Behavioral Benefits of Sensorimotor Predictions: Directing Attention to Maximize Informational Gain During Motor Learning

Inauguraldissertation

zur Erlangung des Doktorgrades der Naturwissenschaften
(Dr. rer. nat.)

dem Fachbereich Psychologie und Sportwissenschaften
der Justus-Liebig-Universität Gießen
vorgelegt von

Theresa Karoline Brand

geboren in Erlenbach am Main

Gießen, Januar 2026

Als Dissertation vom Fachbereich Psychologie und Sportwissenschaft
der Justus-Liebig-Universität Gießen angenommen.

Erstgutachter: Prof. Dr. Hermann Müller
Zweitgutachter: Prof. Dr. Alexander Schütz

Abstract

Humans internally predict the consequences of their own motor actions using so-called forward models (e.g., Anguera et al., 2009; Flanagan & Wing, 1997; Maurer et al., 2015; Wolpert, 1997). These models simulate the input-output relationship of the musculoskeletal system by integrating sensory information about the current state of the body and the environment with copies of motor commands (Jordan & Rumelhart, 1992; Kawato, 1999; Miall & Wolpert, 1996).

The present dissertation investigates functional benefits of such predictive processing, focusing on how sensorimotor predictions shape visual information uptake during motor learning. Specifically, it examines whether sensorimotor predictions direct visual attention toward spatial locations in the environment that are critical for evaluating movement outcomes and adjusting subsequent actions. To address this research question, three consecutive studies were conducted in which eye movements were recorded while participants performed a semi-virtual, goal-directed throwing task.

Study I showed that sensorimotor predictions can direct gaze toward predicted action effects. The high informational value of these predictively chosen fixation locations for feedback processing was expressed by a systematic modulation of fixation durations as a function of the movement outcome. *Study II* demonstrated that the relevance of outcome-related information is dynamically weighted by both outcome history and the predicted result of a current trial, supporting efficient allocation of attentional resources when multiple gaze targets compete for attention. The comparison of prediction-based top-down attentional mechanisms with salience-driven bottom-up influences in *Study III* suggests that, with sufficient motor expertise, responsiveness to salient distractors can be selectively modulated in feedback-critical situations.

Together, these findings show that during movement execution, gaze can be directed predictively toward information relevant for learning. It can be assumed that this predictive allocation likely ensures that the necessary information for evaluating outcomes and correcting errors is gathered efficiently, particularly in time-critical situations.

Zusammenfassung

Menschen sagen die Folgen ihrer eigenen motorischen Handlungen mithilfe sogenannter Vorwärtsmodelle intern voraus (z. B. Anguera et al., 2009; Flanagan & Wing, 1997; Maurer et al., 2015; Wolpert, 1997). Diese Modelle simulieren die Input-Output-Beziehung des Bewegungsapparates, indem sie sensorische Informationen über den aktuellen Zustand des Körpers und der Umgebung mit Kopien motorischer Befehle integrieren (Jordan & Rumelhart, 1992; Kawato, 1999; Miall & Wolpert, 1996).

Die vorliegende Dissertation untersucht die funktionalen Vorteile einer solchen prädiktiven Verarbeitung und konzentriert sich dabei darauf, wie sensomotorische Vorhersagen die Aufnahme visueller Informationen während des motorischen Lernens beeinflussen. Konkret wird untersucht, ob sensomotorische Vorhersagen die visuelle Aufmerksamkeit auf räumliche Orte in der Umgebung lenken, die für die Bewertung von Bewegungsergebnissen und die Anpassung nachfolgender Handlungen entscheidend sind. Um diese Forschungsfrage zu beantworten, wurden drei aufeinanderfolgende Studien durchgeführt, in denen die Augenbewegungen der Teilnehmenden aufgezeichnet wurden, während diese eine halb-virtuelle, zielgerichtete Wurfaufgabe ausführten.

Studie I zeigte, dass sensomotorische Vorhersagen den Blick auf vorhergesagte Handlungseffekte lenken können. Der hohe Informationswert dieser prädiktiv gewählten Fixationsorte für die Feedback-Verarbeitung spiegelte sich in einer systematischen Modulation der Fixationsdauer als Funktion des Bewegungsergebnisses wider. Studie II zeigte, dass die Relevanz von ergebnisbezogenen Informationen sowohl durch die Ergebnishistorie als auch durch das vorhergesagte Ergebnis eines aktuellen Versuchs dynamisch gewichtet wird, was eine effiziente Zuweisung von Aufmerksamkeitsressourcen unterstützt, wenn mehrere Blickziele um Aufmerksamkeit konkurrieren. Der Vergleich vorhersagebasierter Top-down- und salienzgetriebener Bottom-up-Aufmerksamkeitsprozesse zeigt in Studie III, dass bei ausreichender motorischer Expertise die Responsivität gegenüber auffälligen Distraktorreizen in feedbackkritischen Situationen gezielt moduliert werden kann.

Zusammen zeigen diese Ergebnisse, dass der Blick beim Lösen von Bewegungsaufgaben durch sensomotorische Vorhersagen auf lernrelevante Informationen ausgerichtet werden kann. Es ist anzunehmen, dass diese vorhersagebasierte Blickzuweisung dafür sorgt, dass die für die Bewertung von Ergebnissen und die Korrektur

von Fehlern erforderlichen Informationen – insbesondere in zeitkritischen Situationen – effizient gesammelt werden.

Acknowledgements

First and foremost, I want to express my sincere gratitude to my supervisors, Prof. Dr. Lisa Maurer and Prof. Dr. Hermann Müller, for giving me the opportunity to pursue a doctoral degree. Their continuous support, trust in my decisions, and encouragement to develop my own ideas shaped every stage of this journey. Even during their busiest times, they made time for questions and always came up with brilliant ideas whenever a smart solution was needed. I greatly appreciate the time and effort they invested, as well as their enthusiasm for research, which reignited my motivation during challenging moments. They created an inspiring and enriching working atmosphere that allowed me to grow both scientifically and personally. I could not have wished for better mentors or a more valuable training as a researcher.

I am deeply grateful to Prof. Dr. Alexander Schütz for the valuable collaboration throughout this project. His thoughtful feedback and constructive discussions profoundly strengthened this work, and his openness and reliable communication were deeply appreciated.

My sincere thanks also go to Prof. Dr. Mathias Hegele for laying the conceptual foundation for this line of research and for the insightful discussions that enriched this project. I am likewise grateful to both Prof. Dr. Alexander Schütz and Prof. Dr. Mathias Hegele for kindly serving as members of my examination committee.

Special thanks are extended to Dr. Heiko Maurer for his indispensable technical support. His comprehensive knowledge of the laboratory infrastructure and his readiness to assist were essential for ensuring the smooth execution of the experimental work.

I would also like to thank all other colleagues from the Department of Training Science and the Institute of Sport Science for the pleasant working atmosphere, the enriching time together, and the many shared experiences.

I am deeply grateful to the student assistants who helped collect data for the experiments: Mojtaba Abdollahi, Lena Kloock, Christina McCusker, Parastoo Namaei, Jana Schuster, Merle Thielking, and Nathalie Wester. Their dedication and reliability were invaluable.

Furthermore, I feel very fortunate to have been part of the Collaborative Research Center/Transregio 135 "Cardinal Mechanisms of Perception", led by Prof. Dr. Karl

Gegenfurtner, which made this doctoral research possible and provided an excellent, well-structured, and collaborative environment for scientific development.

I am especially indebted to my bachelor’s and master’s thesis advisor, Dr. Michael Joch, for fueling my interest in science during my student years. I am grateful for his continued availability for advice. Our conversations have always left me with renewed clarity and direction.

Finally, a special thank you goes to my friends and family. After long days consumed by endless thinking, writing, or programming, they helped me “exit the loop” and return to reality.

Table of Contents

I

Synopsis

1 Introduction

> *"I knew [the ball] would go in, it was just one of those feelings."*
> — Talor Battle, American professional basketball player (2011).

Sometimes, in the split second our hand releases a ball or our foot strikes a penalty shot, we experience, as Talor Battle described, an immediate, almost instinctive sense that the action will succeed — or fail — even before the outcome unfolds. In such moments, we briefly glimpse what usually happens unaware to our attention and continuously within our central nervous system when we move: Over the past decades, extensive research in the field of motor control has demonstrated that humans internally predict the consequences of their own actions ahead of time using so-called *forward models* (e.g., Desmurget & Grafton, 2000; Flanagan & Wing, 1997; Jordan & Rumelhart, 1992; Miall & Wolpert, 1996). These models simulate the input-output relationship of the musculoskeletal system by integrating sensory information about the current state of the body and the environment with copies of motor commands (Miall & Wolpert, 1996). Critically, forward models develop over time through motor experience in specific tasks, as the system learns the outcomes associated with particular motor commands (Jordan & Rumelhart, 1992).

The present dissertation centers on the functional benefits of such predictive processing, focusing on the question whether these internally generated action effect predictions (hereafter referred to as sensorimotor predictions) are used to optimize visual information uptake in the context of motor learning.

The introduction will first review the role of sensorimotor predictions in detecting and correcting movement errors. It will then outline how different sensory modalities contribute to outcome evaluation of actions depending on the nature of the task, highlighting the crucial role of visual information when movements produce distal action effects. Further, the predictive nature of gaze in goal-directed actions will be discussed. Disentangling the sources of this predictive gaze behavior and clarifying its functional role imposes specific demands on the experimental task used in this dissertation. This task will be introduced, followed by an overview of the three studies that comprise the present work.

1.1 Behavioral Benefits of Sensorimotor Predictions for Motor Control and Learning

As noted at the start of the introduction, our actions are not always adequate, but can be inaccurate or even fail. Detecting and evaluating errors in action execution is therefore essential for accurate motor behavior and learning (Joch et al., 2017). In this regard, a well-established function of sensorimotor predictions (if sufficiently accurate) is the early detection of movement errors. By continuously comparing *predicted* with *intended* sensory action effects before actual sensory feedback becomes available, the central nervous system can detect potential errors before they occur. This predictive monitoring enables rapid online corrections by bypassing delays in sensory processing (Desmurget & Grafton, 2000; Wolpert & Ghahramani, 2000), thus supporting smooth, continuous movement adjustments in closed-loop tasks such as reaching or grasping.

Despite this online correction capability, actions may still fail to achieve their intended outcomes (Krigolson & Holroyd, 2006). Such failures can arise from internal causes (e.g., inaccurately selected motor commands that cannot be corrected in time) or from external perturbations (e.g., interference by another person). For effective trial-to-trial adaptation, it is crucial to distinguish between these two sources of error: only errors attributed to one's own motor behavior should be followed by movement adjustments, while errors caused by random external perturbations should be ignored (Maurer et al., 2019). Sensorimotor predictions support this error attribution process by enabling comparisons between *predicted* and *actual* sensory action effects. If an error occurs predicted by the model, it likely reflects an internal cause; if the intended action goal is missed but no deviation was predicted, the error can be attributed to external perturbations and should not prompt motor adjustments, provided these perturbations are unsystematic (Maurer et al., 2019). This mechanism also applies to open-loop tasks such as throwing or kicking movements, where influencing the outcome is not possible once the effector has left the hand or foot. Thus, on a behavioral level, predictive mechanisms are beneficial for online movement control in closed-loop tasks and for trial-to-trial adjustments in both closed- and open-loop contexts, thereby contributing to motor learning.

For trial-to-trial adaptations, a reliable comparison between predicted and actual sensory feedback is essential. However, before this comparison can take place, the system must gather information about the actual sensory consequences of its actions. In line with Wolpert and Flanagan (2010), who identify efficient acquisition of sensory information as a core component of motor learning, the following section will discuss the specific sensory information required for the evaluation of action outcomes, depending on the type of motor task.

1.2 The Importance of Different Sensory Modalities for Action Outcome Evaluation

Motor actions differ in the sensory modalities through which their outcomes can be evaluated. Some actions, such as adjusting grip force to prevent slippage of a handheld object, rely mainly on proprioceptive and tactile feedback (Avraham & Nisky, 2020), whereas others produce externally observable effects that can be visually assessed. Among these, it is useful to distinguish between actions that involve direct physical interaction with the environment (e.g., grasping an object; Fig. 1, left) and those that impact it at a distance (e.g., throwing a ball; Fig. 1, right; Illamperuma & Fooken, 2024).

Figure 1. Interacting with vs. impacting the environment (adapted from Illamperuma & Fooken, 2024).

In the first case, the comparison between predicted and actual sensory outcomes can rely on multiple sensory modalities due to the *proximal* nature of the movement effects (Ernst & Banks, 2002) — for example, feeling whether and how a glass lies in one's hand through touch *or* seeing whether and how it is being held. In contrast, when impacting the environment, success is defined by the *distal* effects of a movement, which are typically accessible only through vision and, to a limited extent, audition. Auditory feedback in such contexts is often dichotomous (e.g., hearing or not hearing a ball strike the net, or hearing the crowd's positive or negative reaction after a free throw in basketball) and thus insufficient for deriving precise motor adjustments if necessary. Visual feedback, in turn, is often available only briefly, such as when a basketball hits the rim or the instant a tennis ball bounces on the court.

Therefore, particularly in tasks where movements impact the environment and produce distal action effects, accurate evaluation of outcomes depends on the timely prioritization of relevant visual information, often despite competing attentional demands. Returning to the basketball example, when players take a shot, they must direct their gaze toward feedback-relevant locations in the environment at the right moment to facilitate accurate outcome evaluation and trial-to-trial adaptation, while suppressing irrelevant visual input from the surroundings (e.g., from spectators or teammates).

Since sensorimotor predictions provide reliable estimates of when and where visible effects of one's actions will occur, they could direct visual attention proactively. While several effects of sensorimotor predictions on perceptual processes are well established (such as the attenuation of self-induced sensory consequences, exemplified by the inability to tickle oneself; Blakemore et al., 2000), their potential role in guiding visual attention and information uptake during action outcome evaluation remains largely unexplored. Therefore, the present dissertation investigates whether sensorimotor predictions allow for directing visual attention to spatial locations in the environment that are critical for evaluating movement outcomes and adjusting subsequent actions. This role should be distinctly crucial in tasks involving distal action effects, where outcome evaluation relies primarily on visual information.

1.3 Predictive Nature of Eye Movements in Goal-Directed Actions

Research on eye movements in goal-directed actions with externally observable effects consistently demonstrates the predictive nature of gaze, showing that humans anticipate where task-relevant visual information will become available and direct their eyes accordingly (Bakst & McGuire, 2021; Fiehler et al., 2019; Henderson, 2017). However, the sources on which these predictions rely can vary across tasks (Fiehler et al., 2019; Zago et al., 2009; Zhao & Warren, 2015).

