply more force. However, upon receiving sensory feedback indicating that the object is in fact lighter than anticipated, the grip strength is promptly adjusted to facilitate a smooth handling of the cup, thereby correcting the inaccuracy in the initial prediction. Nevertheless, it can be demonstrated that even in the case of changing object properties, people tend to plan their movements under the assumption that the object in question has the same properties as in the previous interaction (Lukos et al., 2013; Witney et al., 2001). To illustrate, in the experiment conducted by Lukos et al. (2013), participants had to grasp

and lift an object with a varying center of mass. The object was of an inverted T-shape and a mass could be placed in slots at the left or right bottom of the object, resulting in an uneven mass distribution that was unpredictably altered on a trial-by-trial basis. It was demonstrated that sensorimotor memories from the preceding trial were used to select grasping points on the object, resulting in a greater tilting of the object when the mass distribution changed from the previous trial to the current one. Moreover, individuals tend to employ a consistent finger placement when interacting with an object, despite the potential for alternative grasping positions (Dixon et al., 2012). This grasping behavior also results in an object tilting more when its mass distribution is not predictable and varies from one occasion to another, in comparison to the interaction with an object with a constant mass distribution (Voudouris et al., 2019). These findings indicate that the brain attempts to account for the performance error during the previous interaction with the object in order to plan a subsequent movement with the object (Lukos et al., 2013; Scheidt et al., 2001).

In the context of interactions with objects exhibiting unpredictable properties, it can be assumed that enhanced processing of tactile feedback would be advantageous in order to obtain necessary information to adapt trajectories with minimal delay. To date, the potential impact of predictions based on sensorimotor memories on tactile suppression has not been fully explored. One study sought to determine whether the general context of repetitive factors associated with an object, in this case mass distribution, affects tactile suppression when interacting with that object (Voudouris et al., 2019). This experiment demonstrated that when interacting with an object exhibiting a changing mass distribution, tactile sensitivity was enhanced in comparison to an object with a constant mass distribution. The objective was to compare the basic context of object properties (constant or changing mass distribution) between different blocks of the experiment. It remains unclear as to whether sensorimotor memories of the most recent object interaction can influence somatosensory predictions in a manner comparable to the effects observed in movement kinematics. Alternatively, it may be that these predictions are founded upon a higher degree of reliability.

In addition to the influence of sensorimotor memories of the most recent object interaction, the question of whether one is aware of the conditions of the movements being performed must also be considered. For example, whether the properties of the object will remain constant or may change during the interaction may also affect the strength of tactile suppression observed between uncertain and certain movement contexts. The implicit learning of statistical regularities has an influence on various aspects of goal-directed movements. Through haptic exploration, for example, underlying dynamics of an object can be implicitly learned, so that the

collection of necessary tactile information can be improved (Zoeller et al., 2019). Furthermore, the anticipation of specific object properties can be shaped by implicit sensorimotor memories (Schneider et al., 2020), irrespective of whether explicit references to these object properties have been made (Flanagan et al., 2008). The impact of providing explicit information about the consistency of an upcoming series of object interactions with potentially changing object properties on the strength of tactile suppression through predictive control remains unclear.

Influences of action control on somatosensory predictions

Movements are typically performed with the intention of achieving a specific goal, like grasping a cup of coffee in order to drink it. Consequently, individuals are continuously engaged with their surroundings in order to elicit certain perceptual effects through their actions (Dignath et al., 2014; Pfister et al., 2014). Actions can be categorized on a spectrum, ranging from simple actions, such as pressing a bell, to complex sequences of actions, such as cooking a meal. Although most movements may appear simple, they are often a complex sequence of individual actions that must be precisely coordinated. Furthermore, the environment in which the action takes place and the objects that can be interacted with often present a degree of uncertainty that must be responded to adaptively and flexibly (Frings et al., 2020). In addition to the influences on sensorimotor predictions that have already been described, cognitive approaches should be taken into account, such as action control. Action control is defined as the translation of intentions into actual movements (Kuhl, 1984). This process is influenced by past experiences and the context in which an individual is located in. Each situation may involve features of previous actions, including aspects of the stimulus environment, the response that was made in that environment, and the subsequent effects caused by the previous action. When an action is performed, these situational and multisensory features are integrated into a common event-file (e.g. Hommel, 1998, 2004; Treisman, 1996). The occurrence of a previously identified feature will function as a contextual cue, prompting the automatic retrieval of the associated event-file from memory. This will also result in the recall of the preceding reaction. Consequently, the repetition of the same reaction is already available and there is a tendency to execute it automatically. This can result in a performance benefit, such as a faster reaction or more precise execution. In case that the retrieved reaction is deemed inappropriate, it must be suppressed in order to execute a different response. This can result in a performance disadvantage, including slower response times, errors, and inaccurate execution. When planning a goal-directed movement, the brain may access previously stored event-files of similar actions in a specific context. These contextual cues can influence the selection and execution of the current movement by biasing the brain towards actions that have been successful in similar contexts.

A number of studies examining action control have employed paradigms such as task switching (Koch et al., 2018), negative priming (Frings et al., 2015; Mayr & Buchner, 2006), and stimulus-response (S-R) binding (Frings et al., 2007; Hommel, 1998). These paradigms share a sequential trial methodology, whereby the processing in one trial (prime) influences the reaction in a subsequent trial (probe). Notable effects in action control studies include global expectation consistency or mixing costs: Performance is often enhanced when an action is repeated consecutively, compared to when the action or its features change between trials (Los, 1999; Philipp et al., 2008; Rubin & Meiran, 2005; Steinhauser & Hübner, 2005). Moreover, performance is typically enhanced when stimulus-response features are either fully repeated or entirely new, while partial feature repetition typically results in impaired performance, known as partial repetition costs (Hommel, 1998, 2004). For example, in task switching paradigms, alternating between tasks (e.g., odd/even judgement of numbers versus vocal/consonant judgement of letters) using the same keys often results in longer reaction times when switching tasks compared to repeating them from the preceding (prime) trial to the current (probe) trial. Rather than a unified theory, paradigm-specific theories have been proposed, including S-R Binding Approaches to Memory (Henson et al., 2014) and the Theory of Event Coding (Hommel et al., 2001).

A recent approach, the Binding and Retrieval in Action Control (BRAC) framework (Frings et al., 2020) presents an overarching theory that focuses on feature binding and feature-based event-file retrieval. The BRAC framework explains the phenomenon of task switch costs through the integration of both stimulus and task in the prime trial. Here, stimulus repetition in the probe trial prompts the automatic retrieval of the previous task, which can result in interference if a task switch is required (Frings et al., 2020; Koch et al., 2018). The BRAC framework enables the explanation of various results from different paradigms typically used in action control studies. This is achieved through the transfer of the core principles of binding and retrieval. Typical paradigms used to study action control are somewhat artificial in that they include stimulus presentation on a computer screen at the beginning of each trial and require very simple motor responses, such as button presses. As BRAC aims to provide an overarching and universal perspective on action control, the postulated principles should also be applicable to action sequences of higher complexity, such as grasping a cup or preparing a meal. These complex action sequences are composed of several discrete movements. Especially when interacting with everyday objects, it is not always the case that all object features are continuously perceivable; in some instances, they can only be experienced through interaction with the object. For instance, when lifting a box with unknown content, the object's features are

only fully experienced through the act of lifting it. The question thus arises as to whether the BRAC framework can be extended to encompass more complex types of actions.

Rationale of the studies

Overall, the overarching aim of my doctoral research is to examine the intricacies of goal-directed movements and to identify the underlying components that collectively ensure successful movement performance. When interacting in natural environments, it is crucial to select and process relevant information to build predictions to ensure precise motor plans. This process is particularly important when engaging with objects, as previous experiences guide the selection of appropriate movements. These past experiences provide a framework for understanding how somatosensory predictions are used to interact effectively with different objects. However, in some cases, visual information is not available, and the properties of objects can only be experienced through interaction and the collection of somatosensory information, introducing uncertainty in the usage of somatosensory predictions. In such situations, cognitive approaches also become helpful in understanding the building of sensorimotor predictions, as they explain how movements are formed based on previous intentions and the mental mapping of the object's characteristics. Additionally, previous actions influence subsequent ones by retrieving previously bound features, such as environmental cues, the responses performed, and the outcomes of those actions. This retrieval process ensures that each new action is informed by past experiences and contextual cues, enhancing the accuracy and efficiency of motor planning in complex environments. The objective of my doctoral research is to gain a deeper understanding of factors that affect sensorimotor predictions. These include current information, like the significance of somatosensory feedback, past sensorimotor memories and associated expectations about object properties, and cognitive action control principles. To investigate the influence of these factors on the establishment of somatosensory predictions in the context of goal-directed movements, I conducted three studies.

The first study was designed to examine the influence of current information, including task-relevance and feedback signal intensity, on predictions based on efference copies during a pointing movement. Previous studies have found both a reduction (Colino & Binsted, 2016; Juravle et al., 2018; Manzone et al., 2018), as well as an increase in late-reach suppression (Fraser & Fiehler, 2018; Juravle et al., 2010; Voudouris & Fiehler, 2021) during reaching and grasping. The mere predictability of a tactile signal at the end of a movement is not sufficient to account for the observed discrepancies. Is predictable tactile feedback suppressed to a lesser extent when it is relevant? My first study addressed this question and brought new insights on how task-relevance and intensity of tactile feedback signals shape somatosensory predictions.

The objective of the second study was to determine whether predictions based on recent sensorimotor memories besides influencing movement kinematics, also affect tactile suppression in a comparable manner. Previous research has indicated that humans plan their movements on the assumption that an object will retain the same properties as in the previous interaction (Lukos et al., 2013; Witney et al., 2001). Additionally, the general context of a changing mass distribution between trials has been shown to enhance tactile sensitivity (Voudouris et al., 2019). It is yet unclear whether somatosensory predictions are built upon past sensorimotor memories to such an extent that they can influence tactile sensitivity on a trial-by-trial basis in a manner comparable to kinematic behavior when confronted with uncertain object properties. The second study revealed that somatosensory predictions exert different influences on tactile sensitivity and kinematic behavior. Moreover, this study examined the effect of explicit information on predictive control, contrasting it with the impact of implicit anticipation.

The third study was designed to examine if the applicability of central principles of action control approaches can be applied to a sequence of discrete, goal-directed movements and shape the formation of somatosensory predictions. The repetition of features from a previously bound event-file has been observed to automatically influence actions, such as altering response times and error rates in tasks involving simple actions, like pressing buttons to react to cues on a screen (e.g. Frings et al., 2015; Hommel, 2004; Koch et al., 2018; Philipp et al., 2008; Rubin & Meiran, 2005; Steinhauser & Hübner, 2005). A recent approach, the Binding and Retrieval in Action Control (BRAC) framework (Frings et al., 2020), aims to utilize the core concepts of action control, namely feature binding and retrieval, in order to provide an explanation for the various results that are typically observed in action control research. Can these concepts be applied to more complex action sequences involving goal-directed movements and contribute to the formation of somatosensory predictions? The results of my third study demonstrated the influence of binding and retrieval on the building of somatosensory predictions and their impact during the planning and execution of a complex action sequence.

2. Summary of Published, Peer-Reviewed Articles

Study I: Linking Signal Relevancy and Intensity in Predictive Tactile Suppression (Beyvers et al., 2022)

The aim of the first study was to investigate whether the strength of predictions based on efference copies is modulated by the relevance of the task in terms of the anticipated consequences of the movement and the intensity of associated feedback signals, as reflected in the degree of tactile suppression.

In the experiment, two groups of 26 participants each completed a task in which they received either visual or tactile information regarding the location of a hidden target. Participants were instructed to reach out towards the screen and find the target. No additional visual cues were provided to assist with the identification of the target's location. To eliminate potential interference from tactile signals at the end of their reach, participants were required to approach the screen closely without making physical contact. Two vibrotactile stimulators (tactors) were attached to the participants' right index finger – one test and one feedback tactor. First, participants did a baseline task in which they had to report whether they felt vibrations from the test tactor while resting their hand. In the main task, consisting of two blocks, participants were instructed to reach out and move their index finger to a previously cued area until they received tactile or visual feedback indicating that they found the hidden target. One group received strong tactile feedback and the other weak tactile feedback. After completing the movement, participants indicated whether they felt any vibrations from the test tactor, which could be either be transmitted early or late into the movement. To examine perceptual behavior, the proportion of trials in which the probing stimulus was perceived were fitted to a logistic function via maximum-likelihood estimation. From this point, the 50% detection threshold (point of subjective equality, PSE), which refers to the threshold of detectability, was extracted. Tactile suppression was calculated by subtracting the baseline PSE from the PSE of each movement condition, with higher positive values indicating a greater reduction of tactile sensitivity. Given the absence of contact with a surface and the necessity for participants to rely on the feedback provided to ensure task completion, we expected a reduction in late-reach suppression overall. Additionally, reduced suppression was expected when the tactile feedback was weak compared to strong, as suppression would increase the risk of missing relevant feedback. As the tactile feedback condition included a predictable tactile signal, we expected an increase in tactile suppression compared to the visual feedback condition.

As expected, we found that suppression was significantly reduced in the late phase of the movement, when the target was approached. By eliminating any physical contact at the end of a reaching movement, we rendered the feedback provided at the end of the reach as the sole task-relevant tactile signal indicating task completion. Therefore, the reduction in suppression observed in the late phase of the reach supports the view that tactile signals are suppressed when they are predictable and not uniquely relevant to the successful completion of a task. Furthermore, we found that suppression was significantly more pronounced when feedback was delivered through tactile cues rather than visual cues, but only in case of strong tactile feedback. The observed increase in suppression when tactile feedback was presented compared to visual feedback provides further evidence for the predictive nature of tactile suppression (Fraser & Fiehler, 2018; Fuehrer et al., 2022; Gertz et al., 2018; Manzone et al., 2018; Voudouris & Fiehler, 2021). In addition, our findings demonstrate that tactile suppression is not only responsive to the task relevance of the predicted somatosensory consequences of a movement, but also adapts to the signal intensity. The release of suppression when confronted with faint feedback allows the brain to detect signals that would otherwise be missed, and only seems to be used when such an effort is required for successful goal-directed actions.

Study II: Sensorimotor Memories Influence Movement Kinematics but not Associated Tactile Processing (Beyvers et al., 2023)

The second study investigated whether and how predictions derived from sensorimotor memories influence movement kinematics and associated tactile processing during grasping tasks. Based on the premise that our past interactions with objects shape our future motor actions, the aim of the study was to investigate whether somatosensory predictions under uncertainty are established on the basis of the most recently obtained object information (Experiment 1), and whether implicit or explicit knowledge of changing object properties influences tactile suppression (Experiment 2).

The first experiment involved 24 participants who were asked to grasp and lift an inverted T-shaped object with an uncertain mass distribution. A tactor was attached to the participant's right index finger. First, in a baseline block, participants responded to vibrotactile stimuli while their hand was at rest. During the main task, the mass distribution of the object varied in a pseudo-randomized order across trials. Therefore, the trial sequence contained trials where the mass distribution repeated or changed from one trial to the next. In addition, participants were presented with tactile stimuli at the moment of object contact. They were required to report the detection of the stimulus at the end of each movement to probe tactile sensitivity. The kinematic

analysis involved evaluating the vertical separation of digits at the moment of object contact, and the maximal object roll during lifting. Tactile suppression was assessed based on participants' responses to the vibrotactile stimuli during grasping compared to the baseline, as reflected in the resulting PSE difference (see description in Study 1). Consistent with prior research (Lukos et al., 2013; Witney et al., 2001), it was observed that humans utilize sensorimotor memories from the previous trial to plan their next movement when grasping an object with uncertain properties. Participants positioned their fingers in anticipation of a mass distribution that was identical to the one presented in the trial before, leading to a smaller object roll when the mass distribution was repeated, compared to a changing mass distribution. These findings suggest that sensorimotor memories significantly influence the planning and execution of movement kinematics when object properties are uncertain and sensory action consequences are difficult to predict. However, these memories did not appear to affect tactile perception. Participants' ability to detect the tactile stimulus remained consistent regardless of the mass distribution they had previously experienced.

The second experiment introduced a more complex trial structure, which incorporated short sequences with a pseudorandomized mass distribution (mixed sequence parts) into longer sequences with a constant mass distribution (constant sequence parts). In two experimental sessions, another 24 participants were provided with either explicit or implicit information about the trial structure. In the first implicit session, participants were not informed about the structure of the presented sequence to test for implicit learning of the statistical regularities. In the second explicit session, participants were informed about the structure of the upcoming part of the sequence to investigate whether this would alter predictive control and the strength of tactile suppression. The overall procedure was similar to the first experiment. The results of the second experiment confirmed the findings of the first, providing further support for the initial conclusions regarding kinematic behavior. Participants adapted their grasping movements based on previous trial experiences with the object. In contrast to movement kinematics, tactile suppression was not influenced by the division into constant and mixed sequence parts. The intermixing of parts with a changing and constant mass distribution may have limited the establishment of reliable predictions. Furthermore, the provision of explicit information about the sequence or the absence of such information did not affect either kinematics or tactile sensitivity. It can be assumed that recent sensorimotor memories affect motor control and tactile processing in different ways. Although these memories have a significant impact on our motor actions, such as the kinematics of grasping movements, somatosensory predictions seem to require a more stable information base to affect tactile sensitivity during goal-directed movements.

Study III: Episodic Binding and Retrieval in Sequences of Discrete Movements – Evidence from Grasping Actions (Beyvers et al., 2022)

The aim of the third study was to investigate how central principles from cognitive action control approaches can explain the formation of predictions within the context of executing complex sequences of goal-directed actions. The study focused on the episodic binding and retrieval of movement features, such as the memorized object mass distribution and position and their impact on the execution of subsequent grasping and lifting actions. The aim was to understand how previous movement experiences influence future actions, within the context of the Binding and Retrieval in Action Control framework (BRAC; Frings et al., 2020).

A total of 32 participants were asked to grasp an object with an uneven mass distribution from two different positions and lift it as straight as possible. In a sequence of trials, object features such as the mass distribution and object position could either repeat or change from trial to trial. These features were either kept constant on a global level (constant blocks) or varied in a pseudorandomized manner across trials (mixed block). The mixed block contained complete, partial, and no repetition of both factors with respect to the previous trial, whereas the constant blocks only contained complete repetitions. The study employed a combination of constant and mixed blocks that was used to examine mixing costs and partial repetition costs. To analyze motor planning and control, kinematic measures such as digits' separation and object roll were examined. Assuming that the principles of binding and retrieval can be applied to complex, continuous movements, we expected and found that mixing costs are reflected in both variables. A comparison of the results for the two conditions – constant blocks and mixed blocks, both of which exhibited complete repetition of the two features – revealed that in the constant blocks, participants were more efficient in positioning their fingers in a manner that favored the distribution of the weight, which ultimately led to a significant reduction in the tilting of the object. Additionally, our findings indicate that the mixing costs are reflected in the mixed block, with the best task performance observed when both object features were fully repeated from one trial to the next. These results suggest that the features during grasping and lifting the object were stored in a common event-file and retrieved in subsequent actions to influence both digits' separation and object roll.

The findings demonstrate the applicability of the Binding and Retrieval in Action Control (BRAC) framework to a wider range of motor actions, extending its relevance beyond simple tasks such as button presses to encompass more complex actions such as grasping and lifting an object. The findings are comparable to those of previous studies that employed paradigms

involving simple motor actions, such as button presses (Los, 1999; Philipp et al., 2008; Rubin & Meiran, 2005; Steinhauser & Hübner, 2005). Furthermore, the findings indicate that the fundamental processes of action control, specifically feature binding and retrieval, are taken into account in the formation of sensorimotor predictions. The retrieval of event files stored in memory can influence the prediction of movement patterns and the anticipated outcomes of planned movements. Overall, our results support the existence of a common underlying mechanism for action control across different levels of complexity. The use of a more natural and ecologically valid study design allows for the comparison of results across actions of different complexity, thereby enhancing our understanding of action control in everyday tasks. Furthermore, our findings indicate that the formation of sensorimotor predictions and the resulting anticipation of movement outcomes is underpinned by a complex interplay between multiple factors, including action control mechanisms.

3. Discussion

In the present dissertation, I examined influential mechanisms underlying sensorimotor predictions and how they impact tactile perception and the execution of goal-directed movements. A particular emphasis was placed on the establishment of somatosensory predictions based on current information, like task relevance and feedback signal intensity, on past sensorimotor memories when interacting with uncertain object properties, and cognitive action control approaches in the context of complex action sequences.

During movement, the processing of tactile information is influenced by feedforward processes (Wolpert & Flanagan, 2001), which evoke tactile suppression when somatosensory signals are predictable, thereby making the processing of incoming information more efficient (Bays et al., 2006; Chapman & Beauchamp, 2006; Desmurget & Grafton, 2000; Williams & Chapman, 2002). With the first study, I was able to highlight previous research that identified the dynamic modulation of predictions to meet the demands of somatosensory processing during the execution of goal-directed movements (Fuehrer et al., 2022; Voudouris & Fiehler, 2021). Furthermore, my results demonstrated that this adaptation is not solely modulated by the intrinsic predictability of incoming somatosensory signals. The necessity to detect and process anticipated feedback signals in order to complete a task and the related intensity of these signals play a significant role in this process. In this sense, tactile suppression was generally more pronounced when task-relevant tactile feedback was anticipated and exceeded the detection threshold at the same time. Unlike previous studies, in this study, a physical contact with a

surface was eliminated at the end of the reaching movement and participants had to rely on a given feedback signal, making it uniquely relevant for the task. The reliance on given feedback is likely to have contributed to the reduction in suppression observed in the late phase of the reach. This suggests that suppression is released when signal processing is highly relevant, particularly when signals are faint and easy to miss. In such cases, excessive suppression may hinder successful goal-directed actions. A dynamic modulation of tactile perception is consistent with theories of motor control, which propose that the modulation of sensory feedback is based on the goal of an action (Liu & Todorov, 2007; Todorov & Jordan, 2002). To achieve optimal planning and flexible adjustment of goal-directed movements, it is essential to combine predictive mechanisms with somatosensory feedback processing (Voudouris & Fiehler, 2021). The demands on somatosensory processing and the necessity to process incoming feedback signals vary in specific ways over the course of a movement, depending on the task at hand. This provides an explanation for the temporal discrepancies in tactile suppression observed in previous studies (Colino & Binsted, 2016; Fraser & Fiehler, 2018; Juravle et al., 2010, 2018; Manzone et al., 2018; Voudouris & Fiehler, 2021). The necessity to detect and process predicted feedback signals that arise during movement appears to be more crucial than the predictability of a somatosensory action effect alone in determining the strength of tactile suppression.

While the first study examined the modulation of tactile suppression based on current information during pointing, the second study investigated the impact of past sensorimotor memories associated with prior object interactions on sensorimotor predictions. The aim was to investigate whether these predictions exert a similar influence on both kinematic behavior and tactile sensitivity when reaching and grasping an object characterized by uncertain properties. Previous studies have demonstrated a significant impact of the most recent sensorimotor memories when grasping an object on various kinematic movement parameters, including finger placement on an object, grasp aperture, and the resulting tilt of the object (Fu et al., 2010; Lukos et al., 2007, 2013; Scheidt et al., 2001; Voudouris et al., 2019). In line with those findings, participants in my study demonstrated a tendency to compensate for the mass distribution experienced in the previous trial, resulting in a reduction in object roll when the mass distribution was repeated. This finding is consistent with the hypothesis that the brain forms and utilizes sensorimotor memories to predict the properties of objects and plan movements accordingly (Lukos et al., 2010, 2013; van Polanen & Davare, 2015; Voudouris et al., 2019). However, in contrast to the findings regarding movement kinematics, tactile suppression did not elicit a significant variation in response to changes in mass distribution. This indicates that tactile perception is unlikely to be influenced by short-term previous trial effects to the same extent as movement kinematics. Tactile sensitivity appears to require a more stable information

base in order to be affected by sensorimotor predictions. Another potential explanation for the absence of modulation of tactile suppression through previous trial mass distribution may be the timing of the probing stimulus. Tactile sensitivity was probed when the object was grasped, while the current mass distribution could not be fully experienced. On the one hand, this ensured that tactile suppression was primarily affected by somatosensory predictions build initial to the start of the movement. On the other hand, it is possible that somatosensory predictions were equally strong at this time point independent of the mass distribution in the current trial.

In order to enhance the strength of sensorimotor predictions, the trial structure of the second experiment of Study 2 was designed with longer sections of constant mass distribution, which were incorporated into the mixed sequence on a regular basis. Another study found stronger tactile suppression when grasping an object with its properties staying identical than when they changed (Voudouris et al., 2019). In odds with this finding, tactile suppression in my experiment was found to be consistent and uniform across both constant and mixed parts. The constant parts were of shorter duration and alternated directly with the mixed parts of the sequence. This frequent change may have impeded the establishment of reliable predictions that could affect tactile suppression. Furthermore, the efficacy of predictive control was not enhanced by the provision of explicit information regarding the statistical regularities of the provided trial sequence. Neither was there any discernible impact on kinematic behavior or tactile perception. Presumably, the previous trial effects of sensorimotor memories on kinematics are so pronounced that explicit knowledge is rendered inconsequential in this instance. This finding is consistent with those of previous studies, which also demonstrated that individuals tend to plan their movements under the assumption that object properties remain constant (Lukos et al., 2013; Witney et al., 2001). However, it appears that tactile suppression is a rather resource-intensive mechanism, requiring a reliable base for the brain to be able to build somatosensory predictions that would influence tactile perception. The relatively frequent alternation between constant and changing object properties seems to have led to an incalculable degree of uncertainty for the system to overcome.

The third study dived deeper into the basis of sensorimotor memories and explored whether classical principles from action control approaches, such as feature binding and retrieval, contribute to the establishment of sensorimotor predictions. Additionally, the third study explored these action control principles when performing more complex, continuous movement sequences, including the interaction with uncertain object properties. Prior research in the domain of action control has concentrated on simple motor actions (e.g. Frings et al., 2007, 2015;

Koch et al., 2018; Mayr & Buchner, 2006). The existence of previous trial effects in movement kinematics (Broda et al., 2020; Lukos et al., 2013; Voudouris et al., 2019) has demonstrated the viability of observing typical effects investigated in action control, including mixing and partial repetition costs. The results of the third study indicated that when an object was repeatedly grasped and lifted, a change in the object's mass distribution resulted in a significantly larger tilting angle. This suggests that participants planned their movements and the positioning of their fingers in a comparable manner to that observed during their previous contact with the same object. This is consistent with the idea that the features of the object and the movement itself were bound in a common event-file and were retrieved upon repeated exposure to the same object, as the Binding and Retrieval in Action Control (BRAC) framework suggests (Frings et al., 2020).

In addition to demonstrating the general usability of paradigms using complex, continuous actions, the third study also identifies a series of factors that should be considered when designing more naturalistic experiments. The mass distribution was found to exert a more pronounced influence on participants' behavior than the object position. It has been proposed that task-relevance is a crucial factor influencing the binding of a feature into an event-file (Memelink & Hommel, 2013; Mocke et al., 2020). In addition, the two object features used in the third study had varying degrees of accessibility throughout the trial. While the object position was directly visible, the mass distribution was not, and could only be experienced by lifting the object. This is in contrast to previous action control paradigms, in which all features are typically perceivable from the beginning of each trial. The greater complexity of continuous goal-directed movements provides an opportunity to integrate features of differing task-relevance and temporally varying accessibility in a natural manner. It is essential to give both factors careful consideration when designing new paradigms and analyzing results. Together with other studies demonstrating repetition effects in continuous goal-directed movements (Cohen & Rosenbaum, 2004; Dixon et al., 2012; Randerath et al., 2015; Valyear et al., 2019), the findings of the third study provide evidence for the applicability of reflecting the binding and retrieval of previous actions. This allows the design of paradigms that resemble natural real-world scenarios more closely, thereby enhancing ecological validity.

Implications & future directions

The findings of all three studies offer novel insights into the underlying mechanisms of goal-directed movements, with significant implications for future research and applications, including those in rehabilitation, prosthetics, and virtual reality. The influence of predictive mechanisms on tactile suppression is a dynamic process that occurs throughout the course of a

goal-directed movement (Voudouris & Fiehler, 2021). The results of Study 1 reinforce this conclusion and highlight the necessity of considering task relevance and the intensity of tactile feedback in this process. Future studies could examine whether a reduction or absence of tactile suppression is associated with a lack of task relevance of somatosensory feedback at a specific timepoint. Furthermore, it remains unclear whether a specific threshold exists for signal intensity, above which feedback is suppressed, or whether there is a continuous relationship between down-regulation and the benefit of improved sensitivity. A deeper comprehension of the modulation of tactile suppression can facilitate the development of haptic feedback systems in scenarios where precise tactile feedback is crucial, such as virtual reality, prosthetics, and teleoperation. This ensures that the feedback provided is both relevant and accurately processed by the user.

The findings of Study 2 additionally indicate that the investigation of tactile sensitivity at different stages of a movement is crucial. The embedding of the sections with constant object conditions appears to have resulted in the predictions being of insufficient strength. It is plausible that sensorimotor memories exerted no observable influence on the tactile suppression, as this uncertainty resulted in discrepancies between somatosensory predictions and observed outcomes at the timepoint under investigation. Future studies could investigate whether lifting the object and experiencing its current mass distribution would result in a different influence on tactile suppression. This would provide further insight into the influence of a predictive violation on tactile suppression throughout the course of a movement. The results in kinematic behavior corroborate the findings of previous research indicating that the most recent sensorimotor memories exert a pronounced influence on the planning of actions involving object interaction (Fu et al., 2010; Lukos et al., 2007, 2013; Scheidt et al., 2001; Voudouris et al., 2019). Advanced assistive technologies may be able to predict users' intended actions by considering their previous movements and sensorimotor experiences. This prediction can enhance the speed and accuracy of device response, thereby aiding users with reduced mobility and making the use of such a device more natural.

The results of Study 3 provide a basis for action control research in a more naturalistic way, as they showcase the applicability of paradigms involving complex, continuous goal-directed actions in reflecting principles, such as binding and retrieval as suggested by the BRAC framework (Frings et al., 2020). Future studies could investigate the number of motor features that can be bound together and the underlying mechanisms of their integration. This would help to determine whether the integration is dependent on spatial or temporal dependencies of the single action components. Furthermore, future studies could examine whether the varying

relevance of the features that occur in complex, continuous movements affects binding to an event file, as has been previously proposed for simple movements (Memelink & Hommel, 2013; Mocke et al., 2020). In order to gain a deeper insight into the processes that influence binding and retrieval, it may be beneficial to develop a potential feature hierarchy. Furthermore, the task of lifting an object and re-placing it, which was employed in Study 3, did not evoke a strong ecological relevance. The assignment of a higher-level goal to a continuous movement, such as lifting a virtual cup to drink without spilling the water, would serve to increase the proximity to an everyday task. Overall, Study 3 provides guidance for the design of more ecologically valid experimental paradigms that better reflect real-world tasks, thereby enhancing the generalizability of action control principles.

Concluding summary

The present dissertation, based on three studies, elucidates the intricate interplay of various factors in the establishment of somatosensory predictions. A particular emphasis was placed on the examination of somatosensory predictions that are based on current information, past sensorimotor memories, and cognitive action control principles and their influence on tactile perception and motor control during the execution of goal-directed movements. The findings reinforce the hypothesis that tactile suppression is a predictive mechanism, demonstrating sensitivity to the intensity and relevance of anticipated tactile feedback. It is evident that predictions based on sensorimotor memories exert a considerable influence on the planning and execution of movements, which can be further explained through the lens of action control mechanisms. Nevertheless, the reliability of these predictions based on the most recent experiences appears insufficient to affect tactile sensitivity. In conclusion, it can be stated that predictions based on past sensorimotor experiences and event-files exert a significant influence on motor control strategies, such as movement planning and execution. In contrast, tactile processing, as reflected in tactile suppression, remains relatively stable and is primarily influenced by the need to process somatosensory feedback signals that are both task-relevant and difficult to detect.

These findings contribute to a deeper understanding of how the brain uses past experiences, current sensory information, and cognitive control to predict and regulate the outcomes of goal-directed movements. Furthermore, they provide potential avenues for the enhancement of performance in various applied settings.

4 References

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II Publications

Publication I: Linking Signal Relevancy and Intensity in Predictive Tactile Suppression



Linking Signal Relevancy and Intensity in Predictive Tactile Suppression

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Predictable somatosensory feedback leads to a reduction in tactile sensitivity. This phenomenon, called *tactile suppression*, relies on a mechanism that uses an efference copy of motor commands to help select relevant aspects of incoming sensory signals. We investigated whether tactile suppression is modulated by (a) the task-relevancy of the predicted consequences of movement and (b) the intensity of related somatosensory feedback signals. Participants reached to a target region in the air in front of a screen; visual or tactile feedback indicated the reach was successful. Furthermore, tactile feedback intensity (strong vs. weak) varied across two groups of participants. We measured tactile suppression by comparing detection thresholds for a probing vibration applied to the finger either early or late during reach and at rest. As expected, we found an overall decrease in late-reach suppression, as no touch was involved at the end of the reach. We observed an increase in the degree of tactile suppression when strong tactile feedback was given at the end of the reach, compared to when weak tactile feedback or visual feedback was given. Our results suggest that the extent of tactile suppression can be adapted to different demands of somatosensory processing. Downregulation of this mechanism is invoked only when the consequences of missing a weak movement sequence are severe for the task. The decisive factor for the presence of tactile suppression seems not to be the predicted action effect as such, but the need to detect and process anticipated feedback signals occurring during movement.

Keywords: tactile suppression, prediction, feedback, goal-directed movement, task-relevance

INTRODUCTION

Somatosensory feedback plays a crucial role in the control of goal-directed movements. However, delays and noise associated with processing of afferent signals constantly arising from the moving body part can compromise the detectability of somatosensory feedback (Miall and Wolpert, 1996; Faisal et al., 2008). Selecting relevant aspects of incoming sensory information is fundamental for efficient signal processing. It has been suggested that, during movement, somatosensory feedback is combined with predictions about future sensory states of the moving body part in order to compensate for ongoing sensorimotor noise (Desmurget and Grafton, 2000). These predictions are formed on the basis of an efference copy of motor commands in a feedforward fashion (Wolpert and Flanagan, 2001). When somatosensory feedback can be precisely predicted, reliance

on such feedback can be minimized, resulting in a decrease in tactile sensitivity (Williams and Chapman, 2002; Bays et al., 2006; Chapman and Beauchamp, 2006). This mechanism, also referred to as *tactile suppression*, has been investigated during self-touch (Blakemore et al., 1998; Bays et al., 2005; Walsh et al., 2011; Kilteni and Ehrsson, 2017), showing that self-generated stimuli are perceived as less intense compared to externally generated stimuli. Externally generated stimuli are also harder to detect during movement, compared to a resting state (Chapman et al., 1987; Fraser and Fiehler, 2018; Gertz et al., 2018; Manzone et al., 2018; Voudouris and Fiehler, 2021). Importantly, this relative suppression is stronger for predicted compared to unpredicted somatosensory consequences of movement (Voudouris et al., 2019; Führer et al., 2021). In sum, tactile suppression provides a well-established behavioral measure of the strength of somatosensory predictions and allows us to understand how the brain utilizes predictions of future sensory states to efficiently process signals resulting from goal-directed movements.

Tactile suppression can be modulated by various factors. Some studies have reported a positive correlation between movement speed and the magnitude of tactile suppression. For example, Cybulska-Klosowicz and colleagues tested detection of a mild electrical stimulus applied to the finger during elbow extension movements of varying speeds (Cybulska-Klosowicz et al., 2011). They found no evidence of tactile suppression at very slow movement speeds (< 50 mm/s), whereas at higher speeds detection thresholds increased, indicating substantive tactile suppression. Moreover, tactile suppression decreases during haptic exploration (Juravle et al., 2013), which is typically associated with slower movement speeds. Other studies measuring the time course of suppression in goal-directed movements have reported an increase in tactile suppression early in the course of a movement, when movement speed is typically higher (Juravle et al., 2010; Colino and Binsted, 2016). These results are in conflict with more recent findings showing a release from suppression at the time of peak speed (Voudouris and Fiehler, 2021). Thus, it is still unclear how exactly movement speed can modulate tactile suppression or whether there are other factors influencing this relationship.

In a previous study, we sought to examine this ambiguity in more detail by determining whether implicitly generated differences in movement speed had a direct effect on tactile suppression (Fraser and Fiehler, 2018). Participants performed speeded reaching movements to a visual target. By manipulating the target's size, we systematically varied reach kinematics, capitalizing on Fitts' law (Fitts, 1954; Mackenzie et al., 1987), without changing the reach goal or explicit instructions between conditions. We measured suppression of a vibrotactile stimulus applied either early in reach (25% reach time), when higher speeds are expected, or late (75% reach time), when lower speeds are expected. In all conditions, participants significantly slowed down toward the end of the reach (by varying amounts, depending on target size). Despite this, we found an increase in the magnitude of tactile suppression at the later stages of movement, independent of target size. These results support other studies also showing stronger suppression at the end of

goal-directed movements (Juravle et al., 2018; Voudouris and Fiehler, 2021). In a follow-up experiment (Fraser and Fiehler, 2018), we tested whether the expectation of a tactile consequence at the end of the reach would further increase late-reach tactile suppression. Participants reached to visual targets of different colors associated with or without a tactile consequence. We found a selective increase in late-reach suppression only when a tactile consequence of movement was expected. We concluded that tactile suppression is modulated by the expected tactile consequences of movement in a time-sensitive manner. In other words, the ability to detect tactile stimuli seems to depend on a dynamic modulation of suppression, based on the predictability of anticipated feedback signals.

The previously described experiment, along with work showing certain predicted consequences of movement (e.g., expected force; Broda et al., 2020) do not likely modulate tactile suppression, raises questions about the exact nature of dynamic modulation of suppression. Predictability does not appear to be the sole factor modulating the strength of tactile suppression. Instead, specific predictable features of a movement seem to have more influence over modulation of suppression than others. One such influential feature is the *task-relevance* of a predicted sensory outcome. In our previous study, the tactile feedback which led to increased suppression was highly redundant. Visual cues indicating the successful end of the reach were always present. Thus, the selective increase in late-reach suppression we observed might be attributed to a lack of task-relevance of this tactile feedback. There is evidence that the strength of tactile suppression is indeed diminished in contexts where one is required to process somatosensory feedback signals, specifically at task-relevant effectors. For instance, during grasping, the magnitude of suppression is lowest in the fingers involved in the grasp (Colino and Binsted, 2016; Manzone et al., 2018). Furthermore, suppression is diminished during haptic exploration, when tactile information needs to be actively sampled (Juravle et al., 2013). It appears that the modulation of tactile suppression includes an adjustment for signals that, although highly predictable, remain informative and therefore useful.

In addition, the *intensity* of somatosensory feedback may have a potential influence on the dynamic modulation of tactile suppression. When uncertainty about somatosensory input occurs, predictive processes are downregulated to improve the processing of incoming sensory signals (Franklin et al., 2012). Decreasing the intensity of tactile feedback may increase the upweighting of input signals to avoid missing the sensory feedback. Such a strategy would necessarily be accompanied by a reduction in tactile suppression.

In the present study, we investigated whether tactile sensitivity during goal-directed movements is modulated by both the task-relevancy of the predicted consequences of movement and the intensity of related feedback signals. First, to increase task-relevancy of the tactile feedback, we employed a novel task in which (a) given feedback was uniquely informative about task completion, and (b) additional visual information about the target location was not provided during the movement. Second, we eliminated all other expected tactile signals at the end of

the reach as a possible confound by instructing participants to reach close to the screen without touching it. We kept feedback uniquely informative by having visual or tactile feedback as the only indication that a target was found. Thus, a predictable tactile component at the end of the movement was only present with tactile feedback. Visual feedback served as a control to highlight the influence of a predictable, yet task-relevant tactile feedback on the strength of somatosensory predictions. Additionally, we examined further modulation of tactile suppression by varying the intensity of the tactile feedback (strong vs. weak) across two separate groups of participants.

The ability to detect tactile signals was assessed early in the movement, when no feedback was predicted (~25% reaching time) and late in the movement, when anticipated feedback became more likely (~75% reaching time). As participants had to control and stop their movements before touching the screen, we expected an overall reduction in late-reach suppression for both conditions. We further hypothesized a relative increase in suppression in conditions where predictable tactile feedback occurred at the end of the movement, compared to when feedback was visual. We expected this increase in suppression to be most profound for the strong tactile feedback, which should result in better predictions and therefore more suppression of incoming signals. These results would indicate that both the need to process somatosensory information, and the anticipated intensity of this information, modulates suppression of predicted somatosensory signals.