In interception tasks, for example, individuals shift their gaze toward the expected bounce point of a ball, where predictions may be based on learned internal models of environmental dynamics (e.g., Diaz et al., 2013). In everyday activities, the eyes typically lead the hand when making tea (Land et al., 1999), preparing a sandwich (Hayhoe, 2000), moving an object around an obstacle (Johansson et al., 2001), or reaching toward a target (Baldauf et al., 2006; Epelboim, 1998; Herst et al., 2001; Neggers & Bekkering, 2000). Predictive gaze shifts in such contexts may stem from the anticipation of stimuli one has to interact with or from the anticipation of actions one has to perform, both based on experience with the task (Pfeuffer et al., 2016). In addition, gaze allocation can also be influenced by expectations about where objects of interest are most likely to appear (Draschkow et al., 2014; Henderson, 2017; Le-Hoa Võ & Wolfe, 2015). In these continuous, closed-loop actions with proximal action effects (cf. Figure 1, left), predictive gaze shifts are typically associated with movement planning and the online control of movement, supporting functions such as object localization and guidance of contact, or avoidance (for a review, see Fiehler et al., 2019; e.g., Land et al., 1999). Examining the role of sensorimotor predictions in supporting action outcome evaluation in these contexts is inherently challenging, since different predictive mechanisms interact, and movement planning, online movement control, and outcome evaluation are spatially and temporally intertwined.

Such a spatiotemporal overlap is largely absent in tasks with distal action effects. Using a task, in which simple manual actions (key presses) produced simple distal effects (predictable visual stimuli on the left or right side of a screen after a short delay), Pfeuffer and colleagues (2016) demonstrated that individuals predictively directed their gaze toward these distal effects of their actions shortly *after* the manual responses. This pattern suggests a relationship between predictive gaze shifts and action outcome evaluation rather than action planning and online monitoring.

However, the unambiguous and dichotomous action–effect mappings in this task (e.g., a right key press consistently producing a visual effect on the right side) likely engaged explicit cognitive rather than sensorimotor mechanisms in action outcome evaluation: participants may have just verified whether learned action-effect contingencies held (Elsner & Hommel, 2004). With the paradigm lacking natural and continuous contingencies between actions and their effects that are cognitively impenetrable, the role of sensorimotor predictions in guiding visual attention for action outcome evaluation in the context of motor learning remains unclear.

1.4 The Experimental Motor Task

To address this research gap, the experimental task for this dissertation needed to meet several specific requirements derived from the considerations in Chapters 1.2 and 1.3. First, the task needed to involve distal action outcomes, which (a) inherently require accurate and well-timed visual processing of outcome feedback and (b) allow outcome-evaluative functions of gaze to be clearly dissociated from planning and online guiding functions due to a temporal and spatial separation between movement execution and its consequences. Second, to disentangle different sources of prediction, the task needed to provide naturalistic, continuous mappings between movement execution and resulting outcomes — comparable to a basketball free throw, a tennis serve, or a soccer penalty shot. Under such conditions, predictive gaze behavior can plausibly rely on implicit sensorimotor predictions of one's own action consequences rather than on explicit action–effect rules. At the same time, the task had to allow for the masking of unfolding action effects, ensuring that predictive gaze behavior could not rely on internal models of environmental dynamics. This latter requirement is best met by a (semi-)virtual task, which additionally offers high experimental control, precise measurement of motor outcomes, and high-resolution eye tracking as a continuous behavioral trace of visual attention (Lai et al., 2013).

Thus, the present work employed a semi-virtual goal-directed throwing task inspired by the British pub game *Skittles* (Figure 1, right). In this game, a ball attached to a post by a string is swung around the post to hit (a) target object(s) located on the opposite side (Fig. 2*A*). The semi-virtual implementation of this game has been employed in previous research related to motor learning (e.g., Joch et al., 2017; Maurer et al., 2015; Müller & Sternad, 2004). In this version of Skittles, participants perform real ballistic throwing movements using a metal lever (Fig. 2*B*), while the action effects (resulting ball trajectory and terminal outcome) are displayed on a computer screen from a top-down perspective (Fig. 2*C*).

Critically, the task's open-loop nature yields a predictable action effect upon movement completion, cleanly separating movement execution from action outcome evaluation processes. Furthermore, the distal location of the action effect necessitates efficient visual information processing. Importantly, the task's motor redundancy (infinitely many release angle–velocity combinations leading to similar outcomes) ensures that hits and misses are not determined by dichotomous execution differences (cf. Pfeuffer et al., 2016). Moreover, the nonlinear relationship between release parameters and outcomes renders prediction cognitively impenetrable, making the task well suited for investigating implicit sensorimotor computations. Finally, the semi-virtual implementation allows for selective masking of ball trajectories, ensuring that predictive gaze behavior cannot rely on straightforward extrapolation of the ball's flight paths based on learned internal models of environmental dynamics.

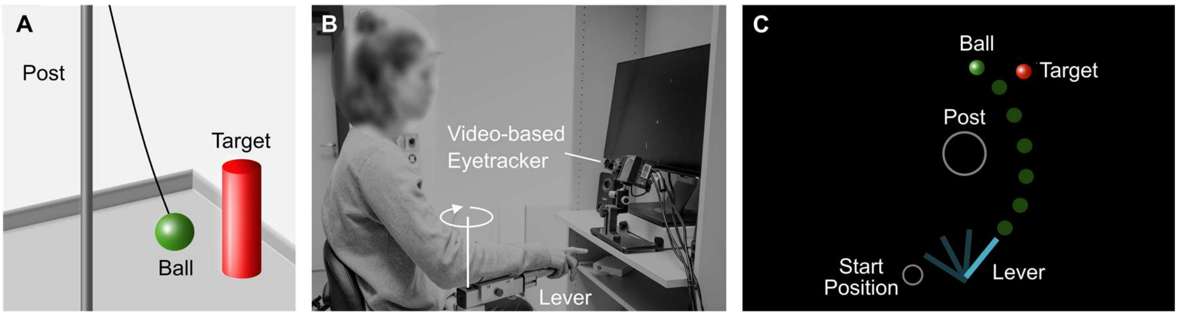


Figure 2. *A*: Schematic illustration of the original Skittles game, in which a ball that is attached to a post by a string must be swung around the post to hit a target object on the opposite side. *B:* Experimental setup of the semi-virtual adaptation of the Skittles game. Participants use a metal lever to execute an outward-rotational throwing movement resembling a Frisbee toss. A virtual ball is released by lifting the index finger from an electrical contact sensor at the tip of the lever, and the resulting action effect is displayed on a screen in front of the participant. Eye movements are tracked during task execution with an Eyelink 1000 Plus on a desktop mount running in remote mode. *C:* Task space displayed on the screen. The movements' starting position is indicated on the left-hand side of the manipulandum's vertical axis. After release, a green ball travels with an elliptical trajectory around a gray center post and toward a red target.

Eye movements were recorded in temporal alignment with throwing movements and their unfolding effects using a video-based eye tracker. To account for the gradual development of forward models with increasing task familiarity and expertise (Jordan & Rumelhart, 1992), each study, outlined in the following section, included one or more practice sessions.

1.5 Outline

Sensorimotor predictions enable the early detection of movement errors, facilitating both online control and trial-to-trial adaptation. Especially in motor tasks with *distal* action effects, efficient adaptation from trial to trial requires directing visual attention to relevant feedback at the right moment despite competing attentional demands. A further, yet underexplored, function of sensorimotor predictions may therefore lie in optimizing visual information uptake during motor learning by proactively guiding attention.

To address this overarching research question, the present thesis employed three sequential studies, in which eye movements were recorded as participants performed the semi-virtual throwing task, Skittles.

Study I examined whether sensorimotor predictions guide gaze toward feedback-relevant locations during motor learning, thereby facilitating essential comparisons between intended, predicted, and actual action effects. To isolate the role of sensorimotor predictions, other potential predictive mechanisms that could influence gaze behavior (e.g., predictions based on environmental dynamics) were carefully controlled.

Building on this, *Study II* investigated whether sensorimotor predictions not only guide gaze to relevant feedback locations but also modulate the *value* assigned to these locations based on predicted action success. As outlined earlier, motor actions in natural environments are often performed under competing attentional demands. Besides the prospective gain of task-relevant information, for example, motivational aspects of stimuli also influence where we direct our gaze (for reviews, see Hayhoe & Matthis, 2018; Schütz et al., 2011; Tatler et al., 2011). In such contexts, the selection of gaze targets is assumed to rely on a dynamic priority map, where each spatial location is continuously assigned a value reflecting its current behavioral relevance (Fecteau & Munoz, 2006). In motor tasks, feedback about action outcomes may vary in value depending on predicted success, becoming especially important when errors are expected and deriving suitable adjustments for motor commands in the subsequent trial is required. Accordingly, *Study II* examined whether sensorimotor predictions, including predictive estimates of action success or failure, modulate this priority map, supporting efficient allocation of attentional resources when multiple potential gaze targets compete for selection.

With visual saliency of stimuli being another factor influencing gaze target selection (Schütz et al., 2011), *Study III* extended the logic of *Study II* by examining whether sensorimotor predictions not only bias gaze toward valuable stimuli but also suppress bottom-up interference from salient distractors, especially in feedback critical moments (i.e., predicted errors).

Through these studies, the present dissertation investigates the broader functional role of sensorimotor predictions in shaping visual attention and learning in motor tasks, offering valuable insights into the interplay between action, prediction, and perception.

Subsequent chapters will summarize the three studies, followed by an integrative discussion and perspectives for future research.

2 Summary of Studies

2.1 Study I: Directing Visual Attention to Relevant Feedback Positions

Reference

Brand, T. K., Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. (2024). Sensorimotor prediction is used to direct gaze toward task-relevant locations in a goal-directed throwing task. *Journal of Neurophysiology*, *132*(2), 485-500.

Background

Previous research has demonstrated that the predictive nature of gaze can arise from different underlying mechanisms and can serve multiple functions in motor control and learning, ranging from online movement control (e.g., Land, 2006) to the evaluation of action outcomes (Pfeuffer et al., 2016). This first study was specifically designed to disentangle whether sensorimotor predictions are used to proactively guide gaze in support of action outcome evaluation in complex motor tasks with distal effects.

Methods

Twenty participants completed 500 ball throws per day, across three days. During the first two sessions, they received continuous visual feedback about the ball's flight. In the third session, the ball flight was masked in a subset of trials, and participants only received static outcome feedback for 500 ms at the moment of minimum distance between the ball and the target (t_{dmin}). This masking should ensure that predictions and potential gaze shifts toward future action effects were based on internal movement-related information (i.e., a copy of efferent motor commands and proprioceptive information). To prevent the visually salient target from attracting gaze (toward the intended action effect) in a situation where outcome prediction becomes particularly challenging due to reduced input signals, in some trials, the target was also masked after ball release.

The expectations included consistent predictive gaze shifts toward future action effects shortly after ball release, both in trials with continuous ball flight information and in trials with masked ball flight. Weaker or no correspondence between predictively chosen fixation locations and action effects was expected when no ball flight information was available, but the visually salient target could be fixated. In addition, if the predictively chosen fixation locations held high informational value for feedback processing, fixation durations at these points would depend on the prevailing processing demands (Henderson, 2017). It is plausible to assume that processing demands vary based on two factors: a) the action outcome (i.e., hit vs. miss), where processing demands should be higher if movement corrections are necessary, and b) outcome uncertainty, where processing demands may increase for outcomes close to the hit/miss boundary due to diminished outcome predictability (Henderson et al., 1999; Maurer et al., 2019).

Results

Across all sessions, a high proportion of trials with predictive gaze shifts toward the target region was observed after ball release, but before the outcome feedback was available. Covariation between the predictively chosen fixation locations and the final position of the ball showed that the subjects apparently directed their gaze toward predicted action effects. Varying the experimental conditions revealed that this gaze behavior occurred both when the ball's flight was visible and when it was masked, *provided that* the target circle was also hidden as a salient visual anchor. Masking of ball flight ensured that predictive gaze shifts were indeed based on sensorimotor predictions rather than solely on extrapolating the visible ball flight.

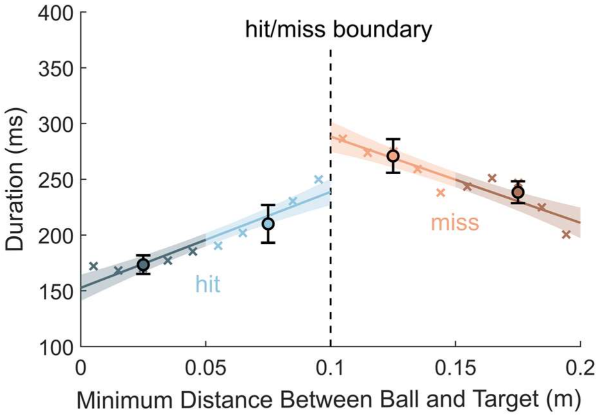


Figure 3. Fixation durations after the time of minimum distance between ball and target (t_{dmin}) in trials with predictive gaze shifts toward future action effects, separated by outcome (hit vs. miss) and outcome uncertainty (clear vs. narrow). Regression lines (±95% CI) depict fixation durations as a function of ball-target deviations, binned in steps of 0.01 m. *n* = 17 subjects.

As expected, fixation durations at the predictively selected locations were modulated by action outcome and outcome uncertainty. Durations were longer for errors than for hits, and longer for outcomes near the hit/miss boundary than for clearly successful or unsuccessful outcomes (Fig. 3). When combining both effects, fixation durations were longest for narrow errors and shortest for clear hits. This result pattern indicates that the predictively selected fixation locations provide high informational value for feedback processing. While a similar hit-miss difference was observed when participants simply fixated the target, the findings as a whole confirm that sensorimotor predictions serve as a mechanism for guiding gaze toward relevant feedback locations.

2.2 Study II: Value Assignment to Competing Fixation Targets

Reference

Brand, T. K., Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. (2025). Predicted task success and outcome history mediate eye movements toward locations with high informational or motivational value. *Journal of Neurophysiology*, *134*(2), 568-579.

Background

The longer fixation durations in errors compared to hits in *Study I* indicate that the outcome feedback in goal-directed actions is of varying value depending on the (predicted) outcome (hit vs. miss). While it is particularly important to process feedback on erroneous trials to derive suitable adjustments (to succeed in the long term), it may be less crucial to guide gaze toward learning relevant information if one is sure that a trial will be a hit. Videos of popular basketball players show that when they expect to make the shot, they sometimes turn around directly after ball release and do not (need to) visually monitor the outcome feedback. To hit a second time under the same circumstances, the same motor command can be used and attention could be directly devoted to cheering spectators rather than outcome feedback. Thus, it is plausible to assume that sensorimotor predictions serve not only to identify locations in the environment with high informational value for feedback processing, as shown in *Study I*, but also to assign those locations a specific value depending on the predicted action outcome. Such a mechanism could provide significant behavioral benefits in case multiple stimuli dynamically compete for attention during and after the execution of a motor task. To examine this proposition, systematic differences in the selection of competing fixation targets with either high informational value (providing graded movement outcome feedback) or high motivational value (showing the monetary reward for a hit in a current trial) were assessed as a function of (predicted) task success in the semi-virtual goal-directed throwing task. A third potential fixation target displayed the progress through the experiment and was considered to be of neutral value.

Methods

The semi-virtual throwing task was practiced by 22 participants over 500 trials in a first session, during which the visual feedback on the ball flight was gradually reduced, to only show static outcome feedback at t_{dmin}. In session two, participants completed another 500 trials with only the first quarter of the ball flight visible. Furthermore, two additional visual targets were introduced, allowing participants to choose where to direct their gaze. That is, depending on the participants' gaze position at t_{dmin}, feedback at only one of the target locations could be perceived for 500 ms. The (i) neutral target indicated the experimental progress, (ii) the throwing or informational target showed the ball position relative to the throwing target, providing graded visual feedback on the throwing outcome, and (iii) the motivational target provided reward information. Each trial offered a pseudorandom reward of either 0 cents (70% of the time), 5 cents (20%), or 25 cents (10%) for a hit. Crucially, reward information was displayed regardless of trial outcome if the motivational target was fixated, and rewards were granted for hits whether or not the target was fixated (see also Daddaoua et al., 2016).

The primary instruction was to hit the throwing target as often as possible to win as much money as possible. Acoustic feedback (the sound of two colliding billiard balls at t_{dmin} in hits and its absence in misses) was consistent across trials regardless of the fixated target. Thus, participants received dichotomous outcome feedback even when fixating on the neutral or motivational target.

It was expected that predicted errors would increase the value of graded outcome feedback, leading to more fixations on the informational target in error trials compared to hits. Conversely, more fixations on the motivational target in predicted hits were expected, as reward-related information would have a higher value in these cases. Additionally, the study examined how outcome history (outcome trial n-1) might influence the integration of sensorimotor predictions regarding the outcome in a current trial into saccadic programming.

Results

In replication of *Study I*, participants consistently fixated the visual targets shortly after release but before outcome feedback. There were large interindividual differences in the proportion of fixations on each target. However, these individual proportions were systematically influenced by the outcome of the previous trial (Fig. 4; e.g., a higher proportion of fixations on the informational target in trials following an error) and the predicted outcome of the current trial (a higher proportion of fixations on the motivational target during trials that resulted in a hit compared to those resulting in an error).

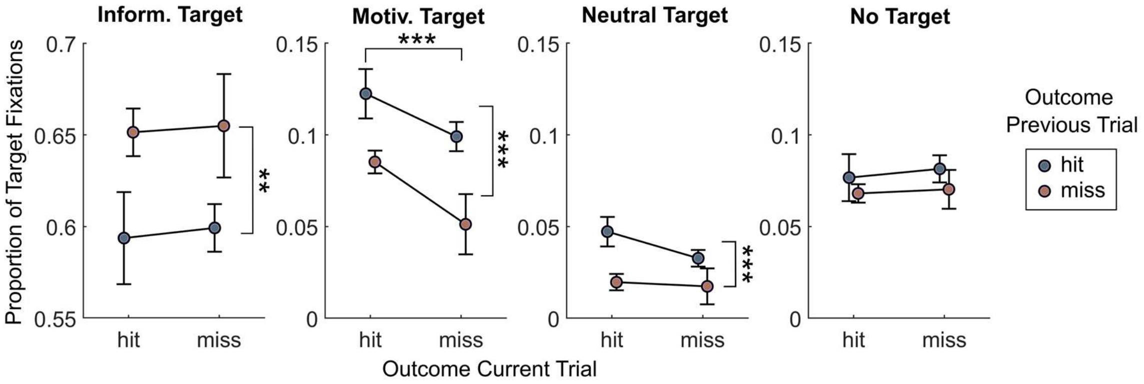


Figure 4. Relative frequencies of target fixations at the time of minimum distance between the ball and the throwing target (t_{dmin}) across different outcome(s) (histories). Values are means ± bootstrapped SE; Data were analyzed using Generalized Linear Mixed Models (GLMMs); $n = 18$ subjects; $^{***}P < 0.001$, $^{**}P < 0.01$.

The results suggest that individuals primarily rely on outcome history to direct their attention to learning-relevant information, while dynamically integrating sensorimotor predictions of current outcomes. In addition, the prediction of a hit can signal available attentional resources and direct selective attention to motivational aspects (e.g., reward information). Taken together, humans combine previous experiences with sensorimotor predictions to attribute value to different parts of the visible space and to guide gaze toward highly valued positions.

2.3 Study III: Shielding Visual Attention from Salient Distractors

Reference

Brand, T. K., Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. Do sensorimotor predictions provide top-down guidance of visual attention against bottom-up distraction? (prepared for submission)

Background

Influencing factors of gaze target selection have been studied extensively (for reviews, see Hayhoe, 2017; Schütz et al., 2011; Tatler et al., 2011). Aside from the prospective gain in task-relevant visual information via gaze shifts and motivational aspects of stimuli, such as a monetary reward linked to fixation targets (Liston & Stone, 2008; Sohn & Lee, 2006), also low-level features of scenes, such as visual saliency (e.g., Itti & Koch, 2000), influence decisions about visual target selection. However, several studies show that task demands can suppress the influence of saliency completely (e.g., Einhäuser et al., 2008; Henderson et al., 2007). This suppression should be particularly effective when sensorimotor predictions indicate an upcoming movement error, and thus the need to direct attention to the feedback information. Hence, *Study III* examined the weighting of top-down attentional shifts based on predictions about movement outcome against bottom-up attentional shifts induced by perceptual saliency.

Methods

The semi-virtual throwing task was practiced by 45 participants over 500 trials in a first session, during which visual information about the ball flight was gradually reduced, and only static outcome feedback was provided at t_{dmin} for 200 ms. In the final 50 trials of session 1, a salient distractor was introduced in 60% of the trials to prepare participants for the conditions of the experimental phase. On the second and third days, only a quarter of the ball flight was visible, and a distractor appeared in 60% of all trials in pseudorandom positions, colors, and shapes to prevent habituation. The procedure was as follows: after ball release, the target was masked, and a distractor occasionally appeared (cf. the gap paradigm by Saslow, 1967). This process was succeeded by showing the ball's position relative to the target to provide feedback on the trial outcome. The distractor could appear either 100 ms or 350 ms after release, with a jitter of 30 ms in both cases.

Gaze behavior was assumed to differ systematically between hits and misses. Based on the findings from *Study II*, it was expected that predicted errors would signal an increase in the value of outcome feedback, leading to enhanced top-down control and fewer fixations on salient distractors. In contrast, predicted hits were expected to yield weaker top-down weighting of the feedback location and hence greater susceptibility to distraction.

Results

There were large interindividual differences regarding distractor fixation rates that were not predictive of task performance. However, high performing participants (classification according to a median split regarding hit rates) fixated salient distractors less frequently in (clear) errors than in hits, suggesting that motor expertise enables the contingent shielding of attention form salient distractors to prioritize action outcome feedback (Fig. 5*A*). In contrast, low performers showed no such modulation, likely due to lower predictive precision.

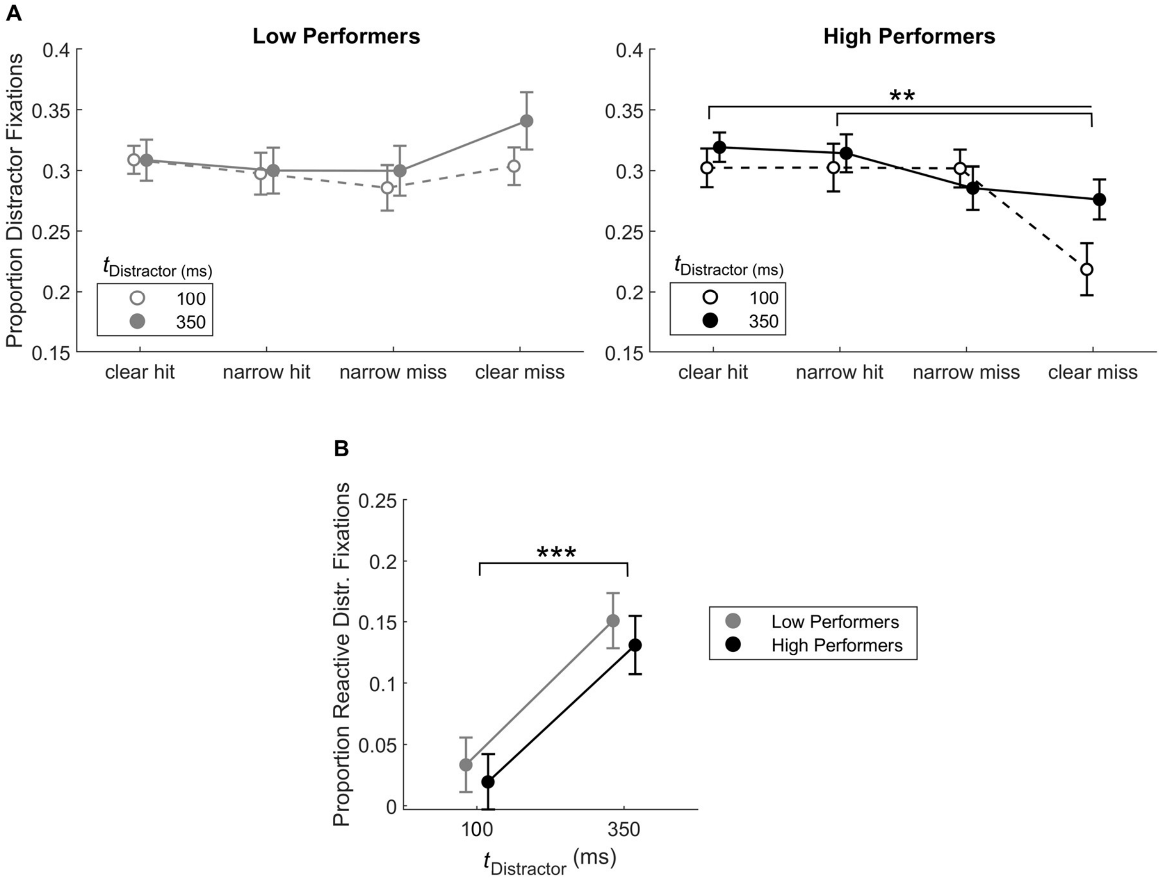


Figure 5. *A:* Proportion of distractor fixations across throwing outcomes (clear hit, narrow hit, narrow miss, clear miss) separately for early and late distractors ($t_{\mathrm{Distractor}}$; appearance either 100 or 350 ms after ball release) as well as low and high performers (median split regarding hitrates). *B:* Proportion of reactive distractor fixations (gaze shift latency relative to distractor onset < 150 ms) for early and late distractors, displayed separately by performance group. Data were analyzed using GLMMs; *n* = 43 subjects; Values are means ± bootstrapped SE; ***P* < .01, ****P* < .001.

When considering only reactive gaze shifts (which were defined as gaze shifts toward the distractor with a latency < 150 ms after distractor onset), both high and low performers were able to suppress gaze shifts toward the distractor when critical information (i.e., ball flight information) was still available. This was the case when the distractor was displayed 100 ms after release (Fig. 5*B*). This result pattern might suggest that, in general, individuals are aware of when critical information is available, and suppression is evident in such cases. However, motor expertise is necessary to assign greater weight to outcome information and to shield visual attention from salient distractors during motor errors.

3 Discussion

The present work examined how sensorimotor predictions shape visual information uptake during motor learning, with a particular focus on tasks in which actions generate distal effects in the environment. In such tasks, effective action outcome evaluation depends on prioritizing the appropriate visual information at the right moment despite competing attentional demands. To address this question, three sequential studies were conducted in which eye movements were recorded while participants performed a semi-virtual, goal-directed throwing task.

Study I aimed to isolate the immediate role of sensorimotor predictions in guiding visual attention. By controlling for other sources of predictive gaze behavior, such as learned internal models of environmental dynamics, this study provided initial evidence that predictions based on movement-related information proactively guide gaze toward feedback-relevant locations, thereby facilitating the evaluation of movement outcomes. Building on this, *Study II* examined whether predictive estimates of success or failure modulate attentional prioritization when multiple stimuli compete for attention. The results showed that the value of learning-relevant information is weighted dynamically based on the history of action outcomes (success vs. failure) and the predicted outcome of the current trial, ensuring a purposeful allocation of attentional resources. Finally, *Study III* explored how such prediction-based top-down control interacts with bottom-up saliency. It suggests that with sufficient motor expertise, salient distractors can be contingently shielded in feedback-critical situations.

Together, these studies show that sensorimotor predictions (I) facilitate efficient feedback processing, (II) dynamically modulate attentional priority, and (III) guide gaze in competition with stimulus-driven saliency, uncovering key mechanisms by which sensorimotor predictions might support motor learning.

In the following section, the significance of such *sensorimotor control of visual attention* for optimizing information processing in the context of motor learning will be discussed. The discussion is organized into two parts: first, considering its relevance across different types of tasks, and second, discussing its influence among other factors that guide gaze during natural behavior.

3.1 Significance of Sensorimotor Control of Visual Attention Across Tasks

Study I demonstrated that participants generated predictive gaze shifts toward future action effects both when ball flight information was available and when neither the ball flight nor the target was visible. In these cases, fixation durations were precisely modulated by action outcome and uncertainty, indicating the high informational value of gaze positions selected via sensorimotor predictions.

However, when the ball flight was masked, but the throwing target remained visible, gaze was consistently drawn to the target. This finding indicates that a visually salient anchor can override gaze guidance based on sensorimotor predictions. Critically, this effect does not reflect stimulus-driven capture per se, but is rather driven by the functional relevance of the target as an approximate reference for the feedback location. That a low-cost, stimulus-driven strategy is reasonably favored when internal predictions were challenging to generate is represented by fixation duration result patterns. Even when participants only fixated the target, fixation durations were prolonged in misses compared with hits, as indicated by a simple hit-miss comparison of fixation durations in the respective experimental condition. This pattern implies that, in the present task, even a simple target fixation provided sufficient information for outcome evaluation, thereby potentially reducing the relative benefit of more precise prediction-based gaze shifts. The present study could not determine whether fixation locations chosen using sensorimotor predictions provided greater informational value with respect to action outcome evaluation than fixating the throwing target. Detecting more subtle differences in the informational value of the selected positions would have required a finer-grained analysis of fixation duration patterns across all experimental conditions, which in turn would have necessitated a larger number of trials per condition.

Notably, in the present throwing task, a) a visual anchor could indicate the approximate effect location, and b) action effects occurred within a small field of vision. In tasks in which action effects can occur across a wider field of vision and no visual cue indicates their future location — as in a tennis serve — the functional significance of sensorimotor control of visual attention might be higher. Consistent with this idea, Massing et al. (2016) showed that restricting gaze did not impair learning when action effects were confined to a narrow visual area, but did impair performance when effects spanned a larger visual angle. Thus, the significance of gaze control through sensorimotor predictions likely depends on the availability of external visual anchors, and scales with the spatial extent of the action effects.