MATERIALS AND METHODS

Participants

A total of 68 students participated in the study and completed the experiment. The sample size was not calculated *a priori*, but was chosen to be comparable to previous studies of tactile suppression (e.g., Fraser and Fiehler, 2018; Gertz et al., 2018; Manzone et al., 2018; Voudouris et al., 2019; Führer et al., 2021). In exchange for their participation, participants received either course credit, or financial compensation at the rate of eight Euro/hour. Owing to exclusion criteria (see section “Data Analysis”), the final sample consisted of 52 participants divided into two groups that received different intensities of tactile feedback during the experiment [strong tactile feedback: $n = 26$ (18 f, 8 m), age = 23 ± 3 ; weak tactile feedback: $n = 26$ (17 f, 9 m), age = 23 ± 3]. Participants were all right-handed, as assessed by the German translation of the Edinburgh Handedness Inventory (Oldfield, 1971; strong tactile feedback: 95, weak tactile feedback: 96). The experiment was approved by the research ethics board at Justus Liebig University Giessen, and was run in accordance with the Declaration of Helsinki (2008).

Apparatus

Participants were seated at an 80×117 cm table (Figure 1C) approximately 60 cm in front of the monitor (ViewPixx/3D, VPixx Technologies Inc., Saint-Bruno, Canada). A small keypad (12.5×8 cm) was placed at the edge of the table closest to the participant, under their right hand (approximately 40 cm

from the screen). A wireless mouse was fixed to the table at the same distance, and participants placed their left hand on it throughout the experiment. The participant's right hand was fitted with two custom-built vibrotactile stimulators (“tactors”; Engineer Acoustics Inc., Florida, United States), each with a 5 mm diameter vibration pad. The first tactor was attached to the dorsal surface of the right index finger, such that the pad rested on the skin, roughly equidistant between the proximal and distal interphalangeal joints (test tactor). The second tactor was attached to the ventral surface of the participant's finger just distal of the metacarpophalangeal joint (feedback tactor). The tactors were controlled using a custom MATLAB (Mathworks, Natick, United States) toolbox developed by Engineering Acoustics Inc. A small infrared-emitting diode was attached to the participant's finger; an Optotrak Certus (Northern Digital, Waterloo, Ontario, CA) mounted on the wall tracked the motion of the diode at a sampling rate of 100 Hz. Motion tracking was controlled via MATLAB using the MOTOM toolbox (Derzsi and Volcic, 2018). Tactors and wires were held in place with medical adhesive tape (Figure 1D).

Procedure

Before starting the experiment, participants completed a *calibration* block. Six white circles (0.5 cm radius) distributed in a ring around the center of the screen (Figure 1A) were presented one after the other. The first circle's location was determined for each participant by a random number generator, and the following five circles were equally spaced apart. When a circle appeared, participants were instructed to hold their finger in the air in front of the circle without touching the screen (Figure 1D). Once their hand was in position, they pressed a mouse button and the recorded finger location generated an invisible “target” location in the air. After recording all six target locations, a test phase began in which participants again had to reach to the targets in a randomized order. When participants felt their finger was in the right location, they clicked the mouse, and the fingertip location was recorded again. The test was considered successful if they recreated their previous pointing location with a 15 mm margin of error in every direction. If all six locations did not pass the testing, the calibration was repeated.

The experiment started with a *baseline* block, where participants kept their right ring finger pressed down a button on the keypad (start button). A ring (4 cm radius, line width 0.015 cm) flashed on the screen for 500 ms around one of the six target locations (location cue, Figure 1B); the target itself was never visible. Immediately after that two consecutive tones (100 ms, 1,000 Hz) were presented separated by a 2 s delay. In the middle of the delay, the test tactor vibrated for a 50 ms pulse (vibration trials) or kept silent (no-vibration trials). Participants were instructed to keep their hand still throughout the trial. Following the second tone, an onscreen message prompted participants to indicate if they had felt a vibration from the test tactor, using the mouse to respond yes or no. Five vibration intensities were tested (peak-to-peak displacement of 1.66, 4.98, 8.3, 11.63, and 14.96 μm), each delivered five times in a random order. In addition, five no-vibration catch trials were randomly interspersed throughout the test, leading to 30 trials in total.

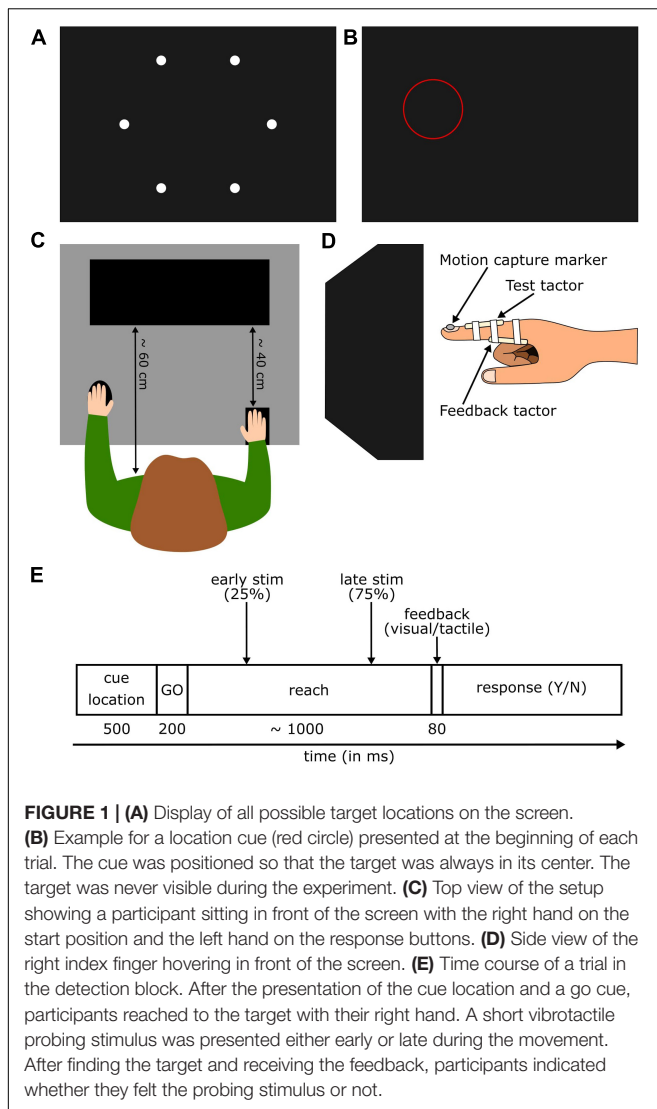


Figure 1E illustrates the trial progression. Participants completed two *detection* task blocks in a pseudorandomly assigned order. At the start of a trial, participants waited with their middle and ring finger on the start button. A location cue flashed for 500 ms on one of the six target locations; location cue characteristics were the same as in the baseline block. After the location cue disappeared, a go cue sounded for 200 ms and instructed participants to reach out with their right index finger to find the invisible target. Hand trajectory was recorded using the Optotrak. When the participant's fingertip reached the target, feedback was given. In the *tactile feedback* block, the feedback tactor on the base of the finger would emit an 80 ms pulse. One group of participants received strong tactile feedback (peak-to-peak amplitude of 134.7 μm , approximately 1,007% of the detection threshold during movement). This value was chosen to be very intense and thus clearly noticeable. The other group received weak tactile feedback (peak-to-peak amplitude of 18.29 μm , approximately 152% of the detection threshold during

movement). In a pilot experiment this value was identified as perceptually "faint" yet still detectable. In both cases the feedback vibration was the only indication that the target was found. In the *visual feedback* block, a message ("Target found") appeared in the center of the screen when the target was found. After receiving the feedback, participants returned to the keypad and pressed the start button again. The screen prompted them to respond whether they felt a vibration on the top of their right index finger during the movement. Participants responded using the mouse to indicate yes or no. Upon response, the next trial began.

Each detection block started with five practice trials wherein no stimulation was delivered. These were used to generate initial stimulation times for the first test trials. Following practice, trials could contain a 50 ms vibration from the test tactor at one of two time points. *Stimulation time* was calculated using either the 25% (early stimulation) or 75% (late stimulation) of the median of the previous five reaches. Eight vibration intensities (peak-to-peak displacement of 1.66, 4.98, 8.3, 11.63, 14.96, 18.29, 21.62, and 24.95 μm) were tested five times, in random order, at each of the two time points during movement. In addition, 16 no-stimulation catch trials were randomly interspersed in the trial order, leading to 96 initial trials for each block. In each trial, participants had 3 s to find the target location. If they took more than 3 s, a message ("Too slow") appeared on the screen. In this case, or if participants reached too quickly and the test stimulus did not fire, or if the stimulus fired during the last 150 ms of the movement, the trial was discarded and added to the end of the block. If participants reached too quickly and received an early stimulus in the second half of the reach time, the trial was reassigned to the late condition and a subsequent late trial of the same vibration intensity was removed. The early trial was added to the end of the block. If participants reached too slowly and received a late stimulus in the first half of the reach time, the trial was reassigned to the early condition, and a subsequent early trial with the same vibration intensity was removed from the block. The late trial was then repeated at the end of the block.

Data Analysis

Data preprocessing was conducted with MATLAB R2019b (MathWorks, Inc., Natick, MA). Motion capture data for a given trial included x, y and z coordinates of the marker from the right index finger from the sounding of the go cue until the target was found. These three vectors were dual-pass filtered using the MATLAB `filtfilt` function using a 2nd order lowpass butterworth filter with a cutoff of 30. The speed of the reaching index finger over the course of the reaching movement was calculated by numerical differentiation of x, y and z velocity. For each participant, speed data were averaged for each feedback type x stimulation time condition, resulting in four reach speed profiles (tactile-early, tactile-late, visual-early and visual-late). *Speed at stimulation* was extracted as the speed of the index finger at the timepoint when the test stimulus was triggered. Speed at stimulation was subjected to a repeated measures ANOVA comparing feedback type (visual, tactile), stimulation time (early, late), and tactile feedback intensity (strong, weak) to determine whether any of these factors influenced movement speed at

critical moments in the task. *Reach time* was calculated as the time between the go cue was given and the participant found the target. Reach time was assessed using a repeated measures ANOVA comparing feedback type (visual, tactile), stimulation time (early, late) and tactile feedback intensity (strong, weak) to determine whether any of these factors influenced the length of time a trial took to complete.

To analyze perceptual behavior, we fitted the proportion of trials in which the probing stimulus was perceived for the baseline and each experimental condition (feedback type x stimulation time x tactile feedback intensity) to a logistic function using maximum-likelihood estimation with the function *psignifit* (Wichmann and Hill, 2001) in MATLAB. The 50% detection threshold (point of subjective equality, PSE), which refers to the threshold of detectability, as well as the difference between the 50 and the 84% threshold (just noticeable difference, JND), which corresponds to one SD from the PSE and refers to the precision of the judgment, were extracted for each condition. Suppression scores were generated by subtracting the baseline PSE from the PSE of each movement condition. As with suppression, precision scores were formed by differences of the corresponding JNDs. Higher positive values for both suppression and precision scores indicated stronger tactile suppression. Participants showing a false alarm rate of 30% or higher ($n = 12$) or a baseline detection threshold or suppression scores that were ± 2.5 standard deviations from the group mean ($n = 4$) were excluded from all analyses. Tactile suppression scores ($n = 52$) were first compared in a one-tailed *t*-test, to determine whether significant tactile suppression occurred in each condition. Furthermore, suppression and precision scores were each subjected to a repeated measures ANOVA with feedback type (visual, tactile), stimulation time (early, late), and tactile feedback intensity (strong, weak) to determine whether any of these factors influenced the detection of the probing stimuli. Finally, to control for a relation of speed (Cybulska-Klosowicz et al., 2011; Fraser and Fiehler, 2018) and the amount of tactile suppression we correlated participants' reaching speed at each stimulation time, with their suppression score for that time. This was performed separately for each feedback type x stimulation time x tactile feedback intensity condition.

All statistical analyses were carried out with JASP (Version 0.14.1). Significant interactions were inspected with *post-hoc t*-tests, Bonferroni-corrected for multiple comparisons ($\alpha = 0.008$). Effect sizes are described as partial Eta squared for ANOVAs and Cohen's *d* for *t*-tests.

RESULTS

In line with previous studies (Fraser and Fiehler, 2018; Gertz et al., 2018; Manzone et al., 2018; Voudouris and Fiehler, 2021), tactile sensitivity was impeded in all reaching conditions, as all suppression scores were significantly greater than zero for both the group with the strong tactile feedback in the visual-early, $t(25) = 4.37$, $p < 0.001$, $d = 0.86$, visual-late, $t(25) = 2.12$, $p = 0.004$, $d = 0.42$, tactile-early, $t(25) = 5.39$, $p < 0.001$,

$d = 1.06$, and tactile-late condition, $t(25) = 4.01$, $p < 0.001$, $d = 0.79$ (see **Figure 2**, upper left panel), as well as for the group with the weak tactile feedback in the visual-early, $t(25) = 5.52$, $p < 0.001$, $d = 1.08$, visual-late, $t(25) = 5.55$, $p < 0.001$, $d = 1.09$, tactile-early, $t(25) = 6.99$, $p < 0.001$, $d = 1.37$, and tactile-late, $t(25) = 5.19$, $p < 0.001$, $d = 1.02$, condition (see **Figure 2**, upper right panel). Further, detection precision was significantly greater than zero in all reaching conditions for both the group with the strong tactile feedback in the visual-early, $t(25) = 2.95$, $p = 0.007$, $d = 0.58$, visual-late, $t(25) = 3.68$, $p = 0.001$, $d = 0.72$, tactile-early, $t(25) = 3.95$, $p < 0.001$, $d = 0.81$, and tactile-late condition, $t(25) = 3.95$, $p < 0.001$, $d = 0.77$ (see **Figure 2**, lower left panel), as well as for the group with the weak tactile feedback in the visual-early, $t(25) = 3.41$, $p = 0.002$, $d = 0.67$, visual-late, $t(25) = 3.37$, $p = 0.003$, $d = 0.66$, tactile-early, $t(25) = 4.25$, $p < 0.001$, $d = 0.83$, and tactile-late, $t(24) = 3.10$, $p = 0.005$, $d = 0.62$, condition (see **Figure 2**, lower right panel).

Participants showed a stronger suppression effect, which represent a decrease in detection threshold relative to baseline, when the feedback was tactile than when it was visual [$F(1, 50) = 8.27$, $p = 0.006$, $\eta_p^2 = 0.14$] (see **Figure 2**, upper panels), and when the stimulation occurred in the early than the late phase of the movement [$F(1, 50) = 35.69$, $p < 0.001$, $\eta_p^2 = 0.42$]. Further, we found a significant interaction between feedback type and tactile feedback intensity [$F(1, 50) = 5.47$, $p = 0.015$, $\eta_p^2 = 0.11$]. *Post-hoc t*-test revealed a significant difference between visual and tactile feedback only in case of strong tactile feedback, $t(25) = -3.82$, $p_{\text{bonf}} = 0.002$, $d = 0.75$ (see **Figure 3**). When tactile feedback was strong, participants showed more suppression for tactile than for visual feedback (tactile: $M = 3.78$, $SD = 4.11$; visual: $M = 2.35$, $SD = 3.70$), whereas when tactile feedback was weak, there was no difference between feedback conditions (tactile: $M = 3.75$, $SD = 3.34$; visual:

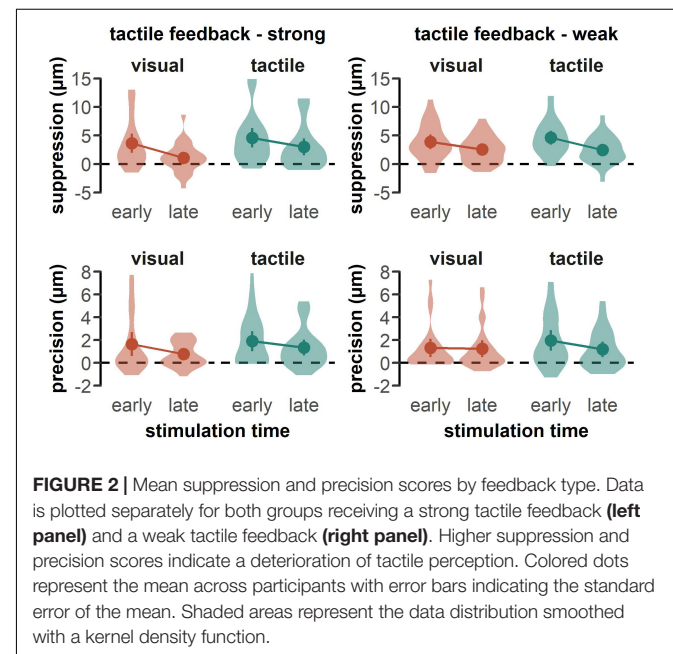


FIGURE 2 | Mean suppression and precision scores by feedback type. Data is plotted separately for both groups receiving a strong tactile feedback (**left panel**) and a weak tactile feedback (**right panel**). Higher suppression and precision scores indicate a deterioration of tactile perception. Colored dots represent the mean across participants with error bars indicating the standard error of the mean. Shaded areas represent the data distribution smoothed with a kernel density function.

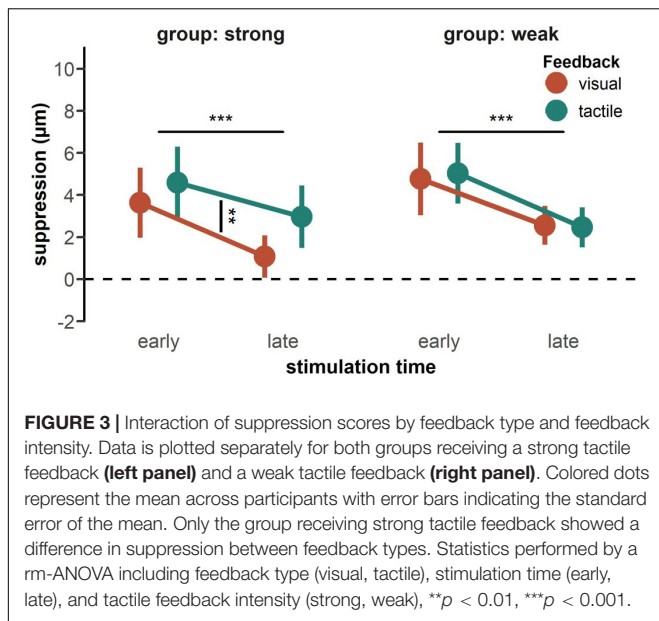


FIGURE 3 | Interaction of suppression scores by feedback type and feedback intensity. Data is plotted separately for both groups receiving a strong tactile feedback (left panel) and a weak tactile feedback (right panel). Colored dots represent the mean across participants with error bars indicating the standard error of the mean. Only the group receiving strong tactile feedback showed a difference in suppression between feedback types. Statistics performed by a rm-ANOVA including feedback type (visual, tactile), stimulation time (early, late), and tactile feedback intensity (strong, weak), ** $p < 0.01$, *** $p < 0.001$.

$M = 3.66$, $SD = 3.66$). There was no other significant main effect or interaction. In line with the suppression scores, the detection precision thresholds decreased relative to baseline in the late phase, compared to the early phase of the movement [$F(1, 50) = 8.22$, $p = 0.006$, $\eta_p^2 = 0.14$] (see Figure 2, lower panels). We found no other systematic differences in the precision scores.

Average reach time and average speed at stimulation are shown in Figure 4. Reach times, reflecting the time from the start of the movement until the target was found, were dependent on the timing of the probing stimulus, [$F(1, 50) = 113.48$, $p < 0.001$, $\eta_p^2 = 0.69$]. Receiving a probe in the late phase of the movement significantly reduced reaching time, compared to when it was presented in the early phase of the movement. There was also a significant feedback type x stimulation time interaction [$F(1,$

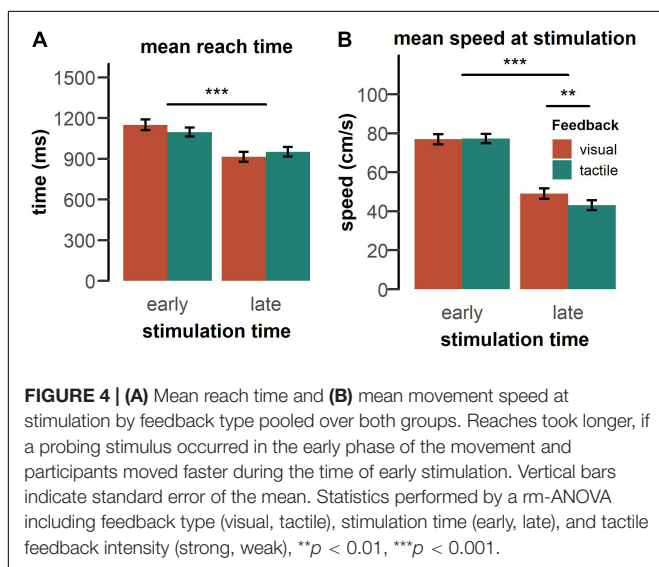


FIGURE 4 | (A) Mean reach time and **(B)** mean movement speed at stimulation by feedback type pooled over both groups. Reaches took longer, if a probing stimulus occurred in the early phase of the movement and participants moved faster during the time of early stimulation. Vertical bars indicate standard error of the mean. Statistics performed by a rm-ANOVA including feedback type (visual, tactile), stimulation time (early, late), and tactile feedback intensity (strong, weak), ** $p < 0.01$, *** $p < 0.001$.