This differentiation regarding task specificity extends the distinction made in the introduction, where the significance of sensorimotor predictions in guiding gaze for outcome evaluation was argued to be higher in tasks with distal action effects compared to tasks producing proximal effects. In the latter case, action outcome evaluation could rely on other sensory modalities such as proprioception or haptics (Avraham & Nisky, 2020), and gaze may primarily serve online control of movements (Land et al., 1999). Nonetheless, the role of sensorimotor predictions in guiding visual attention in such tasks should be examined explicitly, even though this is methodologically challenging because online movement control and outcome evaluation are tightly intertwined both spatially and temporally.

In summary, the significance of sensorimotor predictions for the spatial positioning of gaze and its potential contribution to motor learning appears to be contingent upon the task taxonomy.

Mechanisms identified in *Study II* (value assignment) and *Study III* (shielding visual attention from salient distractors) become particularly relevant when tasks contain multiple competing gaze targets or potential distractors — conditions characteristic of open, dynamic environments such as team sports rather than highly constrained tasks like Skittles or darts. How sensorimotor control of visual attention is weighted against other factors influencing the allocation of visual attention in such settings is discussed in the following section.

3.2 Significance of Sensorimotor Control of Visual Attention Among Other Factors Influencing Gaze Allocation

Available visual input far exceeds the processing capacity of the visual system, necessitating a selection of scene elements for prioritized processing (Klink et al., 2014). A widely accepted framework assumes that gaze selection is governed by a dynamic priority map, in which each spatial location is continuously assigned a value that reflects its current behavioral relevance (e.g., Fecteau & Munoz, 2006; Zelinsky & Bisley, 2015). Priority signals can arise from several sources: for example, bottom-up sensory factors such as feature contrast (i.e., saliency), top-down goal states associated with planned actions, or expectations shaped by past experience (Failing & Theeuwes, 2018; Zelinsky & Bisley, 2015).

Typical goal-directed actions — such as making tea — have been conceptualized as sequences of sensorimotor decisions made under uncertainty (Domínguez-Zamora & Marigold, 2021; Gallivan et al., 2018; Hayhoe, 2017; Maloney & Zhang, 2010; Wolpert &

Landy, 2012). In this view, gaze primarily serves to provide visual information needed for the online control of movement and for selecting immediate actions (Hayhoe et al., 2025). However, viewing goal-directed behavior solely as a sequence of actions that serve an overarching goal, like having a warm cup of tea, neglects a motor learning perspective, in which individuals must assess the accuracy of each individual action to maintain or improve performance.

By using a task in which accurate visual evaluation of action outcomes is essential (i.e., a task with distal action effects), the present dissertation demonstrates that sensorimotor predictions represent an additional source of priority signals that shape gaze behavior in ways that support action outcome evaluation. *Studies II* and *III*, in particular, show how these predictions contribute to value assignment within the priority map. Because the priority map integrates multiple types of signals, the values assigned to potential gaze targets can conflict (Zelinsky & Bisley, 2015). The following sections discuss how sensorimotor predictions are weighted relative to other contributing factors when determining where gaze is directed.

In *Study II*, participants systematically modulated their fixation proportions toward competing gaze targets — one carrying informational value and the other motivational value — depending on both sensorimotor predictions and the history of recent action outcomes. Importantly, outcome history appeared to exert a dominant role in guiding visual attention to *learning-relevant* information. This is likely because outcome history provides a more reliable value-predictive cue than sensorimotor signals. If a previous trial was an error, it is indispensable to assess whether movement corrections led to the desired corrective effect. In such cases, the informational target addresses an evident information gap, closure of which has high task relevance for learning and long-term task performance. Sensorimotor predictions were meanwhile flexibly integrated to assign value to learning-relevant information. By contrast, sensorimotor predictions, like outcome history, signaled spare attentional capacity and enabled gaze allocation to positive reinforcement cues.

Importantly, these modulations of value assigned to competing targets occurred within stable individual preferences for either informational or motivational cues. Participants differed consistently in the proportion of fixations devoted to each target type, and these tendencies were not predictive of task performance. Rather, they likely reflect person-specific factors such as learning style, and cognitive costs associated with processing information (Daddaoua et al., 2016).

Together, these findings contribute to a broader understanding of how previous action outcomes and sensorimotor predictions interact to allocate perceptual resources in the context of motor learning. Furthermore, they show that sensorimotor predictions seem to play a subordinate role in value assignment among stable individual preferences regarding informational or motivational cues. Future research should address whether the relative influence of sensorimotor predictions increases with practice, as more reliable internal models may progressively bias the assignment of attentional priority.

A similar hierarchy of influences in value assignment emerged when contrasting sensorimotor predictions with bottom-up saliency. In *Study III* participants showed robust, person-specific attraction toward salient stimuli that did not correspond to task performance. Yet these baseline tendencies were modulated by sensorimotor predictions: with sufficient motor expertise, salient distractors were fixated less often when error feedback was pending. The influence of sensorimotor predictions may have been stronger if fixations on the distractor and feedback perception had been in more direct temporal competition. In the present design, participants could fixate on the distractor first and still perceive the outcome feedback afterward. Furthermore, task performance in *Study III* was worse than in *Studies I* and *II*, possibly going along with insufficient forward models for reliable outcome predictions. This may have reduced the capacity of predictive signals to shield attention from salient but irrelevant stimuli in feedback-critical situations, i.e., in errors. Thus, although sensorimotor predictions can counteract saliency under certain circumstances (i.e., sufficient motor expertise), their influence here remained limited and subordinate to stable, person-specific attraction to salient stimuli. The precise contribution of sensorimotor predictions in competition with saliency (especially in direct competition with outcome feedback) remains an open question and warrants further investigation, though.

The combined results from *Study I* (showing attraction to the throwing target when outcome prediction was non-trivial) and *Study III* (demonstrating generalized suppression of salient distractors when ball flight information was visible) further indicate that explicit knowledge of task-relevance can outweigh gaze guidance through sensorimotor predictions.

Taken together, the findings across *Studies I - III* suggest that the control of visual attention through sensorimotor predictions is flexibly integrated with more stable interindividual traits, recent experiences, and top-down biases based on explicit knowledge of task-relevant anchors. Sensorimotor predictions appear to function as one component within a broader system of gaze control mechanisms, whose relative contributions may vary across contexts and stages of learning.

3.3 Future Directions

In all three studies, participants first had to acquire sufficient task expertise to establish reliable forward models (Jordan & Rumelhart, 1992). Thus, the mechanisms uncovered in this dissertation primarily describe characteristics of skilled performance. This is particularly notable in *Study III*, where the contingent shielding of salient distractors in feedback-critical situations was only observed in participants with adequate motor expertise. To investigate the direct benefits of gaze control through sensorimotor predictions for motor learning, learning experiments utilizing between-subjects designs with retention tests are necessary. Specifically, future studies could directly manipulate the predictive gaze strategies that emerge from sensorimotor predictions in an intervention group, comparing them to a control group. This methodology would allow for the assessment of how gaze behavior shaped by sensorimotor predictions translates into performance gains. Furthermore, it might be valuable to test whether novices can profit from training predictive gaze strategies – for example, through augmented reality-based guidance to task-relevant information. Such an approach could foster an error-oriented gaze strategy, thereby enhancing the perception of outcome-critical movement information.

3.4 Conclusion

This dissertation investigated how sensorimotor predictions shape visual information uptake in the context of motor learning. Across three studies employing a semi-virtual throwing task, the results reveal key mechanisms through which sensorimotor predictions can support learning: they proactively direct gaze toward feedback-relevant locations, modulate attentional prioritization according to predicted success, and shield attention from salient stimuli in feedback-critical situations.

The significance of such sensorimotor control of visual attention appears to be dependent on task-taxonomy and is shaped by its interaction with other factors governing gaze allocation. Since predictive skills emerge with task expertise, the observed mechanisms reflect characteristics of skilled performance. Thus, while the present studies provide strong evidence that sensorimotor predictions influence gaze control and attentional selection, clarifying their direct contribution to motor learning remains a key open question for future research.

References

Anguera, J. A., Seidler, R. D., & Gehring, W. J. (2009). Changes in Performance Monitoring During Sensorimotor Adaptation. *Journal of Neurophysiology*, *102*(3), 1868–1879. https://doi.org/10.1152/jn.00063.2009

Avraham, C., & Nisky, I. (2020). The effect of tactile augmentation on manipulation and grip force control during force-field adaptation. *Journal of NeuroEngineering and Rehabilitation*, *17*(1), 17. https://doi.org/10.1186/s12984-020-0649-y

Bakst, L., & McGuire, J. T. (2021). Eye movements reflect adaptive predictions and predictive precision. *Journal of Experimental Psychology: General*, *150*(5), 915–929. https://doi.org/10.1037/xge0000977

Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Research*, *46*(26), 4355–4374. https://doi.org/10.1016/j.visres.2006.08.021

Blakemore, S.-J., Wolpert, D., & Frith, C. (2000). Why can't you tickle yourself?: *NeuroReport*, *11*(11), R11–R16. https://doi.org/10.1097/00001756-200008030-00002

Daddaoua, N., Lopes, M., & Gottlieb, J. (2016). Intrinsically motivated oculomotor exploration guided by uncertainty reduction and conditioned reinforcement in non-human primates. *Scientific Reports*, *6*(1), 20202. https://doi.org/10.1038/srep20202

Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, *4*(11), 423–431. https://doi.org/10.1016/S1364-6613(00)01537-0

Diaz, G., Cooper, J., Rothkopf, C., & Hayhoe, M. (2013). Saccades to future ball location reveal memory-based prediction in a virtual-reality interception task. *Journal of Vision*, *13*(1), 20. https://doi.org/10.1167/13.1.20

Domínguez-Zamora, F. J., & Marigold, D. S. (2021). Motives driving gaze and walking decisions. *Current Biology*, *31*(8), 1632-1642.e4. https://doi.org/10.1016/j.cub.2021.01.069

Draschkow, D., Wolfe, J. M., & Vo, M. L.-H. (2014). Seek and you shall remember: Scene semantics interact with visual search to build better memories. *Journal of Vision*, *14*(8), 10–10. https://doi.org/10.1167/14.8.10

Einhäuser, W., Rutishauser, U., & Koch, C. (2008). Task-demands can immediately reverse the effects of sensory-driven saliency in complex visual stimuli. *Journal of Vision*, *8*(2), 2. https://doi.org/10.1167/8.2.2

Elsner, B., & Hommel, B. (2004). Contiguity and contingency in action-effect learning. *Psychological Research*, *68*(2–3), 138–154. https://doi.org/10.1007/s00426-003-0151-8

Epelboim, J. (1998). Gaze and retinal-image-stability in two kinds of sequential looking tasks. *Vision Research*, *38*(23), 3773–3784. https://doi.org/10.1016/S0042-6989(97)00450-1

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433. https://doi.org/10.1038/415429a

Failing, M., & Theeuwes, J. (2018). Selection history: How reward modulates selectivity of visual attention. *Psychonomic Bulletin & Review*, *25*(2), 514–538. https://doi.org/10.3758/s13423-017-1380-y

Fecteau, J., & Munoz, D. (2006). Salience, relevance, and firing: A priority map for target selection. *Trends in Cognitive Sciences*, *10*(8), 382–390. https://doi.org/10.1016/j.tics.2006.06.011

Fiehler, K., Brenner, E., & Spering, M. (2019). Prediction in goal-directed action. *Journal of Vision*, *19*(9), 10. https://doi.org/10.1167/19.9.10

Flanagan, J. R., & Wing, A. M. (1997). The Role of Internal Models in Motion Planning and Control: Evidence from Grip Force Adjustments during Movements of Hand-Held Loads. *The Journal of Neuroscience*, *17*(4), 1519–1528. https://doi.org/10.1523/JNEUROSCI.17-04-01519.1997

Gallivan, J. P., Chapman, C. S., Wolpert, D. M., & Flanagan, J. R. (2018). Decision-making in sensorimotor control. *Nature Reviews Neuroscience*, *19*(9), 519–534. https://doi.org/10.1038/s41583-018-0045-9

Hayhoe, M. M. (2000). Vision Using Routines: A Functional Account of Vision. *Visual Cognition*, *7*(1–3), 43–64. https://doi.org/10.1080/135062800394676

Hayhoe, M. M. (2017). Vision and Action. *Annual Review of Vision Science*, *3*(1), 389–413. https://doi.org/10.1146/annurev-vision-102016-061437

Hayhoe, M. M., & Matthis, J. S. (2018). Control of gaze in natural environments: Effects of rewards and costs, uncertainty and memory in target selection. *Interface Focus*, *8*(4), 20180009. https://doi.org/10.1098/rsfs.2018.0009

Hayhoe, M., Rothkopf, C., Goettker, A., & Powell, N. (2025). Natural visually guided behavior. *Brain Research*, *1866*, 149899. https://doi.org/10.1016/j.brainres.2025.149899

Henderson, J. M. (2017). Gaze Control as Prediction. *Trends in Cognitive Sciences*, *21*(1), 15–23. https://doi.org/10.1016/j.tics.2016.11.003

Henderson, J. M., Brockmole, J. R., Castelhano, M. S., & Mack, M. (2007). Visual saliency does not account for eye movements during visual search in real-world scenes. In R. P. G. V. Gompel, M. H. Fischer, W. S. Murray, & R. L. Hill (Eds.), *Eye Movements* (pp. 537–562). Elsevier. https://doi.org/10.1016/B978-008044980-7/50027-6

Henderson, J. M., Weeks, P. A., & Hollingworth, A. (1999). The effects of semantic consistency on eye movements during complex scene viewing. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(1), 210–228. https://doi.org/10.1037/0096-1523.25.1.210

Herst, A. N., Epelboim, J., & Steinman, R. M. (2001). Temporal coordination of the human head and eye during a natural sequential tapping task. *Vision Research*, *41*(25–26), 3307–3319. https://doi.org/10.1016/S0042-6989(01)00158-4

Illamperuma, N. H., & Fooken, J. (2024). Towards a functional understanding of gaze in goal-directed action. *Journal of Neurophysiology*, *132*(3), 767–769. https://doi.org/10.1152/jn.00342.2024

Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, *40*(10–12), 1489–1506. https://doi.org/10.1016/S0042-6989(99)00163-7

Jablonski, D. (2011, January 9). Cold-shooting Battle heats up just in time. *The Columbus Dispatch*. https://eu.dispatch.com/story/sports/college/2011/01/09/cold-shooting-battle-heats-up/23831928007/

Joch, M., Hegele, M., Maurer, H., Müller, H., & Maurer, L. K. (2017). Brain negativity as an indicator of predictive error processing: The contribution of visual action effect monitoring. *Journal of Neurophysiology*, *118*(1), 486–495. https://doi.org/10.1152/jn.00036.2017

Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye–Hand Coordination in Object Manipulation. *The Journal of Neuroscience*, *21*(17), 6917–6932. https://doi.org/10.1523/JNEUROSCI.21-17-06917.2001