$50) = 20.95$, $p < 0.001$, $\eta_p^2 = 0.30$]. The difference in reach time between the early and late stimulation condition was more pronounced with visual feedback, compared to tactile feedback, $t(51) = 4.60$, $p < 0.001$, $d = 0.64$. No other main effect or interaction was significant.

As expected on the basis of the typical speed profile of a goal-directed movement (see Figure 5), the speed at the moment of receiving the tactile stimulation was substantially higher in the early phase of the movement, compared to the late phase [$F(1, 50) = 176.60$, $p < 0.001$, $\eta_p^2 = 0.78$] (Figure 4). There was also a significant feedback type x stimulation time interaction [$F(1,50) = 19.55$, $p < 0.001$, $\eta_p^2 = 0.28$]. For the late stimulation condition, participants moved slower in anticipation of tactile feedback, compared to visual feedback, $t(25) = 3.52$, $p_{\text{bonf}} = 0.005$, $d = 0.40$, whereas there was no difference in movement speed in the early stimulation condition. No other main effect or interaction was significant.

For stimulation times, 25 and 75% of movement times were targeted. In fact, across all trials, stimulations occurred on average at 27.48 and 66.58% of the movement for visual feedback and at 27.88 and 67.36% for tactile feedback (see Figure 5). Thus, stimulation times for both feedback conditions were comparable and were in the early and late phases of reaching movement.

Finally, Figure 6 shows within-condition correlations between movement speed at stimulation and suppression scores. In the group receiving strong tactile feedback, we found a positive relationship between speed at time of stimulation and suppression in the late phase of the movement both for visual, $r = 0.45$, $p = 0.023$, and tactile feedback, $r = 0.40$, $p = 0.043$.

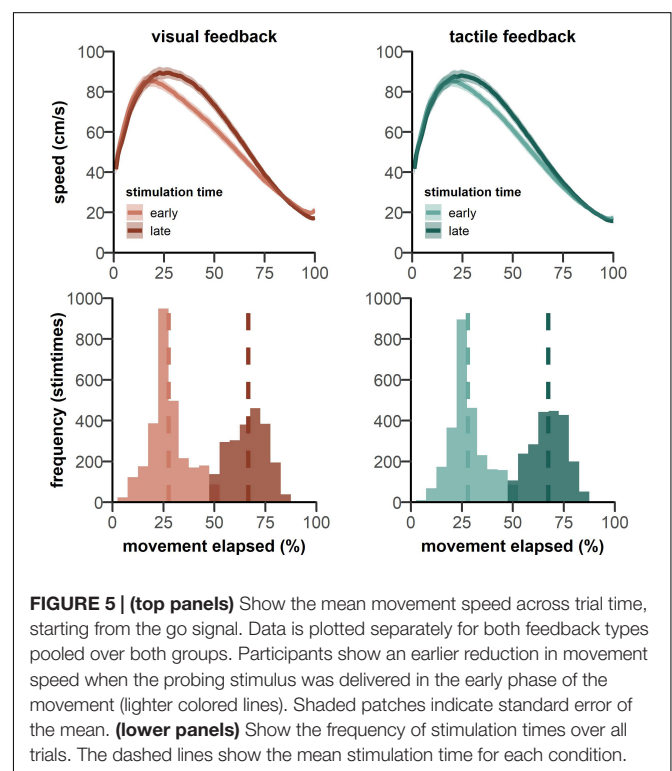
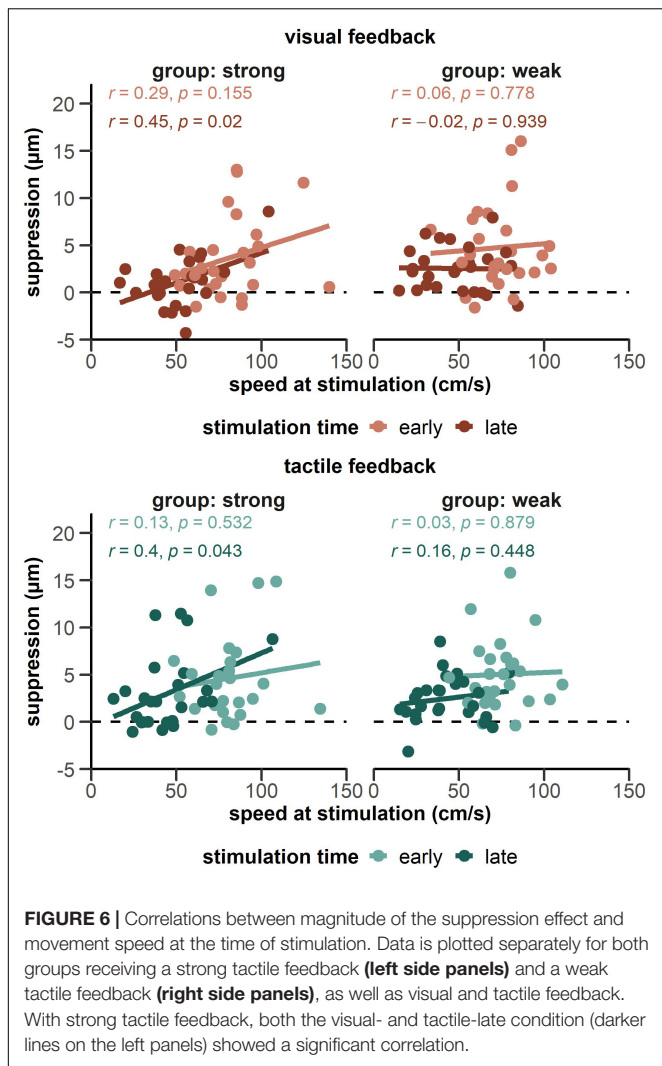


FIGURE 5 | (top panels) Show the mean movement speed across trial time, starting from the go signal. Data is plotted separately for both feedback types pooled over both groups. Participants show an earlier reduction in movement speed when the probing stimulus was delivered in the early phase of the movement (lighter colored lines). Shaded patches indicate standard error of the mean. **(lower panels)** Show the frequency of stimulation times over all trials. The dashed lines show the mean stimulation time for each condition.



DISCUSSION

In the present study, we aimed to investigate whether tactile suppression is modulated by (a) the task-relevancy of predicted somatosensory signals and (b) the intensity of these signals. We asked participants to reach to an invisible target in a cued area in the air. We varied the task-relevancy of predicted somatosensory feedback by providing either a visual or a tactile signal to indicate that the reach was successful. In addition, we varied the relative difficulty of detecting the tactile feedback by varying its intensity: one half of the participants received strong tactile feedback, while the other half received weak tactile feedback. Tactile probing stimuli were applied to the reaching finger, either early or late in the movement. We found that tactile suppression decreased in the late compared to the early phase of the movement. With strong, tactile feedback, suppression was more pronounced compared to visual feedback. There was no difference between weak tactile and visual feedback. Overall, our results support the view that tactile sensitivity is upregulated when the predicted somatosensory

consequences of a movement are task-relevant *and* associated feedback signals are faint. Such modulation of tactile sensitivity is advantageous, as it allows one to detect stimuli that would otherwise be missed. We suggest that such modulation may be characterized as a “release” from suppression if it is potentially resource-intensive to implement, and thus only invoked when such expenditure is required for successful goal-directed actions.

A novel component of this study was our attempt to reduce predictable touch at the end of a goal-directed movement. Predicted action effects can result in an increase in tactile suppression in the late phase of a movement, when manual contact becomes more likely (Juravle et al., 2010; Fraser and Fiehler, 2018; Voudouris and Fiehler, 2021). This could be explained by a forward model which suppresses somatosensory feedback when it can be reliably predicted, based on future sensory states of the moving body part to free capacities for efficient information processing (Desmurget and Grafton, 2000; Williams and Chapman, 2002; Bays et al., 2006; Chapman and Beauchamp, 2006). Certainly, such movements are characterized by highly detectable tactile outcomes. However, the increase in late reach suppression reported in these studies could also be attributed to a lack of task-relevance of the tactile feedback. For example, in the study by Fraser and Fiehler (2018), participants suppressed *more* when given paired tactile and visual feedback about task completion, compared to visual only feedback. In this case, the additional tactile feedback did not provide unique task-relevant information, as participants could solely rely on visual feedback. In contrast, reduced suppression can be found in haptic exploration when tactile information must be actively obtained for task completion (Juravle et al., 2013). Overall, it appears that increased suppression at the end of a movement is primarily related to the expectation of touch at the end of the reach that is not uniquely relevant to task performance.

Other studies have reported decreased tactile suppression at the end of a goal-directed movement (Colino and Binsted, 2016; Colino et al., 2017; Juravle et al., 2018). For example, during grasping the strength of tactile suppression is locally dependent and, thus, less pronounced on the index finger than on the pinky or the forearm of the involved limb (Colino et al., 2014; Colino and Binsted, 2016; Juravle et al., 2018). These data also suggest that suppression on the moving hand seems to be reduced when feedback signals become more relevant for the ongoing task (Colino and Binsted, 2016; Manzone et al., 2018; Voudouris and Fiehler, 2021). Theories of motor control, such as optimal feedback control, assume that sensory feedback is modulated according to the goals of an ongoing action (Todorov and Jordan, 2002; Liu and Todorov, 2007). An optimal estimate of the system’s state is predicted by combining sensory feedback and estimates from a forward model. Optimization of motor output is then accomplished by a controller that tunes feedback gains. Both predictive mechanisms and somatosensory feedback processing are combined in goal-directed movements to enable optimal action planning and flexible responses to incoming sensory information (Voudouris and Fiehler, 2021). A reduction in suppression could be explained by an increased reliance on

somatosensory feedback when it is necessary to perform the task. Depending on the task, this may affect different timepoints in the course of the movement and thus explain the temporal differences of tactile suppression found in different studies. Altogether, the relevance of processing somatosensory signals to successfully accomplish a task appears to be important in modulating tactile suppression, beyond the prediction of tactile stimuli in general.

In the present study, we observed stronger suppression in the early, compared to the late phase of the reach, although a predictable action effect was present only at the end of the reach. However, this action effect was much weaker compared to previous studies (Fraser and Fiehler, 2018), which included contact with a surface at the end of the movement, creating a highly predictable and detectable tactile consequence that may have increased late-reach suppression. Excluding this predictable touch signal at the end of the movement significantly reduced the temporal suppression profile. As the movement had to be stopped before the screen, participants needed to wait for visual or tactile confirmation that their movement was successful. Thus, the received feedback was uniquely relevant for the task and participants were required to detect it. For tactile feedback in particular, tactile suppression would impede task performance. In line with previous studies (Juravle et al., 2010; Voudouris et al., 2019), in our task participants had to rely on feedback signals to successfully accomplish their goal. This feedback processing is increasingly necessary in the late phase of the reach in order to appropriately control the movement and detect task-relevant feedback signals. This may explain a reduction in suppression in the late phase of the movement, compared to the early phase. To the best of our knowledge, our study was the first to show this pattern of suppression without a predictable touch at the end of a movement. Thus, our results suggest that it is not the predictable action effect alone being suppressed, but that the need to process task-relevant feedback signals that would otherwise be missed influences the strength of tactile suppression.

Further, the modality of received feedback influenced tactile suppression. As expected, we observed an overall increase in suppression for tactile compared to visual feedback, both in the early and in the late phase of the movement. This differential effect argues against a general gating mechanism, leading to an overall suppression of external somatosensory signals during movement (Press et al., 2020; Kilteni and Ehrsson, 2021). The increase in suppression for tactile compared to visual feedback points to a predictive component based on the expected tactile feedback at the end of the reach. Together with other studies (Fraser and Fiehler, 2018; Gertz et al., 2018; Manzone et al., 2018; Führer et al., 2021; Voudouris and Fiehler, 2021), our results support the assumption that suppression of external tactile probing stimuli cannot be explained by unspecific gating alone but is adjusted to predicted somatosensory consequences of the movement.

This assumption is further supported by the dependency of suppression on the intensity of tactile feedback, as we only observed a difference between visual and tactile feedback when tactile feedback was strong and not when it was weak.

Suppressing feedback signals that are already weak and thus harder to detect would increase the chance of missing relevant somatosensory information. As a consequence, weak feedback signals become less reliable, which has been associated with weaker suppression (Blakemore et al., 2000; Klever et al., 2019; Voudouris et al., 2019). Overall, it seems conceivable that feedback signals need to be stronger than the sensory noise associated with processing of afferent signals to be detected (Blakemore et al., 2000; Voss et al., 2008; Voudouris et al., 2019). If tactile suppression is strong, weak tactile consequences of movement will go undetected. In cases where such consequences are valuable to the moving agent (i.e., they are task-relevant), downregulating the predictive mechanisms which give rise to tactile suppression can improve task performance. This downregulation is only useful if the agent receives a marked improvement in detection. If somatosensory input signals are already strong, further increasing their strength does not seem to increase tactile suppression (Broda et al., 2020). Further research is needed to investigate whether there is a specific sensory threshold for somatosensory feedback signals to be suppressed, or whether there is a continuous relationship between downregulation and the apparent benefit of improved sensitivity.

Reach characteristics did not depend on the intensity of the tactile feedback received at the end of the movement; reaches were comparable between the two feedback groups. Movement speed profiles show that participants tended to decelerate fairly early in the movement on trials with a probing stimulus occurring in the early phase of the movement, compared to the late phase. This was also reflected in longer reaching times for the early stimulation condition. We speculate that this deceleration may be an effect of the probing stimulus, that is, participants are slowing down as they register or react to the sensation. The difference in reach time between the early and late stimulation condition was even more pronounced with visual feedback, compared to tactile feedback, pointing out a stronger deceleration in movement speed for this condition. As there was no strong expectation of a tactile sensation in the visual condition, the early probing stimulus may have been more surprising and therefore resulted in more online adjustment of the movement. These results raise an interesting question about how reach characteristics may be influenced by the detection task itself, which inherently distracts from the movement. However, as stronger suppression occurred consistently at both stimulation times for tactile feedback, movement differences alone cannot explain the differences in tactile suppression found for the two feedback types.

In addition to these differences in movement characteristics, the highest suppression occurred in the early phase of the movement together with the time of maximum speed during the reach. Interestingly, there was no correlation between movement speed and suppression in the early, but in the late phase of the movement. Only when tactile feedback was strong we observed a positive relation between speed at stimulation and suppression. At the same time, speed at stimulation time was greatly reduced in the late phase of the movement, even more in anticipation of tactile compared to visual feedback.

Overall, higher speed can therefore not explain the increase of suppression during movement. The previously reported positive relationship between the speed of movement and the amount of tactile suppression appears rather context-dependent (Angel and Malenka, 1982; Schmidt et al., 1990; Cybulska-Klosowicz et al., 2011). Since there was no contact with a surface in our current experiment, an increase in the expected force due to higher speeds (e.g., by hitting the surface harder) cannot explain the correlation with suppression scores in the late phase of the reach. In addition, the relationship between suppression and speed at time of stimulation occurred equally for both feedback modalities and yet there was more overall suppression in the tactile condition. This again argues against the assumption that differences in movement trajectories alone can explain the differences in suppression. Rather, the partly contrasting results of different studies regarding the extent of suppression, especially at the end of a movement, might reflect different demands in somatosensory processing caused by specific movement conditions.

CONCLUSION

In summary, the present study supports the view that tactile suppression is based on a predictive mechanism, which is modulated by the need to process incoming somatosensory information that is both task-relevant and difficult to detect. Consequently, tactile suppression can to some extent be adapted to different demands in somatosensory processing. We showed that a reduction in predictability of an action effect at the end of the reach can lead to a general reduction in tactile suppression. Nevertheless, the mechanism proved sensitive to the modality of received feedback. Tactile suppression was more pronounced with tactile feedback, compared to visual feedback. Further, a reduction in tactile suppression was shown by reducing the intensity of anticipated feedback signals, suggesting that downregulation occurs when the consequences of missing a weak movement sequence are severe. We conclude that it is not the predicted action effect alone which influences the extent of tactile suppression, but rather the need to detect and process predicted feedback signals occurring during the movement which matters most.

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article are publicly available at <https://doi.org/10.17605/osf.io/v7q9n>.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Research Ethics Board, Department of Psychology and Sports Science, Justus Liebig University Giessen. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

MB: data curation, formal analysis, investigation, project administration, software, validation, visualization, roles and writing—original draft, and writing—review and editing. LF: conceptualization, data curation, methodology, project administration, software, and writing—review and editing. KP: conceptualization, funding acquisition, methodology, project administration, resources, supervision, and writing—review and editing. All authors contributed to the article and approved the submitted version.

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**Publication II: Sensorimotor Memories Influence Movement Kinematics but not
Associated Tactile Processing**



OPEN

Sensorimotor memories influence movement kinematics but not associated tactile processing

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When interacting with objects, we often rely on visual information. However, vision is not always the most reliable sense for determining relevant object properties. For example, when the mass distribution of an object cannot be inferred visually, humans may rely on predictions about the object's dynamics. Such predictions may not only influence motor behavior but also associated processing of movement-related afferent information, leading to reduced tactile sensitivity during movement. We examined whether predictions based on sensorimotor memories influence grasping kinematics and associated tactile processing. Participants lifted an object of unknown mass distribution and reported whether they detected a tactile stimulus on their grasping hand during the lift. In Experiment 1, the mass distribution could change from trial to trial, whereas in Experiment 2, we intermingled longer with shorter parts of constant and variable mass distributions, while also providing implicit or explicit information about the trial structure. In both experiments, participants grasped the object by predictively choosing contact points that would compensate the mass distribution experienced in the previous trial. Tactile suppression during movement, however, was invariant across conditions. These results suggest that predictions based on sensorimotor memories can influence movement kinematics but not associated tactile perception.

Successful human-world interactions require processing of relevant sensory signals. For example, when grasping an object, humans choose grasping points based on visual information about the object's size¹, orientation², shape³, or surface material⁴. However, vision is not always the most reliable sense to work out relevant object properties. Indeed, although object mass can be inferred from visual information, as mass typically increases with object size, there are occasions when vision misleads our judgements, such as the size-weight illusion⁵. Likewise, although an object's mass distribution can be inferred by the object's shape, some objects that appear to be symmetric may actually have an asymmetric mass distribution. When grasping objects with properties that cannot be reliably inferred from vision, such as of unknown mass distribution, humans *appear* to adopt a generic grasping behavior⁶. If the mass distribution remains invariant over repeated trials, humans rapidly learn and establish more reliable predictions about the object's properties, which helps to tailor their motor behavior by adopting more suitable grasping postures and by applying more efficient digit forces that foster a stable grasp and object manipulation⁷. In such cases, it is evident that humans learn the object dynamics through prior experiences that arise from somatosensory feedback during object interactions.

Despite the importance of somatosensory feedback for motor control and learning, somatosensory afferents, in particular those from the tactile domain, are typically suppressed during movement^{8–13}. This phenomenon of tactile suppression is primarily explained by an internal feed-forward model that predicts future sensory states of the moving limb and suppresses associated sensory signals^{14, 15} based on efferent signals related to the underlying movement^{16–18}. Tactile suppression is typically assessed by presenting tactile stimuli on a limb when it is moving compared to resting. It has therefore been suggested that tactile suppression may not be sensitive only to sensorimotor predictions, but also to other factors, such as backward masking or attentional processes due to dual-tasking. For instance, peripheral mechanisms, such as proprioceptive afferents arising from the movement itself may obstruct the perception of the tactile stimulus on the moving limb through backward masking¹⁹. However, tactile suppression is not stronger at moments when sensory feedback signals are stronger, such as

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when grip and load forces are increased²⁰. Tactile suppression is also robust to increased cognitive demands when performing more than one task²², and it occurs only when the probing tactile stimuli are presented on the moving limb, and not on a static limb while another limb is moving¹², further supporting the idea that suppression does not simply occur due to *any* type of movement. Instead, tactile suppression is a process related to sensorimotor predictions¹⁴, reflecting the interplay between predictive and sensory feedback signals^{6,21}.