Jordan, M. I., & Rumelhart, D. E. (1992). Forward Models: Supervised Learning with a Distal Teacher. *Cognitive Science*, *16*(3), 307–354. https://doi.org/10.1207/s15516709cog1603_1

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, *9*(6), 718–727. https://doi.org/10.1016/S0959-4388(99)00028-8

Klink, P. C., Jentgens, P., & Lorteije, J. A. M. (2014). Priority Maps Explain the Roles of Value, Attention, and Salience in Goal-Oriented Behavior. *The Journal of Neuroscience*, *34*(42), 13867–13869. https://doi.org/10.1523/JNEUROSCI.3249-14.2014

Krigolson, O. E., & Holroyd, C. B. (2006). Evidence for hierarchical error processing in the human brain. *Neuroscience*, *137*(1), 13–17. https://doi.org/10.1016/j.neuroscience.2005.10.064

Lai, M.-L., Tsai, M.-J., Yang, F.-Y., Hsu, C.-Y., Liu, T.-C., Lee, S. W.-Y., Lee, M.-H., Chiou, G.-L., Liang, J.-C., & Tsai, C.-C. (2013). A review of using eye-tracking technology in exploring learning from 2000 to 2012. *Educational Research Review*, *10*, 90–115. https://doi.org/10.1016/j.edurev.2013.10.001

Land, M. F. (2006). Eye movements and the control of actions in everyday life. *Progress in Retinal and Eye Research*, *25*(3), 296–324. https://doi.org/10.1016/j.preteyeres.2006.01.002

Land, M. F., Mennie, N., & Rusted, J. (1999). The Roles of Vision and Eye Movements in the Control of Activities of Daily Living. *Perception*, *28*(11), 1311–1328. https://doi.org/10.1068/p2935

Le-Hoa Võ, M., & Wolfe, J. M. (2015). The role of memory for visual search in scenes. *Annals of the New York Academy of Sciences*, *1339*(1), 72–81. https://doi.org/10.1111/nyas.12667

Liston, D. B., & Stone, L. S. (2008). Effects of Prior Information and Reward on Oculomotor and Perceptual Choices. *The Journal of Neuroscience*, *28*(51), 13866–13875. https://doi.org/10.1523/JNEUROSCI.3120-08.2008

Maloney, L. T., & Zhang, H. (2010). Decision-theoretic models of visual perception and action. *Vision Research*, *50*(23), 2362–2374. https://doi.org/10.1016/j.visres.2010.09.031

Massing, M., Blandin, Y., & Panzer, S. (2016). Magnifying visual target information and the role of eye movements in motor sequence learning. *Acta Psychologica*, *163*, 59–64. https://doi.org/10.1016/j.actpsy.2015.11.004

Maurer, L. K., Joch, M., Hegele, M., Maurer, H., & Müller, H. (2019). Predictive error processing distinguishes between relevant and irrelevant errors after visuomotor learning. *Journal of Vision*, *19*(4), 18. https://doi.org/10.1167/19.4.18

Maurer, L. K., Maurer, H., & Müller, H. (2015). Neural correlates of error prediction in a complex motor task. *Frontiers in Behavioral Neuroscience*, *9*, 209. https://doi.org/10.3389/fnbeh.2015.00209

Miall, R. C., & Wolpert, D. M. (1996). Forward Models for Physiological Motor Control. *Neural Networks*, *9*(8), 1265–1279. https://doi.org/10.1016/S0893-6080(96)00035-4

Müller, H., & Sternad, D. (2004). Decomposition of Variability in the Execution of Goal-Oriented Tasks: Three Components of Skill Improvement. *Journal of Experimental Psychology: Human Perception and Performance*, *30*(1), 212–233. https://doi.org/10.1037/0096-1523.30.1.212

Neggers, S. F., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology*, *83*(2), 639–651. https://doi.org/10.1152/jn.2000.83.2.639

Pfeuffer, C. U., Kiesel, A., & Huestegge, L. (2016). A look into the future: Spontaneous anticipatory saccades reflect processes of anticipatory action control. *Journal of Experimental Psychology: General*, *145*(11), 1530–1547. https://doi.org/10.1037/xge0000224

Saslow, M. G. (1967). Effects of Components of Displacement-Step Stimuli Upon Latency for Saccadic Eye Movement. *Journal of the Optical Society of America*, *57*(8), 1024. https://doi.org/10.1364/JOSA.57.001024

Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Eye movements and perception: A selective review. *Journal of Vision*, *11*(5), 9. https://doi.org/10.1167/11.5.9

Sohn, J., & Lee, D. (2006). Effects of reward expectancy on sequential eye movements in monkeys. *Neural Networks*, *19*(8), 1181–1191. https://doi.org/10.1016/j.neunet.2006.04.005

Tatler, B. W., Hayhoe, M. M., Land, M. F., & Ballard, D. H. (2011). Eye guidance in natural vision: Reinterpreting salience. *Journal of Vision*, *11*(5), 5–5. https://doi.org/10.1167/11.5.5

Wolpert, D. M. (1997). Computational approaches to motor control. *Trends in Cognitive Sciences*, *1*(6), 209–216. https://doi.org/10.1016/S1364-6613(97)01070-X

Wolpert, D. M., & Flanagan, J. R. (2010). Motor learning. *Current Biology*, *20*(11), R467–R472. https://doi.org/10.1016/j.cub.2010.04.035

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3*(11), 1212–1217. https://doi.org/10.1038/81497

Wolpert, D. M., & Landy, M. S. (2012). Motor control is decision-making. *Current Opinion in Neurobiology*, *22*(6), 996–1003. https://doi.org/10.1016/j.conb.2012.05.003

Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2009). Visuo-motor coordination and internal models for object interception. *Experimental Brain Research*, *192*(4), 571–604. https://doi.org/10.1007/s00221-008-1691-3

Zelinsky, G. J., & Bisley, J. W. (2015). The what, where, and why of priority maps and their interactions with visual working memory. *Annals of the New York Academy of Sciences*, *1339*(1), 154–164. https://doi.org/10.1111/nyas.12606

Zhao, H., & Warren, W. H. (2015). On-line and model-based approaches to the visual control of action. *Vision Research*, *110*, 190–202. https://doi.org/10.1016/j.visres.2014.10.008

II

Publications

Study I

Published as: **Sensorimotor prediction is used to direct gaze toward task-relevant locations in a goal-directed throwing task**

Brand, T. K., *Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. (2024). Sensorimotor prediction is used to direct gaze toward task-relevant locations in a goal-directed throwing task. Journal of Neurophysiology, 132(2), 485-500.*

american physiological society®

JNP JOURNAL OF NEUROPHYSIOLOGY®

J Neurophysiol 132: 485–500, 2024.
*First published June 26, 2024; doi:*10.1152/jn.00052.2024

RESEARCH ARTICLE

Control of Movement

Sensorimotor prediction is used to direct gaze toward task-relevant locations in a goal-directed throwing task

Theresa K. Brand,[1,3] Alexander C. Schütz,[2,3] Hermann Müller,[1,3] Heiko Maurer,[1] Mathias Hegele,[1,3] and Lisa K. Maurer[1,3]

[1]Neuromotor Behavior Laboratory, Department of Psychology and Sport Science, Justus Liebig University Giessen, Giessen, Germany; [2]General and Biological Psychology, Department of Psychology, Philipps University Marburg, Marburg, Germany; and [3]Center for Mind, Brain and Behavior (CMBB), Universities of Marburg and Giessen, Giessen, Germany

Abstract

Previous research has shown that action effects of self-generated movements are internally predicted before outcome feedback becomes available. To test whether these sensorimotor predictions are used to facilitate visual information uptake for feedback processing, we measured eye movements during the execution of a goal-directed throwing task. Participants could fully observe the effects of their throwing actions (ball trajectory and either hitting or missing a target) in most of the trials. In a portion of the trials, the ball trajectory was not visible, and participants only received static information about the outcome. We observed a large proportion of predictive saccades, shifting gaze toward the goal region before the ball arrived and outcome feedback became available. Fixation locations after predictive saccades systematically covaried with future ball positions in trials with continuous ball flight information, but notably also in trials with static outcome feedback and only efferent and proprioceptive information about the movement that could be used for predictions. Fixation durations at the chosen positions after feedback onset were modulated by action outcome (longer durations for misses than for hits) and outcome uncertainty (longer durations for narrow vs. clear outcomes). Combining both effects, durations were longest for narrow errors and shortest for clear hits, indicating that the chosen locations offer informational value for feedback processing. Thus, humans are able to use sensorimotor predictions to direct their gaze toward task-relevant feedback locations. Outcome-dependent saccade latency differences (miss vs. hit) indicate that also predictive valuation processes are involved in planning predictive saccades.

NEW & NOTEWORTHY We elucidate the potential benefits of sensorimotor predictions, focusing on how the system actually uses this information to optimize feedback processing in goal-directed actions. Sensorimotor information is used to predict spatial parameters of movement outcomes, guiding predictive saccades toward future action effects. Saccade latencies and fixation durations are modulated by outcome quality, indicating that predictive valuation processes are considered and that the locations chosen are of high informational value for feedback processing.

action monitoring; forward model; predictive eye movements; sensorimotor prediction; throwing task

INTRODUCTION

Past research has shown a consistent and intricate behavioral interdependency between eye and hand movements in goal-directed actions (for a review, see Ref. 1). On the one hand, it is known that the accuracy of smooth pursuit eye movements can be enhanced by an active arm movement, indicating that nonvisual signals, such as the motor commands for an arm movement, can be used by the visual system to guide gaze (2–5). On the other hand, eye movements are used to support accurate hand and body movements. In interception tasks, for example, people shift their gaze toward the location where a moving target that is occluded for a certain time is expected to reappear (6–8) or toward the bouncing point of a ball in racket games (9–14). Thereby, the timing of such so-called predictive saccades is tightly linked to the execution of interceptive hand movements, and their accuracy

Correspondence: T. K. Brand (theresa.brand@sport.uni-giessen.de).

Submitted 2 February 2024 / Revised 17 June 2024 / Accepted 19 June 2024

is correlated with interceptive performance (15). Furthermore, it has also been demonstrated that humans predictively direct their gaze toward the location of the endpoints of their own movements (for reviews, see Refs. 16 and 17). Examples of such gaze shifts are that the eyes regularly lead the hand when making tea (18) or a peanut butter sandwich (19), when moving an object around an obstacle (20), when copying an arrangement of blocks (21, 22), when navigating a cursor from one target to another on a screen (23), when grasping an object (24–26), or simply when reaching to a target (27–31). Fixating an action site ahead of the arrival of the hand (or other end effectors) has been proposed to help direct the effector toward the action site (e.g., see Ref. 32), which indicates a connection of predictive saccades to action planning. Predictive gaze shifts in these situations could either result from an anticipation of stimuli one has to interact with or from an anticipation of actions one has to perform, both based on experience with the task (33).

A core characteristic of the examined tasks is that the action site and the effects produced are spatially overlapping. Furthermore, movements are under closed-loop control, meaning that motor commands can be updated during movement execution based on incoming sensory feedback. For these reasons, it is not possible to discern whether predictive saccades could also be guided to the intended effect that a certain action was meant to produce, as hypothesized by Pfeuffer et al. (33). This would rather indicate a connection of predictive saccades to outcome valuation of actions than to action planning.

To disentangle the possible functional mechanisms giving rise to predictive saccades, Pfeuffer and colleagues set up a task in which simple manual actions (key presses) produced simple distal effects (predictable visual stimuli on the left or right side of a screen after a short delay). Participants predictively directed their gaze toward these distal effects of their actions, and the predictive saccades occurred almost exclusively after the manual responses. These observations confirm—at least for tasks in which the action site is dissolved spatially from the effect the movement produces—that predictive saccades were less related to action planning but rather to outcome valuation [i.e., a comparison between intended and actual action effects as proposed by Pfeuffer et al. (33)].

That predictive processes play an essential role in the outcome valuation of actions has convincingly been shown in a plethora of studies. Over the past decades, it has been proposed that the human nervous system uses so-called internal forward models (e.g., see Refs. 34–37). In analogy to computational models, those forward models mimic the input-output relationships of the musculoskeletal system, allowing predictions of sensory action effects based on information about the current states (of the body and the environment) and on copies of the efferent motor commands (38–40). By determining the deviations of these predicted action effects from intended action effects before actual sensory feedback becomes available, actions can be evaluated online, and erroneous outcomes can be detected before they occur (predictive valuation). This can facilitate continuous adjustments during movement execution in closed-loop tasks (41, 42). Moreover, those sensorimotor predictions also support error attribution (dissociation between internally and externally caused errors) after movement execution by allowing comparisons between predicted and actual action outcomes, which supports performance improvements on a trial-by-trial basis (43, 44).

To optimally use the information that can be obtained from sensorimotor predictions for trial-by-trial adjustments, a reliable comparison of actual with predicted action effects is necessary. Thus, for visually observable effects, we propose a direct relationship between eye movements and sensorimotor predictions, in which the gaze is predictively directed toward predicted action effects. More specifically, we suggest that using sensorimotor predictions to direct gaze toward the predicted action effects offers the following two advantages for the valuation of own actions: first, it should allow precise quantification of actual deviations from a known target or intended action effect (in direction and amplitude)—which might be especially helpful if outcome feedback is only available for a short duration, and, therefore, could be easily missed. Second, the location of the predicted action effect should contain useful information on deviations of the actual from the predicted action effect, which is a critical aspect for error attribution. The idea of predictive saccades targeted toward predicted action effects is also based on the findings about predictive gaze behavior in interception tasks, where eye movement patterns seem to be shaped by learned internal models of the dynamic properties of the environment, showing that model-based prediction is likely to be a pervasive component in natural gaze (6–15).

In the case of the unambiguous and dichotomous action effects produced in the task used by Pfeuffer et al. (33; e.g., right key press = effect on the right side of the screen), it is not possible to discriminate whether the saccades were made to the intended effect of the action or to the predicted effect of the action. To differentiate between intended and predicted effects, tasks with more natural and continuous contingencies between actions and action effects are needed. It has been widely shown that visual and cognitive processing demands influence how long specific locations are fixated on (e.g., see Refs. 45–47; for reviews, see Refs. 48 and 49). With different processing demands depending on movement execution and its respective feedback, such tasks may be able to reveal more precisely the links between predictive gaze behavior and outcome valuation.

Thus, we investigated whether sensorimotor predictions of action effects could be used to facilitate visual information uptake in the context of (error) feedback processing. For this purpose, participants performed a goal-directed throwing task with a natural temporal delay of the distal action outcome relative to movement execution, allowing predictions about the action effect before outcome feedback became available. After a physical ballistic throwing movement (resembling a frisbee toss), a ball presented on a screen traveled around a post to hit a target on the opposing side, leading to a natural spatial decoupling between movement execution and the observation of action effects. Despite varying planning signals depending on previous outcomes including uncertainties (50), the environmental goal and, thus, the intended action effect (hitting the center of the target) remained constant throughout the experiment. In contrast, action effects varied from trial to trial depending on the quality of the planning signals and movement execution.