Sensorimotor predictions are based on a combination of current sensory feedback and prior knowledge about the prevailing dynamics²³. When statistical regularities are highly systematic, such as when repeatedly grasping an object of constant mass distribution, sensorimotor predictions are used both to adopt a suitable grasping posture and to suppress associated tactile feedback⁶. Likewise, when the object's mass distribution changes on a trial-by-trial basis in an unpredictable manner, the adopted grasping configuration remains similar and the associated tactile suppression is substantially weaker⁶. However, even in such unpredictable environments, humans plan their movements on the basis of predictions inferred through their most recent sensorimotor memories^{24,25}. Specifically, people grasp an object of unknown mass distribution *as if it had* the mass distribution experienced in the previous trial. Thus, predictive control seems to be preserved even when acting within unpredictable worlds, and even if these predictions may eventually be incorrect.

In the present study, we sought to examine whether such predictions based on sensorimotor memories influence grasping kinematics and associated tactile processing. We asked participants to grasp and lift an object with a mass distribution that could not be inferred from visual information. The object's mass distribution changed in a pseudo-randomized order across trials but, unbeknownst to the participants, consecutive trials could involve either the same or different mass distributions. At the moment of object contact, a brief vibrotactile probe stimulus on the index finger of the grasping hand was presented to probe tactile suppression^{6,10} and participants had to report whether they detected that probe stimulus or not. We probed tactile suppression right at the moment of contact, and not later, to isolate the effects of the sensorimotor prediction, without contamination from subsequent sensory feedback that could either confirm or contradict this prediction. This time of probing is used to assess participants' reliance on predictive and feedback processes, with stronger suppression reflecting weaker reliance on feedback signals and a stronger reliance on predictive processes^{6,14}. Specifically, when reliance on sensory feedback is reduced, for instance because participants rely more on predictive signals, then sensory sampling from the moving limb will be downweighed, leading to the suppression of the probe tactile stimulus. Likewise, in cases where sensory sampling is more important, the associated sensory feedback from the moving limb will be prioritized, and therefore the probing tactile stimulus on the moving hand will be less suppressed or even enhanced.

Based on previous work²⁴, we expected previous trial effects on various kinematic variables. We also expected tactile suppression during grasping compared to rest^{6,10}. If tactile suppression is modulated by predictions established on the basis of sensorimotor memories, we expected stronger tactile suppression when the mass distribution of an object is repeated from one trial to another compared to when it changes.

Experiment 1

Methods

Participants

Twenty-four participants (18 female, 6 male) aged 19–34 years ($mean = 23 \pm 3.6$) participated in this experiment. In the context of tactile suppression, our study is the first to examine sequence effects. Thus, no data were available on the basis of which we could have calculated an a priori power analysis. Therefore, our sample size was based on previous studies on tactile suppression^{6,8,11,14,22,26}. Participants were all right-handed as measured by the German translation of the Edinburgh Handedness Inventory²⁷ ($range = 60–100$), free from any known neurological conditions, and had normal or corrected-to-normal visual acuity. All participants gave informed written consent to participate in the experiment and received 8 €/hour or corresponding course credits as compensation for their effort. The experiment was approved by the research ethics board of the Department of Psychology and Sports Science, Justus Liebig University Giessen and was in accordance with the Declaration of Helsinki (2013, except pre-registration of the study).

Apparatus

Participants had to grasp and lift an inverted T-shaped object (Fig. 1a). The object had a depth of 5 cm. The lower part was 15 cm wide and 3 cm high, while the upper part was 5 cm wide and 7 cm high. At the backside of the lower part of the object, invisible to the participants, three tubes were distributed laterally. A cylindrical piece of brass (116 g) was inserted in either the left or the right tube, creating an asymmetric object's mass distribution (MD). The total mass of the object, including the brass, was 273 g.

Participants were seated comfortably in front of a 117 cm × 80 cm table (Fig. 1b). A small keypad (12.5 cm × 8 cm) on the table was under the participant's left hand at a comfortable position. The start position for each reaching-to-grasp movement was aligned to the participants' right shoulder and was marked by a round piece of felt pad located ~30 cm in front of their body. To avoid stereotyped movements, two different lateral object positions were used, each 34 cm from the start position. To prevent participants from seeing in which tube the experimenter inserted the brass prior to each trial, participants wore liquid-crystal shutter glasses (PLATO, Translucent Technologies, Toronto, Canada) throughout the grasping block (see below).

To track the movement of the participants' hand and of the object, the position of five infrared markers were recorded at 100 Hz with an Optotrak Certus motion tracking system (Northern Digital Inc., Waterloo, ON, Canada). One marker each was attached to the fingernail of the participants' right thumb and index finger. The other three markers were attached in a triangular arrangement on the backside of the object.

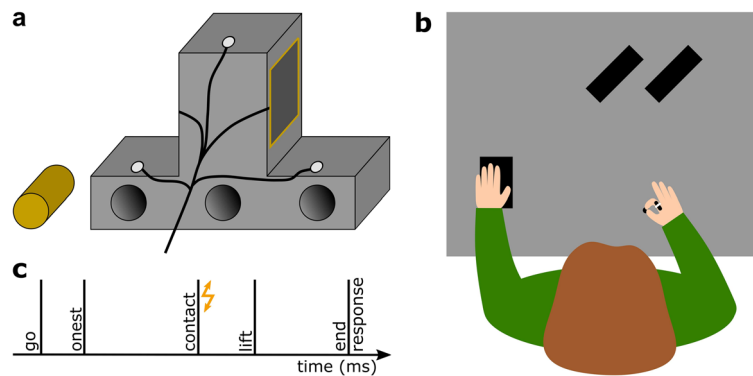


Figure 1. Experimental setup. (a) Illustration of the backside of the inverted T-shaped object with three infrared markers (white circles) and touch sensors (here only one visible) fixed to the grasping area of the object. The three tubes in the object's base were never visible to the participant. The brass mass is depicted to the left of the object. (b) Top view of the setup with the right index finger and thumb resting on the start position and the left hand resting on the numpad. A vibrotactile sensor was fixed on the dorsal part of the participant's right index finger. Both object positions are also depicted (black rectangles). (c) Timeline of a single trial with the flash illustrating the vibrotactile stimulation at the moment of object contact.

Vibrotactile stimulations, always given at the moment of object touch, were triggered by a touch sensor (4.37 cm × 4.37 cm; Interlink Electronics Inc., Westlake Village, CA, USA) that was mounted on each grasping side of the upper part of the object and that was connected through a NI USB-6009 device (National Instruments Corporation, Austin, TX, USA) to the host PC. A vibrotactile stimulation device (Engineering Acoustics Inc., Casselberry, FL, USA) was attached to the dorsal part of the medial phalanx of the participants' right index finger. To allow for a natural grasp, we did not cover the fingertip of the participants with the tactor but chose to stimulate close to the site critical for the movement, as tactile suppression has a rather low spatial specificity across the hand¹⁹. The presented vibrotactile stimuli (250 Hz, 50 ms) differed in intensity; six stimuli had a peak-to-peak displacement ranging from 9.4 to 56.7 μm in steps of 9.4 μm, while one third of the trials involved no stimulation. As tactile information becomes increasingly relevant the closer the hand moves to an object's surface¹¹, we applied tactile stimulation at the moment of first object touch, just before participants lifted the object and received sensory information about its mass distribution. This enabled us to pick up the original prediction regarding object dynamics and examine its impact on tactile processing. This is also in line with previous studies^{6,20} showing that the timepoint when participants made first contact with the object is sensitive to predictive tactile suppression.

Care was taken to ensure that motion tracking markers, the tactor and the connected cables did not constrain the participants' freedom of movement.

Procedure

The experiment consisted of three blocks: two baseline blocks and one grasping block. In the baseline blocks, participants rested their right hand in a comfortable position in front of them. Each baseline trial started automatically: a probe vibrotactile stimulus was presented, if at all, 500 ms after the beginning of the trial. An auditory cue 500 ms after that moment prompted participants to press a button underneath their left index finger or thumb and indicate whether they felt a vibration or not, respectively. The next trial started automatically 500 ms after the response was given. During each of the two baseline blocks, each of the six stimulus intensities was presented five times, while the no-stimulation catch trials were presented 15 times, resulting in a total of 45 trials presented in a pseudorandom order. One baseline block each was presented before and after the grasping block in order to account for possible changes in tactile sensitivity over time.

During the grasping block, each trial started with the shutter glasses being opaque and the participant bringing their right thumb and index fingertips together at the start position. The experimenter inserted the brass mass into the appropriate tube and then placed the object on the appropriate position. Even if the mass distribution was similar between two consecutive trials, the brass was always pulled out and inserted into the given tube to keep auditory cues constant. After the experimenter pressed a key to start the trial, the shutter glasses turned transparent and an auditory signal indicated that participants could start their movement. They were to reach out and grasp the object with their right thumb and index finger at both sides of its upper part, where the touch sensors were attached, lift it as straight as possible for ~ 10 cm, before placing it back down on the table and returning their hand to the start position. Once participants first touched the object, as this was detected by the first activation of the touch sensors, a probe vibrotactile stimulus could be presented on the participant's right index finger. These probe stimuli were identical to those presented in the baseline blocks. After five seconds following the auditory signal, data collection was stopped, the shutter glasses turned opaque, and an auditory cue prompted participants to indicate whether they had felt a probe stimulus (yes/no response). Participants responded in the same way as in the previously described baseline procedure. Figure 1c illustrates the progression of a single grasping trial.

In the grasping block, each participant was presented with a trial sequence of mixed mass distributions. This was designed in a way that all possible combinations of consecutive mass distributions occurred equally often during the block: left followed by left (LL), right followed by left (RL), left followed by right (LR), and right followed by right (RR). For each of these four combinations, 30 trials with vibrotactile stimuli and 15 without a stimulation were presented, identical to those presented in one baseline block. The sequence was designed so that there would appear to be no regularity in the sequence of combinations, either in the mass distribution or in the intensities of the tactile stimuli. This mixed sequence consisted of trials where the mass distribution repeated (*mixed_{same}*; LL and RR) or changed (*mixed_{different}*; LR and RL) from one trial to the next. Overall a total of 180 trials were presented, with 90 trials having the object on the left and the other 90 trials on the right target position in a pseudorandom order across trials. Before starting the grasping block, participants performed nine practice trials to familiarize with the task and the object weight. For those trials, the brass cylinder was placed into the central tube of the object, and this was the only case when the symmetric mass distribution was used. In these practice trials, each stimulus intensity was presented once, in addition to three catch trials with no stimulation. The object was randomly placed five times on the left position and four times on the right position, or the other way around, counterbalanced across participant.

Data analysis

The first goal of the study was to examine whether participants plan their upcoming movement on the basis of sensorimotor memories, i.e. sensorimotor information experienced in the previous trial. To analyze the relevant kinematic behavior, we examined the influence of the previous trial's MD on (a) the vertical separation of the digits at the moment of first object contact, (b) the time between first object contact and object lift, and (c) the maximal object roll during lifting. To determine the relevant kinematic measures for each trial, we first calculated the speed of the hand and of the object by numerical differentiation of the mean position of the markers on both digits and on the object, respectively. These two speed vectors were dual-pass filtered using the MATLAB *filtfilt* function with a 2nd order lowpass butterworth filter and a cutoff frequency of 0.3 Hz. Object lift onset was defined as the first timepoint at which the object speed was greater than 10 cm/s. The moment of object contact was determined as the last timepoint before object lift onset with a hand speed lower than 10 cm/s. For each trial, we calculated the *digits' separation* as the mean vertical distance between the thumb and the index finger within the first 100 ms from the moment of object contact, with positive values indicating that the thumb was placed higher than the index finger⁶. *Loading time* was defined as the time between the moment of contact and object lift onset. Finally, *object roll* was defined as the absolute maximal tilt angle within the first 250 ms after the onset of the object lift.

Next, we examined whether kinematic behavior on a trial with a given MD was influenced by the MD experienced in the previous trial. We defined two configurations of consecutive MDs: *MD_{same}* involved consecutive MDs that were identical (LL, RR), whereas *MD_{different}* involved different consecutive MDs (RL, LR). Overall, each trial (*n*) was classified based on the mass distribution presented in the preceding trial (*n* - 1). For instance, if the MD in the first four trials of a block was RRL, we classified the second trial (R) as '*MD_{same}*', the third trial (L) as '*MD_{different}*', and the fourth trial (L) as '*MD_{same}*' (see also Fig. 2a). For each trial, we calculated the *digits' separation* as the difference in the vertical position between the markers on the thumb and index fingers at the moment of object contact, with positive values indicating that the thumb was positioned higher than the index finger. Please note that each trial, except the first of the block, was both the first and the second trial of a possible pair, and that only the second trial of each pair was used to calculate the digits' separation. After calculating this for all trials, we averaged the values across the four conditions (LL, RR, LR, RL) to obtain four average vertical distance values per participant. To avoid negating the actual effect, the average digits' separation in trials with left MD were subtracted from the corresponding value in trials with right MD, separately for *MD_{same}* (RR-LL) and *MD_{different}* (LR-RL) configurations. Based on previous work^{6,24}, we expected participants to place their thumb lower and higher than the index finger when they anticipated the mass to be on the right and left side, respectively, which would minimize object roll during object lift (see Fig. 2b). As these would lead to negative and positive digits'

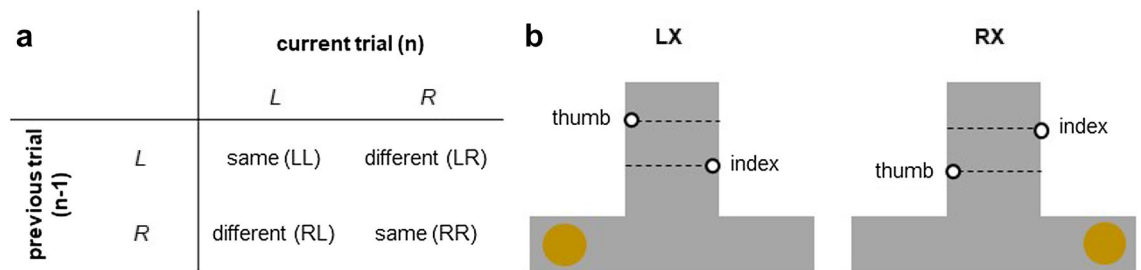


Figure 2. Previous trial configurations. **(a)** Possible combinations of previous and current trial MDs. The *MD_{same}* configuration involved repeats of the same MD in two consecutive trials (LL & RR), whereas the *MD_{different}* configuration involved a change of MD (RL & LR). **(b)** Expected positioning of the digits on the object, based on previously experienced MD. The previous position of the brass mass is represented by a golden circle. With a previous MD on the left (LX), a higher placement of the thumb was expected in the current trial X, and with a previous MD on the right (RX), a higher placement of the index finger was expected in the current trial X.

separation indices (see above), respectively, the MD_{same} calculation (RR–LL) should yield negative indices and the $MD_{different}$ calculation (LR–RL) should yield positive indices. In other words, if the resulting index is negative when the mass distribution is repeated and positive when the mass distribution is switched, this should indicate that participants use predictive control and adopt in trial n a grasp configuration to match the dynamics experienced in trial $n - 1$, independently of whether the adopted grasping posture is suitable for the mass distribution of the current object. *Loading time* and *maximal object roll* were calculated based on the average values that were obtained for each trial for both configurations (MD_{same} , $MD_{different}$).

The second goal of the study was to examine whether sensorimotor memories influence somatosensory processing on the grasping hand. In accordance with previous work^{6,10}, we expected decreased sensitivity to the probing vibrotactile stimuli during grasping compared to the resting trials. If participants consider the MD experienced in the previous trial in order to predict the MD in the upcoming trial, tactile sensitivity should change accordingly: tactile suppression should be stronger in the second of two consecutive trials with identical MD, as the predicted and experienced movement dynamics match. Alternatively, if tactile suppression is affected by backward masking, we expect stronger suppression in trials with different MD than predicted, due to increased feedback processing²⁸. To assess tactile suppression, we first merged the responses of both baseline blocks and fitted each participant's responses in each condition (baseline, MD_{same} , $MD_{different}$) with separate logistic functions using maximum-likelihood estimation with the function *psignifit 3*²⁹ in MATLAB 2019b (MathWorks, Natick, MA). For each of these three psychometric functions that we obtained for each participant, we estimated the detection threshold as the stimulus intensity at 50% of the function. To quantify tactile suppression during grasping while accounting for individual tactile sensitivity, each participant's baseline detection threshold was subtracted from their respective values of the two grasping configurations (MD_{same} , $MD_{different}$). Each of these suppression values were calculated for each participant, and then averaged across participants, with higher positive values indicating stronger tactile suppression. Participants only took part in the whole experiment if their false positive rate in the baseline trials was below 30%. In the grasping block, false alarm rates were below 30% for all participants. Further, we merged the two baseline blocks because we found no differences in the respective detection thresholds.

After calculating the above-mentioned variables, we examined effects of sensorimotor memories on grasping kinematics and associated tactile suppression. For kinematic behavior, we submitted the index values for digits' separation to two-sided one sample t-tests against zero, which tested whether participants adopted a grasping posture based on the mass distribution experienced in the trial before. For tactile processing, we examined whether detection thresholds during each grasping condition was greater than those during baseline by submitting the suppression scores in two-sided one sample t-tests against zero. In a second level, we investigated the effect of previous mass distribution on all kinematic variables and tactile suppression, by using separate paired samples t-tests for grasping kinematics and tactile processing between trials with repeating (MD_{same}) and changing MD ($MD_{different}$). Effect sizes are described as Cohen's d . All statistical analyses were carried out with JASP (Version 0.14.1) and plots were generated using R (Version 1.4.1717) and the package ggplot2 (Version 3.3.5).

Results

Kinematics

Regarding finger positioning on the object, we found mean index values below zero for the MD_{same} condition ($t_{23} = -5.07$, $p < 0.001$, $d = -1.04$) and above zero for the $MD_{different}$ condition ($t_{23} = 8.08$, $p < 0.001$, $d = 1.65$), indicating that participants positioned their fingers in anticipation of a MD that was identical to the one presented in the trial before, independently of whether this prediction was correct or not. Accordingly, the index value was smaller for MD_{same} than $MD_{different}$ ($t_{23} = -10.83$, $p < 0.001$, $d = -2.21$; Fig. 3a).

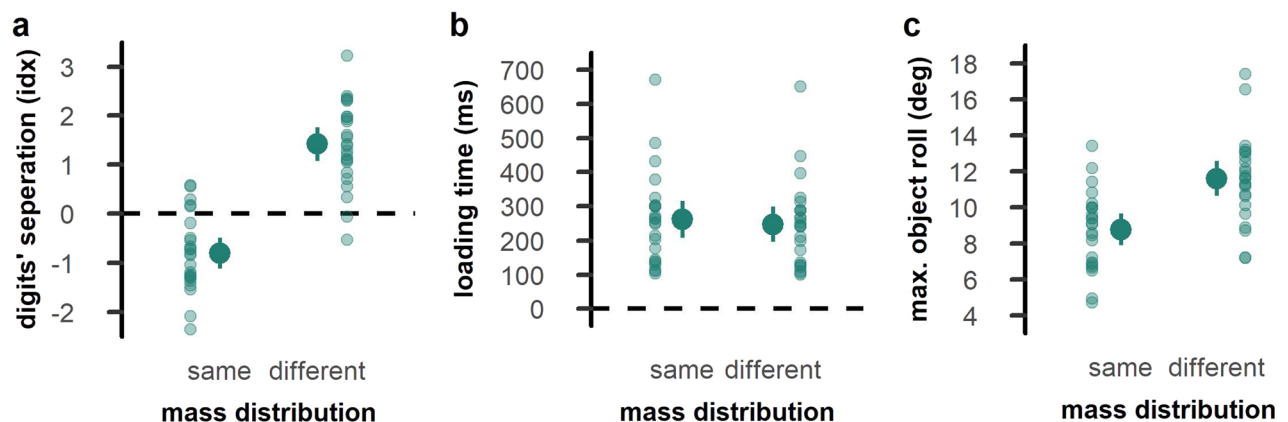


Figure 3. Kinematic performance in Experiment 1. (a) Digits' vertical separation at the moment of object contact, (b) loading time, and (c) maximal object roll during the first 250 ms after object lift. The left side of each panel shows trials with a repeated mass distribution, and the right side for trials with a changing mass distribution. Opaque dots represent the mean across participants with error bars indicating the confidence interval. Transparent dots represent individual participants.

The MD experienced in the previous trial also affected loading time ($t_{23} = 5.42$, $p < 0.001$, $d = 1.11$; Fig. 3b) and maximal object roll ($t_{23} = -18.93$, $p < 0.001$, $d = -3.87$; Fig. 3c) in the current trial. Specifically, loading times were longer and object roll was smaller when the MD was repeated from one trial to another compared to when it was changed.

Tactile sensitivity

As expected^{6,10}, tactile suppression was evident during grasping compared to rest. This was the case for both the MD_{same} ($t_{23} = 7.04$, $p < 0.001$, $d = 1.44$) and $MD_{different}$ ($t_{23} = 8.452$, $p < 0.001$, $d = 1.72$). Yet, we found no effects of previous trial MD on tactile suppression ($t_{23} = 0.33$, $p = 0.742$, $d = 0.07$; Fig. 4).