This allowed us to clearly discriminate the intended action effect (the task goal, i.e., hitting the target with the ball) from the predicted action effects (future ball positions) and, thus, whether predictive saccades were made in the direction of one or the other. In addition, movement outcome quality was precisely quantifiable so that fixation durations at the locations after predictive saccades could be used as a measure of whether those predictively chosen locations were of informational value for feedback processing.

MATERIALS AND METHODS

Participants

Twenty participants (11 females, 9 males) from the student population of the Justus Liebig University, Giessen, Germany, with an age of 25.10 ± 3.08 yr (means ± SD), completed the study. All participants were right-handed, had normal or corrected-to-normal vision, and had no history of injuries in the upper limbs. Each subject participated in the study over three days for ∼1 h, and received a small compensation (either course credit or payment) for participation. The experiment followed the ethical standards laid down in the Declaration of Helsinki (2013, except § 35, preregistration). The protocol was approved by the Ethical Review Board of the Justus Liebig University, Giessen, and subjects gave written informed consent to participate in the study.

We excluded one participant because of inaccurate eye movement calibration results. Another two participants were excluded due to a high prevalence of blinks during a critical phase in the trials (precisely defined in *Eye movement analysis*), resulting in a sample size of 17 participants for the analyses.

Task and Setup

Participants performed a complex goal-directed throwing task inspired by the British pub game “Skittles.” In the original version of the game, a ball attached to the top of a post by a string must be swung around the post to hit target objects on the opposite side (Fig. 1*C*). Apart from the ballistic nature of the task preventing online corrections during movement execution, this throwing task allows a temporal as well as spatial separation of movement execution and its final outcome. Specific action effects can arise from an infinite number of angle-velocity combinations at release, which means that the task is redundant, and hits and misses are not functions of a dichotomous difference in throwing execution. Furthermore, the relationship between execution variables (release angle and velocity) and outcomes in the Skittles task is nonlinear, so outcome prediction is not trivial. The chosen variant of the Skittles task was performed semivirtually (see also Refs. 36 and 51). Participants executed a real ballistic throwing movement using a metal lever device (manipulandum), while the action effect was only visible on a computer screen from an overhead perspective (Fig. 1*A*). On the screen (Model: Dell Alienware AW2521HF, active screen size: 37.7 (*H*) × 30.2 (*V*) cm—full-screen size: 55 (*H*) × 31 (*V*) cm, screen resolution: 1,280 × 1,024 pixels, refresh rate: 120 Hz) in front of each subject, a virtual representation of the metal lever (whose position continuously represented the position of the physical manipulandum), a green virtual ball (Luminance: 93.81 cd/m^2, RGB: [25 153 0]), a gray center post (Luminance: 2.49 cd/m^2, RGB: [30 30 30]), a red target (Luminance: 25.44 cd/m^2, RGB: [153 25 0]), and a predefined start position were displayed (Fig. 1*B*). As the subjects’ heads were not fixed by a chin- or forehead rest, the distance between their head and the monitor could vary slightly. At a typical eye-to-screen distance of 70 cm, stimulus sizes were 0.7° of visual angle for the ball and target, 3.4° for the center post, and 0.9° for the start position.

The calculation of the elliptical ball trajectory around the center post in each trial was based on a physical model of the task (52), where the sizes and positions of the task stimuli were as follows: center post (radius = 0.25 m; position: $x = 0.0$ m, $y = 0.0$ m), target (radius = 0.05 m; position: $x = 0.8$ m, $y = 0.9$ m), ball (radius = 0.05 m; mass = 0.1 kg), and spring constant (1.0 N/m). The two parameters, angle and velocity of the manipulandum at the moment of ball release, which clearly defined the resulting trajectory, were acquired using a magnetic angle sensor integrated into the manipulandum with a resolution of 12 bits (0.09°), and a

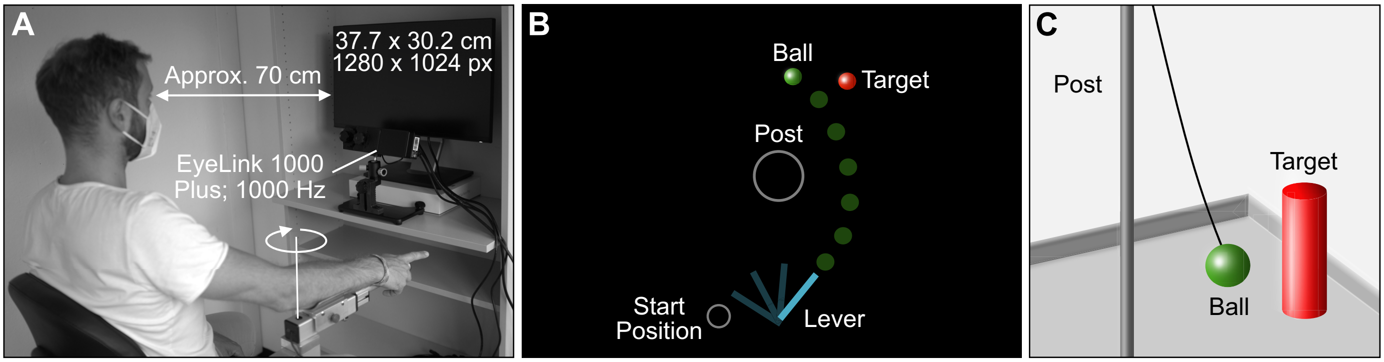


Figure 1. *A*: setup of the semivirtual adaptation of the Skittles task. During the task, participants use a metal lever to conduct throwing movements in an outward-rotation manner. A virtual ball is released by lifting the index finger from an electrical contact sensor at the tip of the manipulandum. Action effects are displayed on a screen in front of the participant. Eye movements are tracked during task execution with an Eyelink 1000 Plus with desktop mount running in remote mode; the participant depicted above gave written informed consent for the publication of this picture. *B*: task space displayed on the screen. The movements’ starting position is indicated on the left-hand side of the manipulandum’s vertical axis. After release, a green ball travels with an elliptical trajectory around a gray center post and toward a red target. *C*: schematic illustration of the real version of Skittles where a ball attached to a post by a string must be swung around the post to hit (a) target object(s) on the opposite side.

sampling rate of 1,000 Hz. To virtually pick up and release the ball, participants placed or removed their index fingers from an electrical contact sensor at the tip of the lever.

In the regular task version, participants could see the ball flying toward the target after the ball was released. The ball collided with the target (a hit) whenever the distance between the ball center's trajectory and the target center ($d_{\min}$) was equal to or smaller than twice the radius of the ball/target. In these cases, the target was pushed away from its position, and the sound of two colliding billiard balls was heard. Depending on the collision angle, the ball bounced off the target at an angle defined by the laws of energy transmission between rigid objects (akin to billiard balls). In trials where $d_{\min}$ was greater than twice the radius of the ball/target, the ball missed the target. Note that depending on the throwing strategy, the time between release and outcome feedback varied minimally between trials of individual participants ranging around 632 ± 58 ms. During task execution, eye position signals of the subjects' right eyes were recorded with a video-based eye tracker (EyeLink 1000 Plus on Desktop Mount; SR Research, Ottawa, ON, Canada) with a sampling rate of 1,000 Hz running in remote mode. This mode enables precise eye tracking without the need for physical head stabilization and thus allows for natural behavior during task execution. The experimental software that enabled task execution and synchronized eye movement data acquisition was created using MATLAB R2021b (The MathWorks, Inc.) and the Psychophysics Toolbox version 3.0.18 (53).

Participants were seated on a height-adjustable stool to align their horizontal line of vision with the center of the screen. The foam-padded manipulandum with a forearm rest was fixed on a height-adjustable stand with the vertical rotation axis below the right elbow joint of the participants. The movement was restricted to the horizontal plane, specifically to rotations around a fixed vertical axis. Window blinds and artificial light ensured constant lighting conditions during data acquisition.

Procedure and Study Design

Participants performed the experimental task on three days. At the beginning of the first session, the task was explained to the participants using a miniature model of the real Skittles game. In addition, five test trials preceded the experimental schedule to clarify the semivirtual task execution. Each session was initialized by a 13-point calibration and validation procedure for eye tracking, in which calibrations were not accepted until average and maximum errors were less than 0.5° and 1°, respectively. Fixations on each fixation target were accepted manually by the experimenter, and fixation targets were displayed in random order. To pick up the virtual ball at the beginning of each trial (the ball gets visually attached to the virtual equivalent of the lever), participants placed their right index fingers on the electrical contact sensor at the tip of the lever, thereby closing an electrical circuit. At the same time, their arms rested on the foam-padded manipulandum. Participants were instructed to initiate each trial by moving the tip of the virtual lever into a red circle positioned left to the fixed end of the lever while simultaneously fixating on this point. Upon reaching the circle, its color turned yellow, and an online drift check was performed. The data for the drift check were recorded for 100 ms after the lever had been inside the start circle for 1 s. The circle turned green when the gaze remained within 2° of the center of the start point on all measurements during the 100-ms drift check. The green start circle signaled that participants could start the movement. They were free to start at any moment after the green signal, and were instructed not to start as fast as possible in reaction to it. If drifts were detected, eye positions were re-calibrated and re-validated (with a 13-point procedure) before movement execution. Participants "threw" the virtual ball by moving the manipulandum in an outward horizontal movement resembling a frisbee toss, starting in front of their upper bodies. Upon lifting their fingers from the contact sensor, the virtual ball was released from the virtual lever and traveled in a counterclockwise trajectory around the center post. The drift check procedure described earlier prevented fast, rhythmic executions of subsequent trials. Thus, the task can be regarded as being discrete.

During each session, participants conducted 500 throws interspersed with short rest periods after each block of 100 trials. Before each new block, the eye tracker was re-calibrated. During the first two sessions, participants received continuous visual feedback about ball flight (C_{full}) to build up task expertise. This means that participants could see the ball flying toward the target after it was released. In this condition, saccades toward future action effects could be based on learned internal models of the dynamic properties of the ball flight (as shown in studies on interception tasks, e.g., see Refs. 6–14). To exclude this explanation for the expected gaze patterns, we included additional conditions without information about ball flight that alternated with C_{full} in *session 3*. In these conditions, predictions and possible predictive saccades toward future action effects could only be based on internal information about the movement (efference copy and afferent proprioceptive information, Fig. 2), i.e., on sensorimotor prediction. In C_{noBall}, the ball was masked immediately after ball release (t_{Release}) and reappeared for 500 ms at the time of minimum distance between target and ball (t_{dmin}), providing static outcome feedback for the participants. To avoid the visually salient target attracting gaze (toward the intended action effect) in a situation where outcome prediction is particularly challenging due to reduced input signals, we additionally masked the target from t_{Release} until t_{dmin} in condition $C_{\mathrm{noBallnoTarget}}$ to uncover the expected gaze behavior. Acoustic feedback was the same in all conditions (the sound of two colliding billiard balls at t_{dmin} in cases of hits), and conditions did not differ in visual input during the planning and movement phase ($t < t_{\mathrm{Release}}$).

The concrete procedure in *session 3* was as follows:

- Twenty trials C_{full},
- Blocks of 10 trials C_{noBall} or $C_{\mathrm{noBallnoTarget}}$ separated by five trials C_{full}.

The order of the two additional experimental conditions was pseudorandomized to control for sequencing effects by simultaneously ensuring the same number of trials in each condition (160 trials each, after the 20 trials in C_{full} at the beginning of *session 3*; see Fig. 2 for a depiction of conditions and experimental schedule).

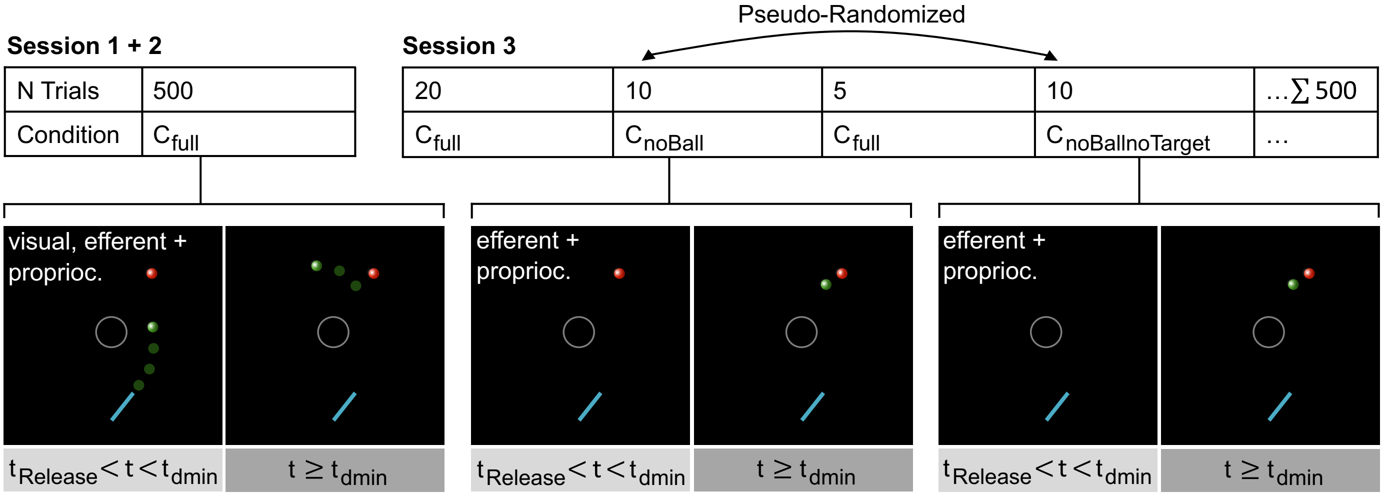


Figure 2. Experimental schedule. In each of three sessions, participants executed 500 throwing trials. In the first two sessions, the ball flight was visible after release (C_{full}). In *session 3*, trials with ball flight (C_{full}) alternated with trials in which the ball was masked after the time of release ($t_{Release}$) and not shown until the time of minimum distance between ball and target (t_{dmin}). Thereafter it reappeared for 500 ms to provide static outcome feedback (C_{noBall} and $C_{noBallnoTarget}$). In $C_{noBallnoTarget}$, the target was also masked during the time between $t_{Release}$ and t_{dmin}.

Participants were informed of the upcoming condition through on-screen instructions before each block of trials under a new condition.

Hypotheses

If sensorimotor predictions are included in the selection of saccadic fixation locations, we expected the following:

- Consistent predictive gaze shifts toward future action effects (i.e., future ball positions) in trials with continuous ball flight information (C_{full}), but also in trials with masked ball flight when only internal information about the movement (efference copy and proprioceptive information) can be used for prediction ($C_{noBallnoTarget}$).
- Weaker or no correspondence between predictively chosen fixation locations and action effects when no ball flight information is available, but the visually salient target can be fixated (C_{noBall}).

In addition, if the predictively chosen fixation locations are of high informational value for feedback processing, fixation durations at this point should depend on the prevailing processing demands (54). It is plausible to assume that processing demands vary depending on the following:

- Action outcome (i.e., hit vs. miss), where processing demands should be higher when movement corrections are necessary.
- Outcome uncertainty, where processing demands may increase for outcomes close to the hit/miss boundary due to a decrease in outcome predictability (45, 55).

In case predictive valuation processes (predictive detection of outcome valence) are also considered in the planning of predictive gaze shifts, there could be differences in the latency of predictive gaze shifts depending on the action outcome (hit vs. miss) as, for example, it has been shown that saccade latencies in simple saccadic choice tasks are sensitive to the expected value of potential outcomes (56–58).

Data Processing and Analysis

Task performance analysis.

Data processing and analyses were conducted using MATLAB R2021a (The MathWorks, Inc.). As task performance is assumed to be related to the quality of the internal forward model of the task (38), and is therefore associated with the ability to predict the action effects of self-generated movements, we calculated the participants' hit rates throughout the experiment. Task performance, and thus skill level, was defined as the hit rate in blocks of 100 trials. In addition, we calculated hit rates within all experimental conditions in *session 3* to control for their effects on task performance.

Eye movement analysis.

The decomposition of the eye tracking data into saccades and fixations was carried out with the built-in EyeLink algorithm using the following three thresholds: velocity (>30 °/s), motion (0.1°), and acceleration (>8,000 °/s^2). To prepare analyses of dependent variables, time stamps of the two trial events, $t_{Release}$, and t_{dmin} were determined in the eye data of each trial. Trials were excluded when the center post was hit, in cases a time stamp was not registered, in cases of bad data quality (precision or accuracy >2°, track loss, artifacts), and when blinks occurred between movement onset and t_{dmin}. These exclusion criteria led to a data loss of 6.87% (percentage of trials lost due to technical issues: 2.01%).

To examine the prevalence of predictive saccades to the target region throughout the experiment, we first searched for trials in which a subject's gaze was in a $r = 3°$ target circle around the target at t_{dmin} (Fig. 3*A*, orange). This target circle includes as many ball positions at t_{dmin} as possible (those of 99.49% of the trials) while still ensuring that the target region was fixated foveally (i.e., deliberately). In respective trials, we identified the start time of the last saccade before t_{dmin} that was greater than 1° (Fig. 3*B*, saccade start), and calculated the time between this time point and $t_{Release}$ (Fig. 3*B*, saccade latency). Only saccades with positive latencies (i.e.,

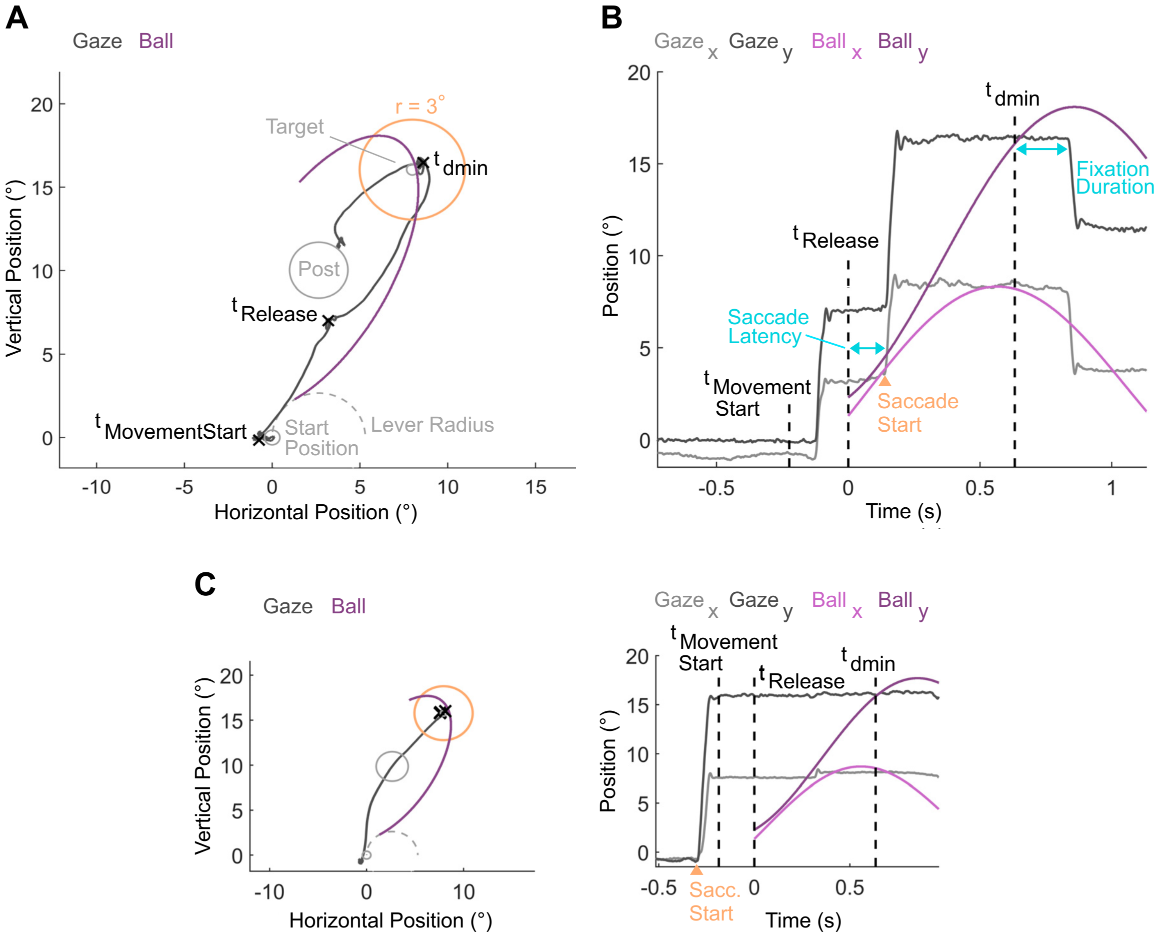


Figure 3. Example trial depicted in space (*A*) and in time (*B*) showing a three-degree target circle around the target and saccade start (both in orange). Both parameters were used to detect whether a predictive saccade was made in a given trial. To be detected as such, a subject's gaze had to be within this target circle at t_{dmin}, and the saccade start needed to follow the release (t_{Release}). In such trials, saccade latency was defined as the timespan between release and saccade start, and fixation duration at the chosen location was defined as the timespan between t_{dmin} and the start of the next event that terminated the fixation (both in cyan). *C*: example of a trial with an anticipatory saccade. In such trials, the gaze was shifted toward the target region before release.

saccades that started after release) were categorized as predictive saccades that could be based on internal information about the movement. Depending on the exact onset, saccades initiated before release should only contain less or no movement-related information and were, therefore, defined as and termed "anticipatory saccades" (see Fig. 3*C* for an example trial with an anticipatory saccade). For predictive saccades, we calculated mean saccade latencies at the subject level after excluding latencies that were rated as extreme outliers (values beyond the threefold interquartile range of a given cell).

To test the extent to which sensorimotor predictions were actually used in predictive saccades, we needed to analyze the correspondence between two elements in a two-dimensional (2-D) space: the predictively chosen fixation location and the action effect in a given trial. If a fully accurate prediction of the action effect was available and could be optimally used to guide a subject's gaze, the predictive saccade should have always landed exactly at the most informative point on the ball trajectory, which could be the ball position at d_{min}. In this ideal case, the minimum spatial distance between the fixation location and ball trajectory should always be zero. Due to the many sources of inaccuracies, we did not expect such a perfect match, though. However, if predictions were at least partially used in gaze control, fixations should, on average, be closer to the action effect than we would expect if only random fluctuations governed gaze variability. The common Pearson correlation does not adequately quantify this correspondence, since it is limited to linear correlations. Yet, the function of the ball trajectories (ellipses) and also the distance calculations show nonlinear relationships. Therefore, we used a generalized correlation coefficient, *R*, which was determined by means of a randomization method based on Müller and Sternad (59). In this respect, we first calculated the mean of minimum distances between the fixation location after a predictive saccade and ball trajectory on the subject level ($\overline{\mathrm{Demp}}$) in degrees of visual angle. Thus, $\overline{\mathrm{Demp}}$ reflects the distance that could be empirically measured in the actual results as the consequence of the co-occurrence of two processes (first, execution of a motor command with its resulting ball trajectory, and second, predictive gaze behaviors), and should be small in cases of successful predictions and their usage for predictive gaze shifts (Fig. 4). Second, we determined the mean of

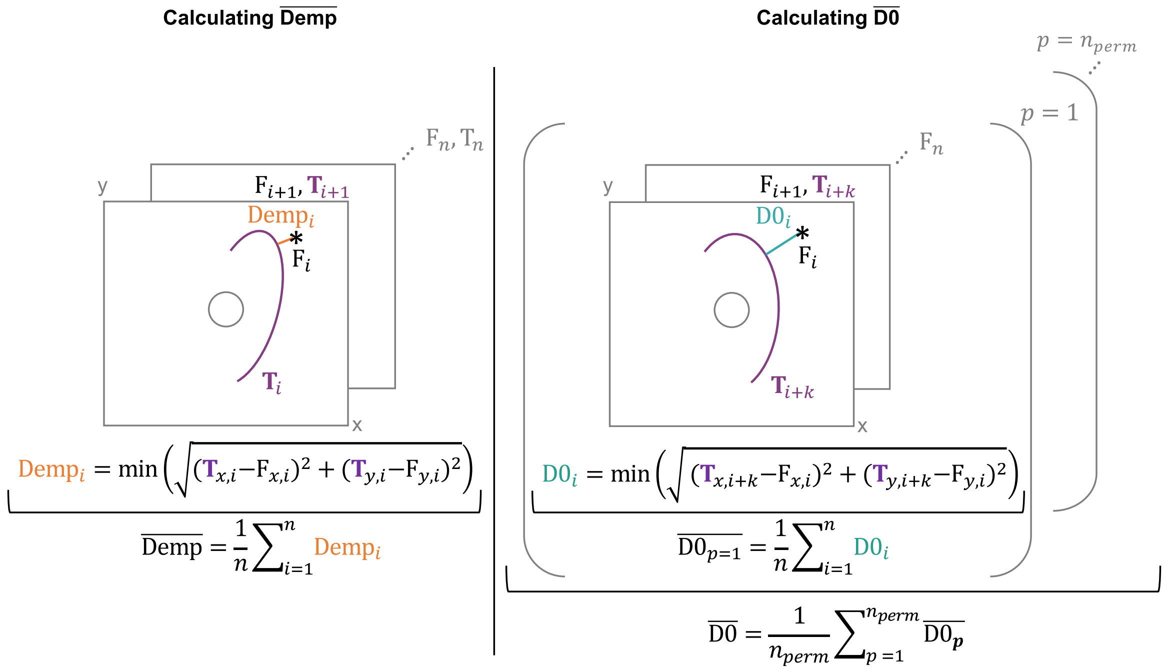


Figure 4. Calculation of $\overline{\text{Demp}}$: mean minimum distance between fixation location after a predictive saccade in a trial (F) and ball trajectory (T), and $\overline{\text{D0}}$: respective distance if covariation between fixation location and ball trajectory was zero. Both metrics were combined as described in Müller and Sternad (59) to calculate covariation between fixation locations after predictive saccades and action effects. i = current trial number, k = random number with $W_k = [-20;20]$ used to associate F_i a random ball flight, p = current permutation run where $n_{\text{perm}} = 50$.

minimum distances between fixation locations and randomly assigned ball trajectories, also on subject level, and in degrees of visual angle. Only neighboring trials (T_{i+k}, where i represents the current trial number and $W_k = [-20;20]$) were used for randomization to avoid overestimating resulting distances due to strategy changes throughout the experiment. Randomization was done $n_{\text{perm}} = 50$ times to calculate a grand mean of the resulting mean distances for each participant. Therefore, $\overline{\text{D0}}$ represents the mean distance that would be observed if the covariation between fixation locations after predictive saccades and ball trajectories was zero (Fig. 4).

The logic of calculating R requires the normalization of the covariance expressed by $\overline{\text{Demp}}$ by the covariation-free $\overline{\text{D0}}$ and is denoted by:

$$R = \frac{\overline{\text{Demp}}}{\overline{\text{D0}}} - 1; \quad W_R = [-1;1].$$

Thus, R is negative in case fixation locations after predictive saccades and ball trajectories are systematically related ($\overline{\text{Demp}}$ smaller than $\overline{\text{D0}}$), indicating that saccades were made to the predicted and not to the intended action effects or any other random position. We calculated distances between the chosen locations after predictive saccades and the target in each trial (Dgt) as an additional indicator of whether predictive gaze shifts were made to predicted or intended action effects.

We further assessed whether locations chosen after predictive saccades were of high informational value for feedback processing by analyzing fixation durations at those locations after feedback (t_{dmin}; Fig. 3*B*, fixation duration). The dependent variable fixation duration was determined by searching for the first saccade after t_{dmin} with a minimum space gain of 1° or, if the fixation around t_{dmin} was terminated by a blink, blink onset was registered. Fixation duration was subsequently defined as the timespan between t_{dmin} and the respective event in milliseconds, and extreme outliers were excluded before further analyses. Assuming that processing demands varied as a function of performance in each trial, we used the trials from *sessions 1* and *2* to get a deeper look into respective result patterns by separating trials by outcome (hit vs. miss), and the sizes of the deviations from the hit/miss-boundary (outcome uncertainty). In detail, we separated trials into narrow and clear hits, as well as misses according to d_{min} in meters (clear hits = [0; 0.05], clear misses =]0.15; 0.2], narrow hits =]0.05; 0.1], narrow misses =]0.1; 0.15]), and compared fixation durations between these four outcome possibilities. A value of 0.1 m represents the boundary between hits and misses. Due to a smaller number of trials in each condition in *session 3*, we only compared fixation durations between the two outcomes (hit = [0; 0.1] or miss =]0.1; 0.2]) in this portion of the data. Trials with error sizes exceeding 0.2 m were excluded from fixation duration analyses (1.88 % of the trials) to ensure a fair comparison between both outcomes.

Finally, we calculated the mean difference in saccade latencies in misses and hits for each subject. A difference in saccade latencies between hits and misses could speak for *1*) differences in the value assigned to the future gaze position according to the predicted outcome (56–58) or *2*) differences in the time needed to evaluate the expected outcome. Therefore, the difference measure is an indirect indicator for also considering predictive valuation processes in planning predictive saccades. To get more distinct results, we only included clear hits ($d_{\text{min}} = [0; 0.05]$) and misses ($d_{\text{min}} =]0.15; 0.2]$) in this analysis.