Discussion Experiment 1

We investigated whether and how sensorimotor memories influence grasping kinematics and associated tactile processing. Our results show that, when grasping an object with uncertain properties, humans utilize sensorimotor memories based on previous trial experience to plan their next movement²⁴. Specifically, participants grasped an object of unknown mass distribution by predictively choosing contact points that would compensate the mass distribution experienced in the *previous* trial, even if the mass distribution in the current trial was different than predicted. These results suggest that sensorimotor memory is used to adjust movement kinematics when object properties are uncertain and sensory action consequences are hard to predict. In line with previous findings^{6,10}, tactile sensitivity was decreased during grasping compared rest reflecting movement-induced tactile suppression. However, tactile suppression was unaffected by the mass distribution of the previous trial, as it did not differ between consecutive trials of repeating and changing mass distributions. These results suggest that tactile suppression is neither affected by predictions based on sensorimotor memories ($MD_{same} > MD_{different}$), nor by backward masking ($MD_{same} < MD_{different}$).

In this experiment, participants had no information about the mass distribution as this could change from trial to trial. We also probed tactile suppression at a moment when the current mass distribution could not be confirmed. Thus, any predictions based on sensorimotor memories might have been equally strong for trials that involved the same (MD_{same}) compared to trials that involved a different mass distribution than the one predicted ($MD_{different}$). To address this possibility, we conducted Experiment 2, where we interleaved longer sequences of trials involving an object of constant mass distribution with shorter sequences of trials with changing mass distribution. We assumed stronger sensorimotor predictions in sequences of constant compared to mixed distributions, and thus expected stronger suppression in those sequences. This experiment was further split into two sessions: in the first session, participants were exposed to the interleaved constant and mixed sequences to test for implicit learning of the statistical regularities of the trial sequence. In the second session, the experimenter informed the participants explicitly about the upcoming sequence (constant or mixed). This was done to explore whether explicit information about the upcoming trial sequence would alter predictive control and the strength of tactile suppression with stronger suppression for the constant compared to the mixed sequence.

Experiment 2

Methods

Participants and apparatus

Twenty-four participants (14 female, 10 male) aged 18–31 years ($mean = 22.71 \pm 3.46$) participated in the study and completed the experiment. None of the participants took part in Experiment 1. They were all right-handed as measured by the Edinburgh handedness inventory (range = 60–100) and had normal or corrected-to-normal visual acuity. As in Experiment 1, participants gave their written informed consent and received monetary

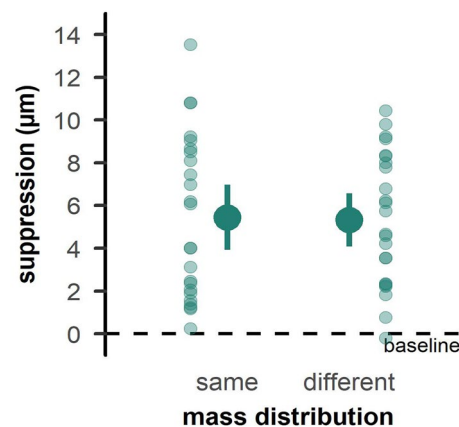


Figure 4. Tactile suppression scores in Experiment 1. The left side of each panel shows trials with a repeated mass distribution, and the right side trials with a changing mass distribution. Zero values indicate no change from baseline, while higher values indicate a deterioration of tactile perception. Details as in Fig. 2.

compensation or course-credits for their efforts. The setup, procedure and analyses were identical to those of Experiment 1, except for the details mentioned below.

Procedure

Experiment 2 consisted of two sessions, each performed on different days. Each session included two baseline blocks, a short practice and a grasping block, all following the same procedure as in Experiment 1. The main difference was the implemented trial sequence. We created a trial sequence with longer parts of 27 trials with a constant MD (*constant*), which were interrupted by short parts of nine trials with a pseudorandomized MD (*mixed*). The longer constant parts should allow building more stable predictions. The mixed interruptions were kept short to limit the total duration of the experiment allowing it to be completed in one session. Since we did not find an effect of the previous trial's MD on tactile suppression in Experiment 1, we did not split the mixed sequence in MD_{same} and $MD_{different}$ trials. Rather, we compared suppression only between mixed and constant parts. We presented three constant parts with a left MD and three blocks with a right MD, always interrupted by a mixed part. The sequence always started with a mixed part and consisted of 216 trials in total. The mixed parts were constructed in the same way as the mixed sequence in Experiment 1. Within the constant, longer parts, one of the two possible MDs was chosen, counterbalanced across participants, but the object position could still change within these parts. During the first session, participants were not informed about the structure of the presented sequence (*implicit version*). At the end of this session, participants filled out a custom questionnaire asking whether they observed a specific trial structure of the presented sequence. Only one of the twenty-four participants indicated that they noted some repetitions. During the second session, performed on average seventeen days later, the very same sequence was presented to each participant. During this session, the experimenter explicitly informed the participant verbally about the structure of the upcoming part of the sequence by indicating whether they would encounter a mixed or constant part (*explicit version*), without however indicating what mass distribution would be presented in the upcoming constant part.

Data analysis

Conditions were divided according to the parts of the sequence (mixed, constant) and the experimental version (implicit, explicit). It should be noted that in Experiment 2, we did not examine the trial-by-trial differences, but rather the differences that could emerge due to the overall context of repetitions or changes in MD. Particularly in the mixed condition, this is expected to result in a mean closer to zero for the digit separation index, which is comparable to calculating a mean for the values as outlined in Experiment 1. The effects of sequence part (mixed, constant) and experimental version (implicit, explicit) on digits' separation, loading time, object roll, and tactile suppression were evaluated using separate 2×2 repeated measures ANOVAs. Significant interactions were inspected with post-hoc t-tests that were Bonferroni-corrected for multiple comparisons. Effect sizes are described as partial Eta squared (η_p^2) for ANOVAs and as Cohen's d for t-tests.

Results

Kinematics

For digits' separation, a negative index occurring when the mass distribution is repeated and a positive when the mass distribution is switched, indicate that participants adopt in trial n a grasp configuration to match the dynamics experienced in trial $n - 1$, independently of whether the adopted grasping posture is suitable for the mass distribution of the grasped object. As expected, and in line with the results of Experiment 1, in the constant parts participants positioned their fingers in anticipation of a repeated MD in both the implicit ($t_{23} = -6.23$, $p < 0.001$, $d = -1.27$) and the explicit version of the experiment ($t_{23} = -6.53$, $p < 0.001$, $d = -1.33$). Likewise, in the mixed parts participants positioned their fingers in anticipation of a repeated MD, irrespective of whether the MD was repeated or changed. This was the case during both the implicit ($t_{23} = 2.39$, $p = 0.026$, $d = 0.49$) and the explicit version ($t_{23} = 3.51$, $p = 0.002$, $d = 0.72$). Evidently, these resulted in a main effect of sequence part ($F_{1,23} = 61.12$, $p < 0.001$, $\eta_p^2 = 0.73$; Fig. 5a). We found no differences between implicit and explicit parts, nor an interaction (both $F < 1.3$, both $p > 0.30$, both $\eta_p^2 < 0.05$).

Participants took longer to start lifting the object when the MD was constant over several trials compared to when the MD changed ($F_{1,23} = 6.82$, $p = 0.016$, $\eta_p^2 = 0.23$). They also took longer to start lifting the object in the first, implicit version of the experiment, compared to the second, explicit version ($F_{1,23} = 11.56$, $p = 0.002$, $\eta_p^2 = 0.33$; Fig. 5b). There was no interaction between the two factors ($F_{1,23} = 0.70$, $p = 0.411$, $\eta_p^2 = 0.02$).

Object roll was smaller during the lift when the MD was repeated over several trials compared to when the MD changed ($F_{1,23} = 470.69$, $p < 0.001$, $\eta_p^2 = 0.95$; Fig. 5c), in line with the results of Experiment 1. There was no effect of the experimental version nor an interaction (both $F < 2.5$, both $p > 0.13$, both $\eta_p^2 < 0.10$).

Tactile sensitivity

Tactile suppression was evident during grasping compared to rest in the implicit version both in the constant ($t_{23} = 7.15$, $p < 0.001$, $d = 1.46$) and the mixed parts of the sequence ($t_{23} = 8.72$, $p < 0.001$, $d = 1.78$), as well as in the explicit version, again both in the constant ($t_{23} = 7.41$, $p < 0.001$, $d = 1.51$) and the mixed part of the sequence ($t_{23} = 7.47$, $p < 0.001$, $d = 1.52$). Suppression appeared stronger in the mixed than constant parts, but this difference was not statistically significant ($F_{1,23} = 4.01$, $p = 0.057$, $\eta_p^2 = 0.15$). There was also no difference in suppression between implicit and explicit versions ($F_{1,23} = 0.45$, $p = 0.510$, $\eta_p^2 = 0.02$; Fig. 6), indicating that the type of knowledge about the statistical regularities of the upcoming trial sequence did not systematically affect tactile suppression. There was also no interaction between the factors ($F_{1,23} = 2.69$, $p = 0.114$, $\eta_p^2 = 0.11$).

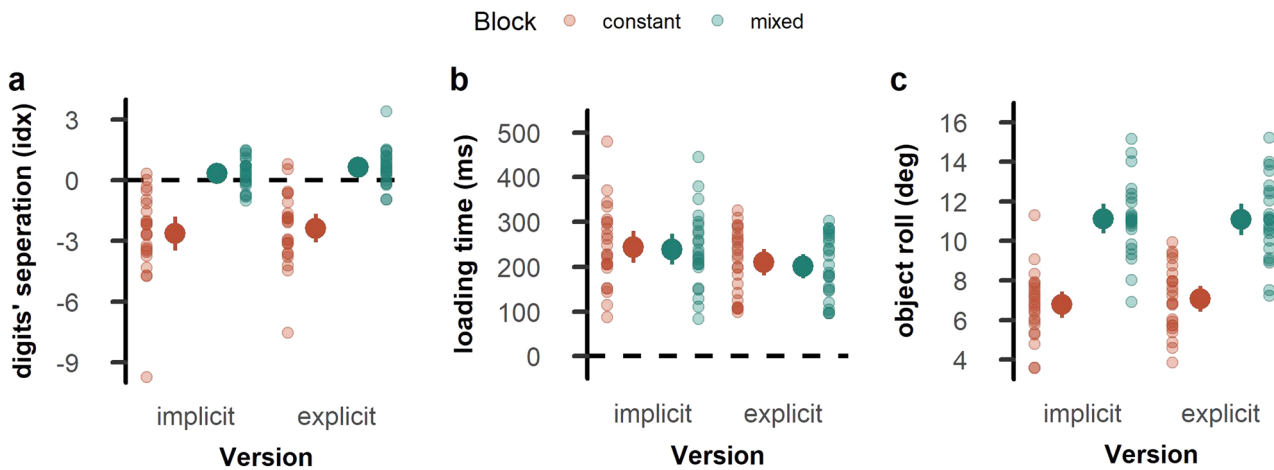


Figure 5. Kinematic performance in Experiment 2. (a) Digits' vertical separation at the moment of object contact, (b) loading time, and (c) maximal object roll during the first 250 ms after object lift. The left side of each panel shows results for the implicit version, and the right side for the explicit version. Mean values for the constant blocks are depicted in red, those for the mixed blocks in green. Opaque dots represent the mean across participants with error bars indicating the confidence interval. Transparent dots represent individual participants.

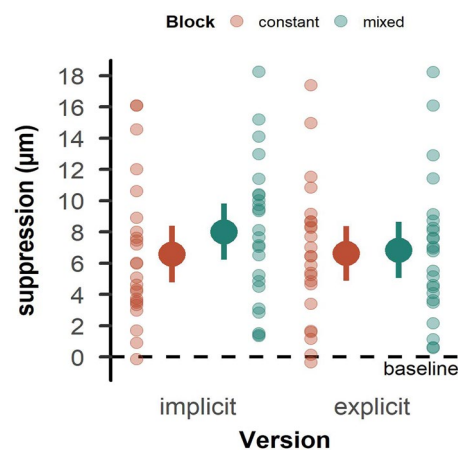


Figure 6. Tactile suppression scores in Experiment 2. The left side of each panel shows the implicit version, and the right side shows the explicit version. Mean values for the constant blocks are depicted in red, those for the mixed blocks in green. Zero values indicate no change from baseline, while higher values indicate a deterioration of tactile perception. Opaque dots represent the mean across participants with error bars indicating the confidence interval. Transparent dots represent individual participants.

Discussion Experiment 2

In Experiment 2 we investigated whether longer parts of repeated object properties would lead to more reliable sensorimotor predictions and hence stronger tactile suppression. Further, we were interested in whether implicit or explicit information about the trial structure would affect tactile suppression. Grasping kinematics were affected similarly to Experiment 1, with grasping postures being predictively chosen to compensate for object roll, even if this prediction might have been wrong. We again found tactile suppression during grasping compared to rest, but suppression was similar between the constant and mixed parts. These results support and further extend the findings of Experiment 1, showing that sensorimotor memories influence movement kinematics but not associated tactile perception. The similar suppression between constant and mixed parts is, however, at odds with previous findings, where suppression was stronger when grasping an object whose mass distribution remained identical over trials than when it changed⁶. One possible explanation is that in the current study, participants were exposed to the constant parts for shorter durations and these constant parts were alternating with mixed parts, which might have limited the establishment of reliable predictions that could affect tactile suppression.

Implicit and explicit information about the upcoming trial structure did not affect the grasping posture or object roll, and it had no effect on tactile suppression. Yet, our results showed that during the explicit session of the experiment, participants started lifting the object earlier than during the implicit session. We interpret this finding with caution, as the explicit version was presented always *after* the implicit version. This does not allow

us to conclude whether this effect is caused by the explicit information itself or whether it is a byproduct of practice, as participants may have lifted the object faster simply because they were more familiar with the task.

General discussion

In this study we examined whether sensorimotor memories influence grasping kinematics and associated tactile processing. Participants reached to grasp an object that could have one of two possible mass distributions. When the mass distributions were presented in a pseudorandom order across trials (Experiment 1), participants grasped the object in the second of two consecutive trials as if it had the mass distribution experienced in the previous trial, demonstrating predictive grasping behavior based on sensorimotor memories. Similar behavior was observed in Experiment 2, when the mass distributions were presented both in a mixed and in a constant order. To assess tactile processing, we employed the well-established phenomenon of tactile suppression and found clear suppression of tactile signals during grasping compared to rest. However, the strength of tactile suppression was unaffected by the statistical regularities of the trial sequence. Our results indicate that sensorimotor memories exert a strong influence on movement behavior but not on associated tactile processing.

Goal-directed behavior is primarily based on visual information. For instance, when grasping an object, humans use vision to extract relevant object properties, such as its size¹, orientation², shape³, or surface material⁴, and they choose suitable grasping points already during movement planning^{30,31}. However, visual information is not always available or informative about certain object properties. For instance, the object's center of mass may not always be inferred from vision. When interacting with such objects, humans initially adopt a 'default' motor behavior, and if object properties remain invariant and occur recurrently, they use somatosensory feedback from the previous interaction to predict the object properties and tailor their movement accordingly⁷. However, when object properties change continuously, predictions are less reliable and can be misleading. Yet, even in such cases, humans plan their movements assuming that the object in question has the same properties as those experienced in the previous trial^{24,25,32}. Our experiments support such predictive behavior. Specifically, participants grasped the object in the second of two consecutive trials as if it had the dynamics experienced in the trial before. Here, the grasping posture cannot have been chosen based on somatosensory feedback from the object of the current trial because we measured this grasping posture before such feedback could be utilized. This tuning of grasping posture demonstrates that motor plans are established based on sensorimotor memories. Evidently, such memories can be advantageous when the prediction is correct but disadvantageous when it is incorrect, as reflected in object roll during object lift.

The second aim of the study was to examine whether tactile processing associated with object grasping and manipulation is affected by predictions established through sensorimotor memories. To capture the original prediction about the object dynamics based on the object's behavior in the previous trial and to examine its influence on tactile processing, we stimulated at the moment of first contact with the object, just before participants lifted it and received sensory information about its mass distribution. It has been shown that tactile suppression is stronger in the early than late phases of a grasping movement suggesting a greater dependence on predictive control during this period^{10,33,34}. The results of our two experiments demonstrate robust tactile suppression during movement, in line with previous findings^{6,10}. This supports the idea that sensorimotor predictions established during movement reduce associated tactile sensitivity¹⁴. In Experiment 1 we show that tactile suppression did not differ between trials of the same than different mass distribution compared to the distribution experienced in the previous trial. This suggests that, although predictions from sensorimotor memories influence grasping kinematics, these predictions do not affect tactile suppression. One possible explanation for this finding is that we assessed tactile suppression at the moment of first contact with the object. At that moment, participants had no access to sensory input about the actual mass distribution. This guaranteed that the measured tactile suppression was influenced only, or at least primarily, from the established sensorimotor predictions, without additional effects of the instantaneous sensory input. However, this experimental decision may also mean that the sensorimotor prediction at that moment might have been equally strong independently of the object's actual mass distribution. In such case, it is unsurprising that tactile suppression is similar between conditions. In Experiment 2 we included a condition with sequences of 27 consecutive trials that involved an object of constant mass distribution. Such constant parts should facilitate predictions about the object's mass distribution compared to the mixed sequence, in which the mass distribution was changing on a trial-by-trial basis. Despite the long sequences of trial repetitions in the constant parts, tactile suppression was similar between constant and mixed parts. This is at odds with previous findings that demonstrated stronger suppression in constant than mixed sequence parts⁶. Such difference may arise due to the fact that in our current experiment the mixed and constant parts were relatively short and were presented interchangeably, whereas in the other study the mixed and constant parts were much longer and were presented in distinct blocks. Thus, in the present study, tactile suppression might not have been adapted as effectively, as participants had to constantly adjust to a switch between constant and mixed intercepts, and as a consequence the sensorimotor predictions in the constant parts might have been weaker compared to the previous study⁶. Future research could explore how tactile sensitivity changes during the grasp and lift movements and how it is affected by predictive violation with different stimulation times throughout the course of the movement.

Tactile suppression has also been explained by peripheral mechanisms, such as backward masking from movement-related afferent signals that mask the tactile probe used to measure suppression¹⁹. In this case, we would have expected stronger suppression in trials where the prediction about the object's mass distribution was wrong, such as in $MD_{different}$ than MD_{same} trials of Experiment 1. This is because, when experiencing an unpredictable sensory event during goal-directed actions, sensory feedback gains increase²⁸, and so such an increase in feedback processing might mask the previously presented tactile probe stimulus. In Experiment 2, it appears that suppression is qualitatively stronger in the mixed compared to the constant condition of the

implicit version, however this was not systematic. All in all, our results do not lend support for the hypothesis of backward masking either, and the apparent invariance in suppression as a function of feedback signals is in line with previous findings²⁰.

In Experiment 2 we further examined whether grasping kinematics and tactile suppression are sensitive to statistical regularities that are implicitly or explicitly inferred. Previous research has demonstrated that implicit learning of the underlying dynamics can be beneficial for sampling, for instance through haptic exploration³⁵. In addition, implicit sensorimotor memories of object properties can influence the anticipation of these properties³⁶, both in the absence and presence of explicit cues³⁷. Yet our kinematic results did not reveal any benefit from the explicit instruction about the trial sequence. Albeit, we observed a slight decrease of loading times when explicit information about the upcoming sequence was provided. However, it is noteworthy that this benefit may simply be due to the repetitive performance of the task, as the explicit session was *always* presented after the implicit session, so we cannot disentangle effects of practice from effects of the type of information. Importantly, we also did not observe any effects of implicit or explicit information on tactile suppression. Informing participants about the fact that the upcoming trials would be of a mixed or a constant sequence does not have any strong effect on motor behavior or associated tactile processing.

In conclusion, we demonstrate that predictions based on sensorimotor memories influence grasping kinematic by adjusting the grip to the previously experienced object properties. However, associated tactile suppression appears robust to such previous trial effects.

Data availability

The data collected for this work will be publicly available at <https://doi.org/10.17605/osf.io/w6ruy>.

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Author contributions

M.C.B.: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing—Original Draft, Writing—Review & Editing, Visualization, Project administration. D.V.: Conceptualization, Methodology, Writing—Review and Editing, Supervision, Project administration. K.F.: Conceptualization, Methodology, Resources, Writing—Review and Editing, Supervision, Project administration, Funding acquisition.

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Competing interests

The authors declare no competing interests

Additional information

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**Publication III: Episodic Binding and Retrieval in Sequences of Discrete Movements –
Evidence from Grasping Actions**



Episodic Binding and Retrieval in Sequences of Discrete Movements – Evidence from Grasping Actions

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RESEARCH ARTICLE

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ABSTRACT

In everyday life humans are confronted with changing environmental demands. In order to act successfully and achieve intended goals, action control is required. A recent approach, the Binding and Retrieval in Action Control (BRAC) framework, attempts to provide an overarching perspective on action control. Based on basic principles such as binding and retrieval, findings from several experimental paradigms could be integrated. However, the focus so far has been on rather artificial paradigms involving very simple motor response requirements, like finger lifting or button presses. We aimed to extend the BRAC framework to more complex movements consisting of a sequence of several discrete actions. Participants were asked to grasp and lift an object with an uneven mass distribution. Object features, like mass distribution and position, were either kept constant on a global level or varied in a pseudorandomized manner. When both object features were kept constant, participants were able to adjust their grasp so that it resulted in a more stable lift and less object roll. Further, with randomly mixed object features, we found best task performance when both object features were completely repeated from one trial to the other. These results suggest that tasks with more complex movements are capable of reflecting principles of action control as defined by the BRAC framework. This offers the possibility to test these principles in even more complex and ecologically relevant paradigms to improve our understanding of everyday life actions.

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Humans continuously perform actions to interact with their environment to produce desired perceptual action effects (Dignath et al., 2014; Pfister et al., 2014). These actions move along a continuum from simple actions, such as flipping a light switch, to more complex action sequences, such as brewing our morning coffee. And even if some actions seem trivial in everyday life, the underlying processes are far more complex. For example, when reaching for our cup of coffee in the morning, many factors must be considered for this action to be successful: the location of the cup, its weight, as well as the nature of the handle and its surface structure. Prior experience or visual cues can help to identify these factors; however, they are always associated with some degree of uncertainty (Faisal et al., 2008; Schultheis, Straub & Rothkopf, 2021). Especially when actions become more complex and occur in situations involving change or uncertainty, they must be adaptive and flexible to respond to these changing environmental demands (Frings et al., 2020). This poses increased demands on processes of action planning and control, which are required to perform such complex movements in order to achieve the intended goals.

Action control is driven by different aspects of cognition, like perception, attention, memory, and motor planning (Frings et al., 2020). To date, a wide variety of theories of action control, such as S-R Binding Approaches to Memory (Henson et al., 2014) or Theory of Event Coding (Hommel et al., 2001), have been developed to explain the results of specific paradigms. Some of the most commonly used paradigms are task switching (Koch et al., 2018), negative priming (Frings et al., 2015; Mayr & Buchner, 2006), or stimulus-response binding (Frings et al., 2007; Hommel, 1998). Theories of action control have several commonalities (Frings et al., 2020). They usually rely on tasks using a sequential trial methodology – the processing of information at one (prime) trial influences the processing and reaction at a subsequent (probe) trial. Binding approaches propose that in the process of motor planning, cognitive mechanisms are often influenced by specific aspects of previous actions. These situational action aspects are coded as elementary features and are thought to be integrated into a common episode or “file” (e.g. Hommel, 1998, 2004; Treisman, 1996). Such an episode is stored in memory and can later be reactivated (i.e., retrieved) through feature repetition. Although there are many commonalities among the different theoretical approaches, paradigm-specific theories have been repeatedly put forward instead of a unified theory.

A recent approach to action control, the Binding and Retrieval in Action Control (BRAC) framework, provides a general and comprehensive theoretical framework for various experimental outcomes from different paradigms (Frings et al., 2020). BRAC focusses on two core processes of action control: feature binding and feature-based event-file retrieval. Following the sequential logic of many experimental paradigms, features of the stimulus environment, a response in that environment, and its subsequent effects are thought to be bound together in an event-file. These event-files can be multisensory, for example, when visual, tactile, and auditory features are combined. If any feature is repeated in a subsequent trial, this will trigger automatic retrieval of the previous event-file from memory. Depending on the requirements of the respective trial the retrieval may result in performance benefits or costs. For example, in task switching paradigms (e.g. Koch et al., 2018), two tasks are performed alternately (e.g. odd/even judgement of numbers vs. vocal/consonant judgement of letters) by using the same keys to make the different judgments. If the task changes, a deterioration in the performance, usually reflected in longer reaction times, can be observed in comparison to a repetition of the task. The hitherto established explanation for this switch cost embraces the interference of the new task with the persistent inhibition of the competing task (see Koch et al., 2010, for a review) or the persistent activation of the previous task, impairing performance (see Koch & Kiesel, 2022, for a comprehensive review of theoretical accounts). Importantly, task switch costs could also be explained by the integration of both the stimulus and task in the prime trial (Frings et al., 2020; Koch et al., 2018). Upon stimulus repetition in the probe trial, the previous task is automatically retrieved, leading to interference in case of a required task switch.

Using the principles described in the BRAC framework, several other effects commonly encountered in the study of action control can be addressed as well. One aspect is the global expectation of consistency of a task, also called *mixing costs*. That is, if a task is performed several times in consecutive order, performance is often better than if the task or features

of the action change from one occasion to the other (Los, 1999; Philipp et al., 2008; Rubin & Meiran, 2005; Steinhauser & Hübner, 2005). When switching between different tasks is required or a task involves mixed features, additional processing is usually needed to switch between the required actions relative to single-task conditions, leading to mixing costs (for reviews see Koch & Kiesel, 2022; Kiesel et al., 2010).

The BRAC framework can also account for results of other paradigms for the study of action control (for an overview see Frings et al., 2020). For instance, it could account for *partial repetition costs* (Hommel, 1998). That is, when confronted with sequences of mixed stimulus-response combinations, participants generally perform better when the current stimulus and response features are either completely repeated or when no feature is identical (Hommel, 1998, 2004). Thus, performance is most likely to be impaired when one feature repeats while another changes. This leads to partial repetition costs, suggesting that previously linked feature bindings are retrieved, which in case of partial repetitions create a conflict between the retrieved action and the action that is actually required (Frings et al., 2020). The retrieved action must be suppressed and therefore results in a relative impairment compared to cases in which all features or no feature are repeated. Overall, the BRAC framework is intended to integrate action-related phenomena from different research areas. This framework should allow for a broader application even beyond the scope of typical cognitive studies on action control.

As BRAC is aimed at providing an overarching perspective on action control, the described core principles of binding and retrieval should be transferable to different experimental paradigms. This transfer has been done to some extent by focusing on rather artificial paradigms using very simple motor response requirements. In these paradigms, stimuli are usually presented on a computer screen and prompt for a button press as the required action. Furthermore, features in these simple paradigms are often clearly perceivable at the beginning of each trial. If the principles postulated in the BRAC framework are universal (as claimed), they should also be applicable to actions involving movements of higher complexity (i.e., more degrees of freedom). Many of our everyday-like actions are characterized by sequences of several discrete movements, e.g. when grasping a cup to drink or preparing a sandwich. Additionally, in such action sequences, not all object features are always continuously perceivable but can sometimes only be experienced through interaction with the object, e.g. when lifting an opaque container filled with liquid. The goal of this study was to test whether the BRAC framework can be generalized to more complex types of actions.

In this study, we examined a situation that required a grasp-to-lift movement, which can be characterized as a sequence of discrete, goal-directed movements, comprising transport, grip, lift, and place phases. In particular, in each experimental trial, participants had to grasp an object with an uneven mass distribution and lift it as straight as possible. Previous studies showed that in such a task participants were more likely to lift the object straight up when the object's mass distribution did not change compared to a situation when it changed in a random manner (Broda et al., 2020; Voudouris et al., 2019). This could be related to the fact that participants tended to grasp the object in the same way as in the previous trial, even though different grasp configurations were possible (Dixon et al., 2012). Moreover, when grasping to lift an object with an unknown mass distribution, participants tended to use a grip that would stabilize the object during lift, expecting it to have the same mass distribution as experienced in the previous trial (Lukos et al., 2013). This previous trial effect even occurred when participants were aware that the mass distribution of the object would randomly change from trial to trial and thus seems to be rather automatic. Action planning in the context of object interaction generally relies on dynamic object representations acquired through previous object interactions (Schneider et al., 2019). In this regard, participants prepare for an action by retrieving features of the action from memory and the object to be grasped represents a decisive cue for this retrieval from memory (Dixon et al., 2012). Overall, there is some evidence that cognitive aspects of action control, like binding and retrieval, also have a substantial influence in more complex actions, but it remains unclear to what extent the BRAC framework can be applied to sequences of discrete actions and what are the similarities and differences compared to effects in single discrete actions (e.g., a single button press).

The aim of this study was to test the principles of the BRAC framework for a sequence of discrete, goal-directed movements which were characterized by a recognizable start and end point (cf., Fitts & Posner, 1967). Participants performed an unimanual object interaction task. They grasped and lifted an object with an uneven mass distribution from two different positions in a sequential order. To examine both mixing costs and partial repetition costs, the trial sequence contained blocks in which object features were either kept constant or changed in a pseudorandomized manner. As participants always viewed the same objects and accomplished the same task, we expect a memory retrieval of all features associated with the object from a previous event file, even if not all object features (mass distribution) are visible at the beginning of each trial. This is comparable to a simple button press experiment where, for example, a circle is displayed at one of two positions on a screen. In this example, the first step would be to respond to the position of the circle by pressing a button. After that, the circle would turn red or blue, which would require another button press response. If the circle is displayed on the right side and then turns blue, it would be assumed that these two features are bound to a common episode. If the circle is presented again on the right side in the next trial, according to the BRAC framework one would assume a bias to respond to the blue color, even if it is not yet visible. If the circle then appears red, a drop in performance would be expected (partial repetition costs). Here, we applied the same experimental logic to more complex movements where features are experienced through object interaction.

Since action sequences involve a longer and more complex temporal structure than single, discrete actions such as button-presses, reaction times might be less sensitive to capture binding and retrieval processes. For this reason, we focused on the kinematic aspects of motion, like the placement of the fingers when grasping an object (digits' separation) and the tilting of this object (object roll), which have already been shown to be strongly influenced by the general movement context and the feature configuration of the previous trial (Broda et al., 2020; Lukos et al., 2013; Voudouris et al., 2019). By examining digits' separation and object roll we were able to test the BRAC framework for motor planning and motor control processes, respectively. Recent studies also investigated response features other than reaction time in the context of binding and retrieval, e.g., percentage of errors or applied force (Pfister et al., 2022; Varga et al., 2022). If there are comparable effects for sequences of discrete actions as for single discrete actions, we expect better performance if (a) object features are constant on a global level, (b) object features are completely repeated within a situation of randomly mixed object features, and (c) no feature at all is repeated within a situation of randomly mixed object features. These results would underline that binding and retrieval processes also play an important role in more complex action sequences and that the BRAC framework can be applied in this context as well. This would indicate that processes of action planning and action control operate on a common, overarching basis, which in turn allows results from different branches of action research to be compared and merged to provide a better understanding of everyday life actions.

METHODS

PARTICIPANTS

In total, 40 participants completed the experiment. Due to a technical problem during data collection, data from eight participants were excluded, resulting in a total sample of 32 participants (26 f, 6 m, $mean_{age} = 23.88 \pm 4.08$ years). In addition, we had to exclude one additional participant from the kinematic data analysis (digits' separation) due to data loss. Due to the lack of a suitable independent data set, we did not perform an a-priori power analysis to calculate the required sample size. Instead, we set the sample size to at least 28 participants that would allow us to detect large effects with a power of 0.95 and effect sizes of $d_z > 0.8$ (corresponding to 19 participants for t-tests) and $\eta_p^2 > 0.14$ (corresponding to 28 participants for ANOVAs; see section Data Analysis). Participants were all right-handed, as assessed by the German translation of the Edinburgh Handedness Inventory (Oldfield, 1971; $mean = 90$, $range = 60-100$).

APPARATUS

Participants were seated in front of an 117 × 80 cm table (Figure 1A). A small keypad (12.5 cm × 8 cm) was placed at the edge of the table approximately aligned to the right shoulder of the participant. They had to grasp and lift one of two inverted T-shape objects (Figure 1B). At the backside of the lower part of the objects, invisible to the participants, three tubes were distributed laterally. A cylindrical piece of brass (116g) was inserted in one of the tubes, creating an asymmetric object *mass distribution* (MD). One of the objects contained the brass mass on the left, the other one on the right side. The total mass of the objects, including the brass, was 270g each. To prevent participants from seeing in which tube the experimenter inserted the brass prior to each trial, participants wore liquid-crystal shutter glasses (PLATO, Translucent Technologies, Toronto, Canada) throughout the whole experiment. On each object, two touch sensors (4.37 × 4.37 cm; Interlink Electronics Inc., Westlake Village, CA, USA) were mounted on the grasping sides of the upper part of the object. The objects were presented at one of two *object positions* (OP) about 33cm from start button, which were about 27cm apart (see Figure 1A). The movement of the participant's hand and the object were recorded with an Optotrak Certus motion tracking system (Northern Digital, Inc., Waterloo, ON, Canada) at 100 Hz. Therefore, infrared markers were attached to the fingernail of the participants' right thumb and index finger and in a triangular arrangement on the backside of the objects. It was ensured that all markers could be correctly detected by the camera system and that cables did not restrict the participants' movement.

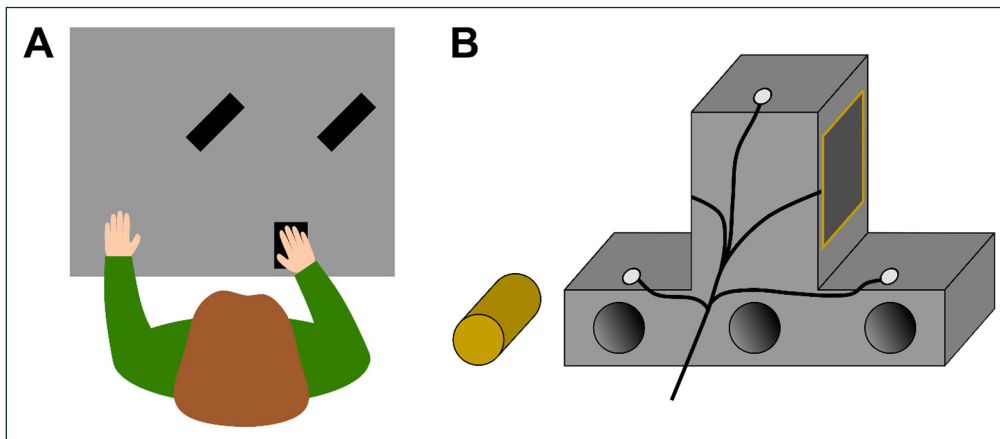


Figure 1 Experimental setup. **(A)** Top view of the setup with the right index finger and thumb resting on the start position, and both object positions (black rectangles). **(B)** Illustration of the backside of the inverted T-shaped object with the three infrared markers (white circles) and the touch sensors fixed to the grasping area of the object. The three tubes in the object's base were never visible to the participant. The brass mass is depicted to the left of the object.

PROCEDURE

The experiment consisted of a blocked sequence of trials differing in the arrangement of the two object features: MD and OP, each on the right or left side. Object features could either repeat (MD+, OP+) or change (MD-, OP-) from trial to trial. Four constant blocks were presented at the beginning and the end of the sequence, in which MD and OP were kept constant (MD+ & OP+, 2 × 4 × 22 trials) and thus there was always a complete repetition of both factors in each of the four constant blocks. The first of the four constant blocks was counterbalanced between participants. The order of the other three constant blocks was randomized. At the beginning and end of the sequence, the constant blocks were presented in the same order for each participant. In between these constant blocks, a longer mixed block was presented (360 trials). This mixed block was designed to prevent participants from predicting the configuration of factors of the upcoming trial (Gellermann, 1933) and to ensure that all possible combinations of consecutive MD and OP occurred equally often during the block. Thus, the mixed block contained complete, partial, and no repetition of both factors with respect to the previous trial. Overall, the sequence contained a total of 536 trials.

Each trial started with the participant pressing the start button on the keypad with their right index finger. The view of the participants was blocked by using shutter glasses. The experimenter inserted the brass cylinder into the left or the right tube of one of the objects, placed it on one of the two positions and started the trial. After the shutter glasses turned transparent, an auditory signal indicated the start of the movement. Participants were instructed to reach out and grasp the object with their right thumb and index finger (precision grip) at both sides of its upper part,

where the touch sensors were attached. They should lift the object at a natural speed straight up for about 15 cm, place it back on the table and return their finger to the start position. Participants had five seconds to perform the whole movement and return to the start button. After the movement was finished, the shutter glasses turned opaque again. Before starting the experiment, participants performed nine practice trials to familiarize with the task and the object weight. For those trials, the brass cylinder was inserted into the center tube of one of the objects. During practice the object was randomly placed on one of the two positions.

DATA ANALYSIS

The main goal of the experiment was to examine the key assumptions of the BRAC framework for more complex movements consisting of a sequence of several discrete, goal-directed movements. The two considered factors (MD & OP) act together from the point where participants grasp the object. To analyze motor planning and motor control, the influence of the previous trial's MD and OP on a) the positioning of the digits at object contact (digits' separation) and b) the maximal object roll during lifting were examined, respectively. In order to determine the relevant kinematic measures for each trial, first the speed of the hand and of the object were calculated by numerical differentiation of the mean position of the markers on both digits and on the object, respectively. These two speed vectors were dual-pass filtered using the MATLAB `filtfilt` function with a 2nd order lowpass butterworth filter and a cutoff of .30. We determined the moment of object contact with the use of the touch sensors as the first timepoint when one of the digits came into contact with one of the sensors. The base value for *digits' separation* was defined as the mean vertical distance between the two digits within the first 100ms starting from the moment of object contact, with positive values indicating that the thumb was placed higher than the index finger. The base value for *object roll* was defined as the absolute maximal tilt angle within the first 250ms after the object was lifted.

To investigate whether kinematic behavior was influenced by MD and OP experienced in the previous trial, different configurations of consecutive factor combinations were defined: MD+ involved trials with consecutive mass distributions that were identical (LL, RR), MD- involved trials with different consecutive mass distributions (RL, LR), OP+ involved trials with consecutive object positions that were identical (LL, RR), and OP- involved trials with different consecutive object positions (RL, LR). Further, the influence of the two different block types within the sequence was considered by averaging the base values of the two kinematic variables within these blocks and the different configurations. Within the constant block, only MD+ and OP+ occurred; within the mixed block, all four combinations of MD and OP were presented (MD+ & OP+, MD+ & OP-, MD- & OP+, MD- & OP-). Since there seems to be a tendency to place the digits in such a way that the MD experienced in the previous trial is compensated (Lukos et al., 2013; Voudouris et al., 2019), calculating the mean values of digits' separation for the different configurations would negate the actual effect. Therefore, the average digits' separation of each participant in trials with left MD were subtracted from the respective value in trials with right MD. Under the assumption that participants position their index finger higher than the thumb when they expected the weight to be on the right and lower than the thumb when they expected the weight to be on the left (Lukos et al., 2013), the resulting index value should be less than 0 when the weight position is repeated and greater than 0 when the weight position is changed. Thus, a negative index value indicates a better performance, as in this case participants positioned their fingers favorable to the distribution of the weight.

To check whether the index values for digits' separation differed from zero, we conducted one sample t-tests against zero separately for each condition. To compare constant and mixed parts of the sequence and to examine whether the general expectation regarding the change in both features had an influence on the task, we conducted one-tailed paired samples t-tests on digits' separation and object roll as dependent variables. We compared the constant blocks with the mixed block trials in which both MD and OP were repeated compared to the previous trial, assuming that both digits' separation index values and object roll to be lower for the constant parts. To examine the influence of the two factors on performance in the mixed parts of the sequence, we conducted a 2×2 within subjects ANOVA on digits' separation index values and object roll as dependent variables with the factors previous MD (MD+, MD-) and previous OP (OP+, OP-). In addition, we calculated the correlation between digits' separation and object roll across all condition (Pearson's r) to test if more efficient grasping of the object (negative digits'

separation) is indeed associated with less tilting of the object (lower object roll). All statistical analyses were carried out with JASP (Version 0.14.1). Significant interactions were inspected with post-hoc t-tests, Bonferroni-corrected for multiple comparisons ($\alpha = .008$). Effect sizes are described as partial Eta squared (η_p^2) for ANOVAs and Cohen's d_z for t-tests.

RESULTS

DIGITS' SEPARATION

First, we analyzed digits' separation as a measure of motor planning processes. We found mean index values below zero for the constant condition (MD+OP+, $t(30) = -12.97, p < 0.001, d_z = -2.33$) and the condition where both features were repeated within the mixed block (MD+OP+, $t(30) = -2.75, p = 0.01, d_z = -0.49$). This indicates that participants positioned their fingers favorable to the distribution of the weight and thus were able to achieve better task performance. The condition where MD was repeated and OP not within the mixed block elicited a mean index value not differing from zero (MD+OP-, $t(30) = -0.27, p = 0.79$). Further, we found mean index values above zero for both conditions where MD was not repeated within the mixed block (MD-OP+, $t(30) = 7.83, p < 0.001, d_z = 1.41$; MD-OP-, $t(30) = 6.63, p < 0.001, d_z = 1.19$), indicating that participants positioned their fingers in anticipation of a repeated MD that did not occur, resulting in worse task performance.

Mixing costs appeared as expected. Comparing parts of the sequence where both object features were repeated (MD+ & OP+), the index value for digits' separation was smaller during the constant blocks compared to the mixed block, $t(30) = -10.12, p < 0.001, d_z = -1.82$ (Figure 2). In a situation where participants were sure to repeatedly grasp the same object, they were able to adjust their grasp so that it compensated for the MD experienced in the previous trial. As such, in digits' separation a better performance was shown when object features were constant on a global level.

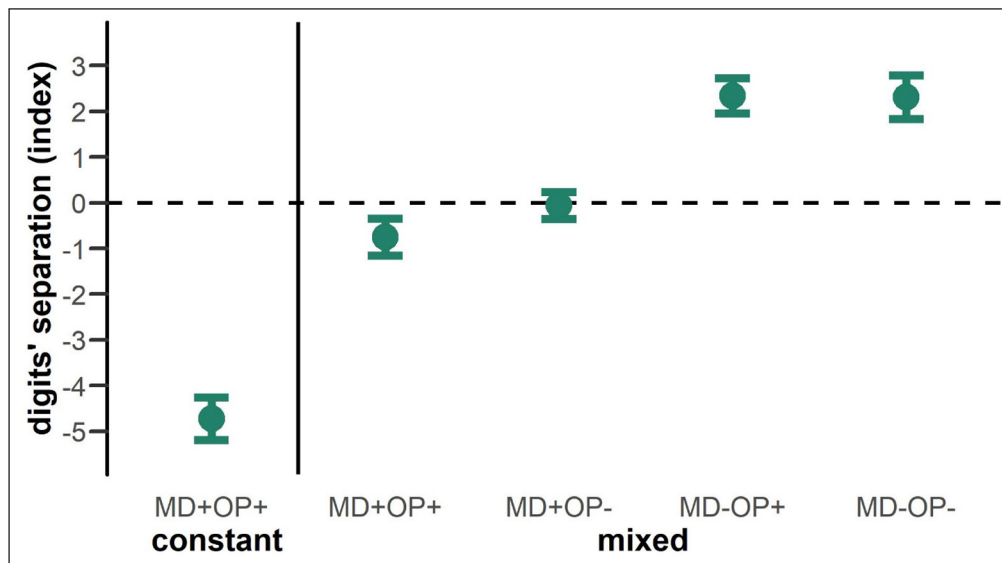


Figure 2 Mean values for digits' separation index. The values are plotted for the different configurations of feature repetitions with regard to the previous trial. Values for the constant and mixed part of the sequence are separated by the vertical line. Negative values indicate that participants positioned their digits in expectation of a repetition of MD that did occur, positive values also reflect this expectation, which, however was not met. Error bars display the 95% Cousineau-Morey within confidence interval.

Within the mixed part of the sequence, participants also grasped the object in a way to compensate for the MD experienced in the previous trial, $F(1,30) = 66.42, p < 0.001, \eta_p^2 = 0.69$, resulting in a mean index value below zero if the MD was repeated ($mean = -0.41 \pm 1.42$), and in a mean index value above zero if the MD changed ($mean = 2.33 \pm 1.79$). In contrast to MD, the OP alone had no influence on the index values in the mixed block, $F(1,30) = 1.17, p = 0.288$. However, we also found a significant interaction between MD and OP, $F(1,30) = 11.13, p = 0.002, \eta_p^2 = 0.27$. The difference in index values between OP+ and OP- was more pronounced within trials with MD+ ($mean_{diff} = 0.70 \pm 1.74$) compared to MD- ($mean_{diff} = -0.03 \pm 1.91$), $t(30) = 3.34, p = 0.002, d_z = 0.60$. In a situation with randomly mixed object features, the best performance was thus shown when both features were repeated.

OBJECT ROLL

Second, we investigated object roll as a measure of motor control processes. Since the positioning of the fingers strongly influences the extent of tilting of the object, mixing costs also showed up in the object roll, as expected. Comparing parts of the sequence where both object features were repeated (MD+ & OP+), the object rolled less during the constant blocks compared to the mixed block, $t(31) = -10.65, p < 0.001, d_z = -1.82$ (Figure 3). When participants were sure to repeatedly grasp the same object, their compensatory grasp allowed them to perform a more stable lift so that the object rolled less in the first 250 ms. Thus, in object roll a better performance was also shown when object features were constant on a global level.

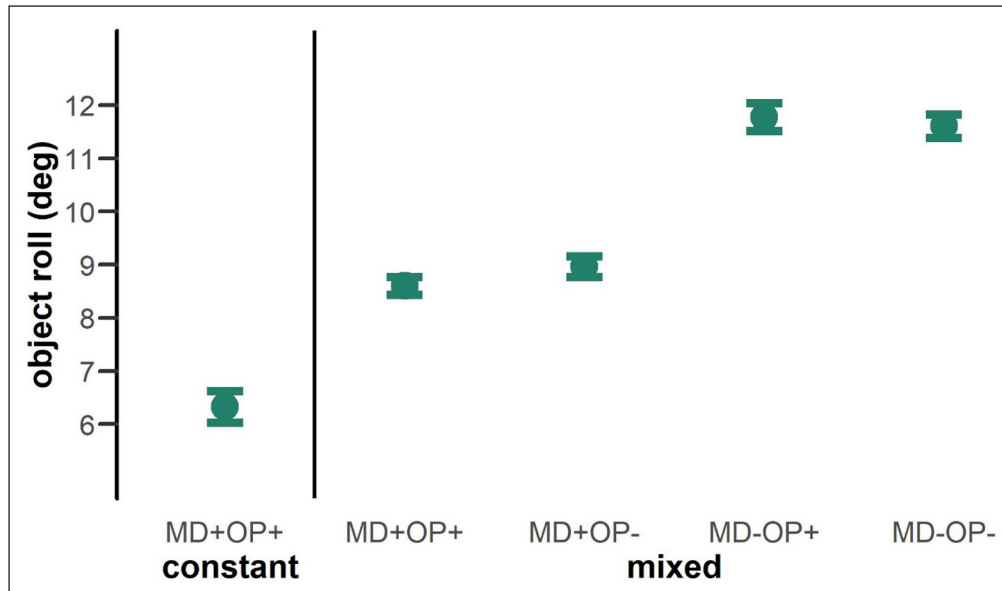


Figure 3 Mean values for object roll. The values are plotted for the different configurations of feature repetitions with regard to the previous trial. Values for the constant and mixed part of the sequence are separated by the vertical line. Values indicate the absolute maximal tilt angle of the object within the first 250 ms of object lift. Error bars display the 95% Cousineau-Morey within confidence interval.

Within the mixed part of the sequence, the object rolled less in the beginning of the lift when MD was repeated, $F(1,31) = 159.24, p < 0.001, \eta_p^2 = 0.84$, resulting in lower values for object roll ($mean = 8.79 \pm 3.39$) compared to situation when MD changed ($mean = 11.69 \pm 3.48$). The OP alone had no significant influence on object roll, $F(1,31) = 2.97, p = 0.095$, but we found a significant interaction between MD and OP, $F(1,31) = 14.943, p < 0.001, \eta_p^2 = 0.33$. When MD was repeated, the object rolled less when also OP was repeated, compared to a change in OP (MD+OP+ < MD+OP-, $t = -4.09, p < 0.001, d = 0.11$). When MD changed there was no such difference (MD-OP+ = MD-OP-, $p = 0.356$). In a situation with randomly mixed object features, the best performance regarding the object roll was thus shown when both features were repeated.

CORRELATION

Last, we analyzed the relationship between digits' separation and object roll to test if more efficient grasping is indeed associated with less tilting of the object. We found a positive correlation between the two variables, $r = 0.63, p < 0.001$ (Figure 4). The object tilted less within the first 250 ms when the participants grasped the object more efficiently (reflected in negative values for digits' separation).

DISCUSSION

In the present study, we aimed to investigate whether the principles of the BRAC framework, like binding and retrieval, also apply for more complex actions consisting of a sequence of discrete, goal-directed movements. Participants performed an unimanual object interaction task. They grasped an object and lifted it as straight as possible. In a sequential order, we varied two features of the object, its mass distribution and position. When both object features were constant on a global level, participants were able to adjust their grasp so that it compensated for the MD experienced in the previous trial, leading to a more stable lift and less object roll. Moreover, within a situation of randomly mixed object features, we found best task performance

when both object features were completely repeated from one trial to the other. These results suggest that even in sequences of discrete movements features of that movement are stored in a common episode. Retrieval of this episode then influenced performance in subsequent actions. As these subsequent trial effects were present for digits' separation and object roll they seem to influence both motor planning and motor control processes. To our best knowledge, this is the first time these basic principles of binding and retrieval, as described in the BRAC framework (Frings et al., 2020), were demonstrated in the context of more complex action sequences.

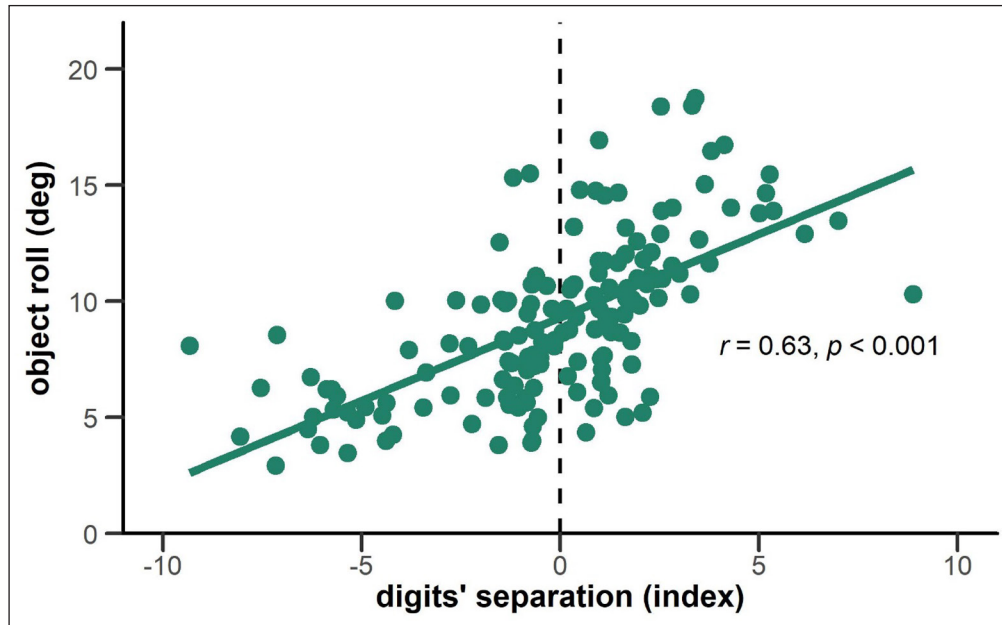


Figure 4 Correlation between digits' separation and object roll. Values for digits' separation are plotted on the x-axis, values for object roll on the y-axis. The two variables show a positive correlation.

In general, grasping and lifting an object is a very familiar task we frequently perform every day. Therefore, it is not surprising that participants performed this task very well, especially in the constant blocks. When confronted with the same object configuration, they could effectively adjust their interaction with the object. This could explain their significantly better performance in the constant blocks compared to the mixed block in addition to short-term binding effects. In the mixed block, where the object configuration changed constantly, a stronger influence of the most recent experience can be assumed.

For both digits' separation and object roll we found mixing costs comparable to those reported in previous studies using more artificial paradigms with simple motor tasks, such as single button presses (Los, 1999; Philipp et al., 2008; Rubin & Meiran, 2005; Steinhäuser & Hübner, 2005). Participants were able to successfully adjust their lifting movements when they were sure that the object's mass distribution or its position did not change from one trial to another. In comparison, the object tilted more when one of the object features could change in consecutive trials, although it did not. These results reflect the global expectation of consistency of the task and suggest that the object features and the action sequence were stored in a common episode. When the same object was presented in a consecutive trial, the action features were retrieved from memory, and thus significantly influenced the choice of action in the next trial. For the constant parts of the sequence, participants could be confident that object features would not change from one trial to another. In contrast, for the mixed part of the sequence, they always had to be prepared for the possibility that object features might change, which required additional processing to switch between the required actions which resulted in mixing costs. In contrast to typically considered temporal variables, such as reaction time, we were able to demonstrate mixing costs for kinematic variables, namely digits' separation and object roll.

Retrieval of action features from memory has also been proposed in the context of grasp planning (Dixon et al., 2012; Rosenbaum et al., 2012). People grasp objects at a similar height as in the immediately preceding grasping movement, even when another grasp location would be more comfortable for the task at hand (Cohen & Rosenbaum, 2004). This grasp-height effect

was explained by the re-use of the motor plan. A motor plan is generated in trial n which is then re-used in trial $n+1$ based on processes which retrieve the grasp location and not the grasp posture (Weigelt et al., 2007). Such retrieval of movement-relevant features is supposed to require the performance of the same movement under similar conditions within a short time frame. This account draws close parallels to principles of the BRAC framework with respect to feature binding and retrieval. To what extent both accounts relate to each other and could explain the various switch and repetition costs in movement planning and control remains a question for future research.

Besides these effects of global expectation, we found interaction effects of both object features for both kinematic variables within the mixed block of the experimental sequence, which are indicative of partial repetition costs. As shown in previous studies using button-response paradigms, participants usually perform better when the current features are completely repeated when confronted with a sequence of mixed stimulus-response combinations (Hommel, 1998, 2004). Repetition effects have also been shown in studies including reaching movement (Dixon et al., 2012; Randerath et al., 2015; Valyear et al., 2019). Here we were able to show a partial repetition effect for a sequence of discrete movements. In case of repetition of the mass distribution of the previous trial, partial repetition costs emerged if the object position was not repeated at the same time. Thus, in case of a repeated mass distribution, the object position appears to have been a crucial cue for retrieving the previous action from memory. In the case of non-repetition of the object position, there seemed to have been a conflict between the retrieved and the actually required action. Thus, especially in digits' separation, there was no clear influence of the previous trial and participants tended to use a default grasp to lift the object. Even though within the mixed part of the sequence there was a general performance decrease when the mass distribution was not repeated. There was no significant advantage of a complete alternation of the two object features, as the BRAC framework would have suggested. Both digits' separation and object roll were comparable irrespective of a change of the object position. There could be several reasons why this effect of a complete alternation did not appear in our results, such as the choice of kinematic variables, the complexity of the task, differences in the relevance of the object features, or even differences in the accessibility of object features throughout the trial.

Temporal parameters, such as reaction time, have been frequently examined in the context of the BRAC framework. These parameters are well suited for discrete actions, but less so for more complex action sequences, which involve a longer temporal structure than simple button-press responses. Thus, these temporal parameters might not be sensitive enough to capture binding processes within action sequences. Therefore, we chose to focus on kinematic aspects of motion, like the positioning of the fingers when grasping an object and the tilting of this object. These parameters are time-independent and at the same time capable to measure retrieval of previous actions. Previous studies investigating the influence of the general movement context and the feature configuration of the previous trial on movement kinematics have already demonstrated the potential of observing effects typically found in action control literature (Broda et al., 2020; Lukos et al., 2013; Voudouris et al., 2019). Additionally, it has been shown that an episode can persist for several seconds before losing their impact (Hommel & Colzato, 2004). Despite the fact that longer temporal distances between binding and retrieval of an episode tend to reduce their influence (Hommel & Frings, 2020), we observed binding effects in a grasping action that lasted about 5 seconds. Future research should examine how many motor features can be integrated into one single event file and whether and how this integration is influenced by spatial and/or temporal dependencies of the single action components (e.g., reach followed by grasp followed by lift).

The two object features, mass distribution and object position, did not seem to have the same relevance for the task performance. The object always had the same appearance (in terms of shape, color, texture, etc.), but could differ in its mass distribution and position. However, only one of these object features, object position, was visible at the start of each trial. The other feature, mass distribution, had to be experienced when grasping the object. Since the task was to lift the object as straight as possible and the mass distribution could vary at the same time, it seems reasonable that the mass distribution had a greater influence on task performance than the object position. This could explain why preceding actions were significantly influenced by the mass distribution and seemed to have been more decisive for the choice of action than

the object position. In general, the position from which to grasp an object is not completely irrelevant. It needs to be considered when planning the grasping movement in order to be able to accurately reach the object. However, for the two performance parameters considered, digits' separation and object roll, the mass distribution of the object still showed a stronger influence. It has been argued that task relevance is a crucial factor in binding features for action planning, and task-relevant features are more likely to become part of an episode (Memelink & Hommel, 2013; Mocke et al., 2020). More complex movements are particularly well suited to investigate features of varying relevance. Such actions offer the possibility to integrate several features in a natural way, not all of which have to be relevant for the task at hand. Future studies examining the BRAC framework could place a stronger focus on the varying relevance of features in order to map out a potential feature hierarchy to gain a more detailed picture of binding and retrieval processes.

Beyond differences in the relevance of the two object features, differences in their accessibility at the beginning of each trial could also explain the diverging effects. Usually, in paradigms investigating binding and retrieval, all features are perceivable throughout a trial. In everyday situations, however, we are also confronted with situations where object features are experienced during object interaction, as in our paradigm. Here, the object position was always visible, whereas the mass distribution could only be perceived by lifting the object. Following the assumptions of the BRAC framework, the retrieval of an episode should result in the retrieval of all object features bound within it and thus have an impact on behavior. Since participants always viewed the same object and performed the same task, we assume that both the object position and the mass distribution of the previous trial were retrieved from memory and consequently influenced their grasping and lifting behavior in the subsequent trial. Additionally, a temporal gradation of the retrieval process would also be conceivable. Retrieval of the object position was possible at the beginning of the trial, i.e. when this object feature was visible, whereas retrieval of the mass distribution could not occur before object lift. Therefore, our focus lay on measuring variables at a time when both features could be perceived and thus interact to influence the participants' motor acts. Nevertheless, we cannot rule out whether the effects we found would change if the mass distribution had been visible from the beginning of the trial. Future studies could examine the role of temporally varying accessibility of features on binding and retrieval processes.

The task we used was considerably more complex and natural than previous tasks studying binding and retrieval processes in action control using single button press responses. It involved an object interaction embedded in an action sequence. However, the task did not involve a strong ecological relevance, as the object had to be lifted and placed back without a higher-level action goal. The present task allowed us to explore the usability of such a paradigm in the context of binding and retrieval and could stimulate further investigations using more complex action sequences. Future studies could create an even more natural context by assigning a higher-level goal to object interaction (e.g., drinking from a cup). For example, a (virtual) object might contain a liquid that should not be spilled during grasping and lifting. The effects found in this study might thus still be underestimated and become more pronounced with greater ecological relevance. Moreover, the BRAC framework should be tested for movements of higher complexity (i.e., more degrees of freedom) than the unimanual object interaction examined here.

CONCLUSION

In summary, the results of the present study support the view that the general principles of action control postulated by the BRAC framework, such as binding and retrieval, appear to operate on a common, overarching basis. We showed that global consistency expectation and partial repetition costs affected how an object with varying mass distribution and position was grasped and lifted. These results suggest that even in more complex action sequences linked features are stored in a common episode and performance is influenced by retrieval of previous actions. Tasks such as these are thus capable of reflecting binding and retrieval and provide the opportunity of designing paradigms that are more natural and ecologically valid than previously used paradigms. Overall, this allows to compare and synthesize results on actions of varying complexity to provide a better understanding of action planning and control in everyday life.

The data collected for this work is publicly available at <https://doi.org/10.17605/osf.io/ux5a7>.

ETHICS AND CONSENT

All participants gave informed written consent to participate in the experiment and received either course credit, or financial compensation at the rate of eight Euro/hour. The experiment was approved by the research ethics board at Justus Liebig University Giessen (reference number 2013–0012), and was run in accordance with the Declaration of Helsinki (2013).

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COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

- M.C.B.: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization, Project administration
- I.K.: Conceptualization, Methodology, Writing – Review & Editing, Supervision, Project administration
- K.F.: Conceptualization, Methodology, Resources, Writing – Review & Editing, Supervision, Project administration, Funding acquisition

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III Appendix

List of all publications

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