Post Hoc Analysis on Post-Error Adaptations

To validate the relationship between predictive saccades and (predictive) valuation processes, we performed an additional post hoc analysis on post-error adaptations in saccade latencies and fixation durations. In reaction time tasks, increases in reaction time in trials following errors (post-error slowing) are a well-documented phenomenon, i.e., thought to be related to increased activity in the performance monitoring system (for review, see Ref. 60). Thus, in our throwing task, post-error adaptations in the form of longer saccade latencies in trials following misses may allow for prolonged collection of information before predictions and subsequent saccades are made. As post-error adaptations are thought to serve performance improvement in the near future (60), it seems plausible that fixation durations could also be influenced by previous results. Such an observation would suggest that information is actively processed during fixations after predictive saccades to improve performance, rather than just reacting to the outcome of the task.

Statistical Analysis

To confirm that participants had learned the task to a point that enabled them to predict the action effects of their movements, we examined performance (hit rate in percent) changes throughout the experiment over blocks of 100 trials with repeated-measures analyses of variance (ANOVA). Moreover, task performance was compared between the three conditions in *session 3*, also with a repeated-measures ANOVA. Repeated-measures ANOVAs were furthermore used for the analysis of the prevalence of predictive saccades and mean latencies of predictive saccades. Factors used were C_{full} *session 1*, C_{full} *session 2*, and C_{full} *session 3* to analyze trends throughout the learning phase, as well as C_{noBall} and $C_{noBallnoTarget}$ to compare results between conditions.

To analyze whether fixation locations after predictive saccades systematically corresponded to future ball positions, indicating gaze shifts toward predicted action effects, we tested whether the *R* values obtained with the randomization method described by Müller and Sternad (59) significantly differed negatively from zero by using one-sample *t* tests. Analysis of the dependent variable fixation duration was done with two-way repeated-measures ANOVAs, including the within-subject factors outcome (hit vs. miss) and outcome uncertainty (clear vs. narrow) for the data from *sessions 1* and *2*, and the factors outcome (hit vs. miss) and condition (C_{full}, C_{noBall}, $C_{noBallnoTarget}$) for the data from *session 3*. To analyze dependencies of saccade latencies on action outcomes, we tested whether calculated difference values (mean latency in clear misses − mean latency in clear hits on the subject level) significantly deviated from zero by using one-sample *t* tests on the data from each experimental condition.

Post hoc analyses of post-error adaptations in the dependent measures fixation duration and saccade latency were conducted using two-way repeated-measures ANOVAs on the data from *sessions 1* and *2*, including the within-subject factors outcome previous trial (hit vs. miss) and outcome current trial (hit vs. miss). The factor outcome current trial was included to reduce residual variance in those analyses.

For repeated-measures ANOVA application, the normality of residuals was checked using Q-Q plots. Sphericity was tested, using Maulchy's *W*. To address violations of the sphericity assumption, the Greenhouse–Geisser correction was applied. Testing normality in the data analyzed with *t* tests was done by applying the Shapiro–Wilk test. The α level for all statistical tests was set at $\alpha = 0.05$, and all reported *P* values correspond to two-sided testing, except for the analyses of covariance where we expected negative *R* values. Extreme outliers were excluded. The analyses described, including the assumption checks, were conducted using JASP (v.0.14.1.0).

RESULTS

Task Performance

As the quality of sensorimotor predictions is related to expertise, task performance was measured as the hit rate over blocks of 100 trials throughout the experiment. In addition, hit rates were calculated for the three different experimental conditions in *session 3*, which differed in the availability of visual feedback about the action effect. As can be seen in Fig. 5*A*, participants improved their performances throughout

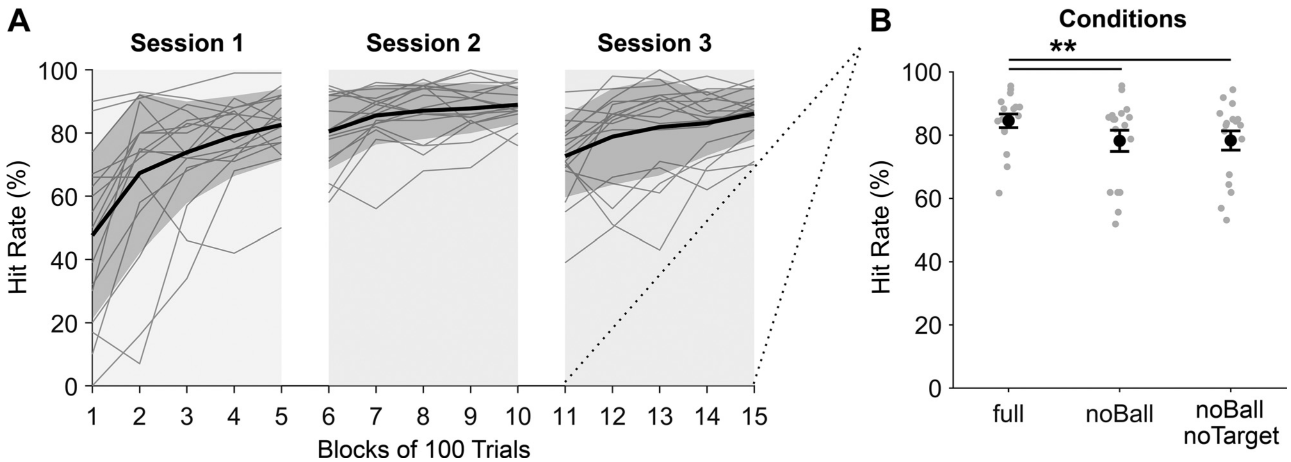


Figure 5. *A*: development of task performance in terms of hit rates over the three experimental sessions for each participant (gray), as well as at the sample level (black). The shaded areas represent standard deviations. *B*: task performance in the three experimental conditions in *session 3*. Values are means ± SE, gray dots represent participant means; $^{**}P < 0.01$.

the experiment, $F(3.11,49.73) = 16.19$, $P < 0.001$, $\eta_p^2 = 0.50$. On average, participants improved from a hit rate of 47.53 ± 26.48% in the first block to a hit rate of 88.94 ± 5.96% in the last block of *session 2*. However, the most significant improvement took place in the first session. In the experimental session (*session 3* with varying conditions), performance significantly dropped to 72.65 ± 13.01% in the first block of 100 trials ($P < 0.01$) compared with the last block in *session 2*, but increased to 86.12 ± 8.00% in the last block of 100 trials again ($P = 0.03$). The significant performance drop was partly caused by a decrease in hit rate in the two experimental conditions C_{noBall} (78.20 ± 13.80%) and $C_{noBallnoTarget}$ (78.31 ± 12.59%), in which less visual information was available, compared with C_{full} [84.54 ± 8.91%; $F(1.42,22.80) = 7.77$, $P < 0.01$, $\eta_p^2 = 0.33$, Fig. 5*B*].

Eye Movement Results

Prevalence and latency of predictive saccades.

Since we expected consistent predictive saccades toward predicted action effects, we analyzed the prevalence of predictive saccades throughout the experiment and in the three experimental conditions using a repeated-measures ANOVA. The prevalence of predictive saccades increased for C_{full} from 80.38 ± 24.69% in *session 1* to 87.87 ± 21.42% in *session 3*, and was lower in the two experimental conditions. Predictive saccades occurred least often in $C_{noBallnoTarget}$ (64.01 ± 22.39%), which gave rise to a significant main effect, $F(1.93,28.94) = 7.83$, $P < 0.01$, $\eta_p^2 = 0.46$, where the prevalence of these saccades in $C_{noBallnoTarget}$ differed from all other cells (Fig. 6*A*, dark gray). In cases where no predictive saccade was performed, a saccade was either made to the target region before release ("anticipatory saccades"; Fig. 6*A*, light gray), or the target region was not fixated at all (Fig. 6*A*, medium gray). This distinction reveals that although the prevalence of anticipatory saccades remained largely consistent across all conditions, the prevalence of trials without a saccade toward the target region increased in $C_{noBallnoTarget}$ and C_{noBall} at the cost of predictive saccades. Nevertheless, trials with predictive saccades predominated across all conditions.

The mean saccade latency for C_{full} decreased from 261.99 ± 76.01 ms in *session 1* to 239.41 ± 66.52 ms in *session 3*. Latency in C_{noBall} (211.21 ± 66.52 ms) was significantly shorter than in C_{full} in *session 1* ($P < 0.01$), and the latency in $C_{noBallnoTarget}$ (310.11 ± 84.25 ms) was longer than in all other conditions, both of which led to a significant main effect in the repeated-measures ANOVA, $F(2.19,32.91) = 13.92$, $P < 0.001$, $\eta_p^2 = 0.48$ (Fig. 6*B*). For reference, the mean ball flight time was 632 ± 58 ms.

Fixation location.

To test the extent to which sensorimotor predictions were actually used in predictive saccades, we calculated covariation between fixation locations after predictive saccades and ball trajectories (i.e., action effects). One-sample *t* tests contrasting generalized correlation coefficients *R* (representing covariation if values were negative) against zero showed significant covariance between those fixation locations and action effects in C_{full} in *sessions 1* and *2* [$R = -0.11 \pm 0.07$; $t(16) = -6.06$, $P < 0.001$, $d = -1.47$], as well as in *session 3*, $R = -0.11 \pm 0.10$; $t(15) = -4.42$, $P < 0.001$, $d = -1.10$. Covariance was also found in $C_{noBallnoTarget}$ [$R = -0.03 \pm 0.04$; $t(15) = -2.97$, $P < 0.01$, $d = -0.74$], despite larger variabilities in fixation locations (Fig. 7), and the largest mean minimum distances between gaze and ball ($\overline{Demp}$, Table 1). In contrast, no covariance was found in C_{noBall} [$R = 0.00 \pm 0.05$; $t(15) = -0.28$, $P = 0.39$, $d = -0.07$], in which no information about ball flight was available, but the target was visible throughout the trial. In this condition, gaze after predictive saccades was more centered on the target ($\overline{Dgt}$, Table 1; see also Fig. 7).

Considering outcome valence, fixation locations in misses were, on average, closer to ball trajectories than to the target in conditions C_{full} and $C_{noBallnoTarget}$, in that both showed covariation between fixation locations and action effects (see Supplemental Table S1, $\overline{Demp}$ vs. $\overline{Dgt}$). This was the opposite for C_{noBall} in which no covariation was found. In trials with saccades toward the target region starting before release (see Fig. 6*A* "anticipatory saccades," which should have contained less or no movement-related information), post hoc analyses

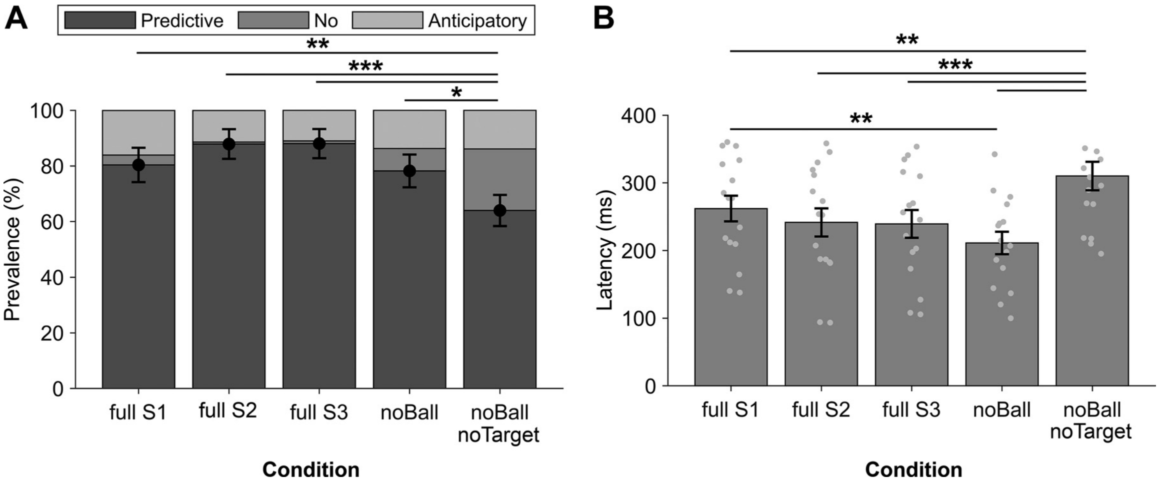


Figure 6. *A*: prevalence of trials with valid predictive saccades (predictive), trials with saccades toward the target region before release (anticipatory), and trials without target region fixations (no) across conditions. *B*: latency of predictive saccades across conditions. S, session. Values are means ± SE, gray dots represent participant means; ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

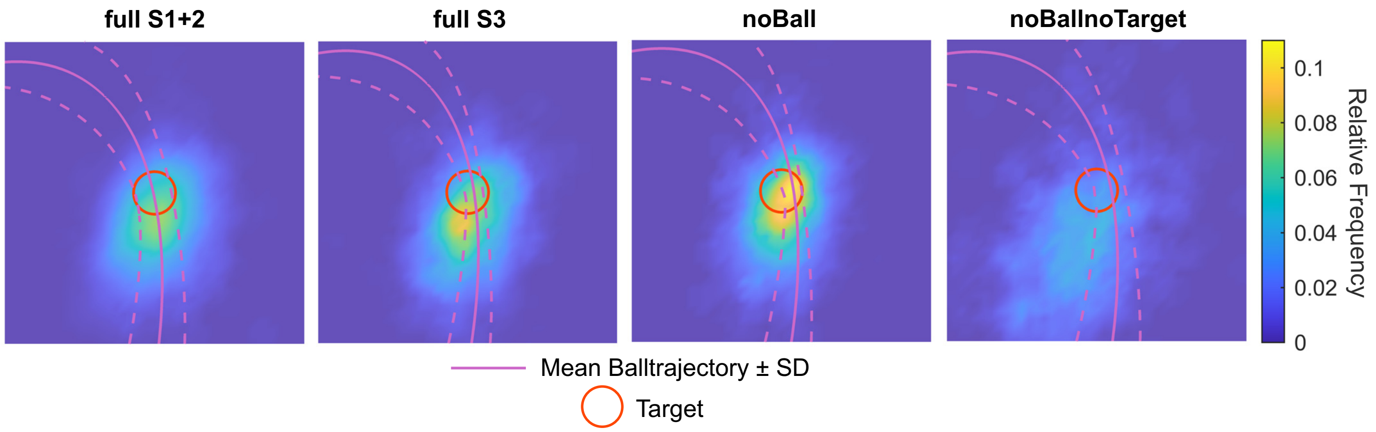


Figure 7. Heatmaps showing fixation locations after predictive saccades in relation to the target and means (±SD) ball trajectories in each condition.

revealed no covariance in either condition (Supplemental Table S3, *R*).

Fixation duration.

Fixation durations at fixation locations after predictive saccades were seen as an indicator of whether the chosen positions were of high informational value for (error) feedback processing. By using a repeated-measures ANOVA, with the within-subject factors outcome (hit vs. miss) and outcome uncertainty (clear vs. narrow) on the data from *sessions 1* and *2*, we found that fixation durations were longer in misses than in hits, $F(1,16) = 29.51$, $P < 0.001$, $\eta_p^2 = 0.65$. In addition, fixation durations depended on the size of deviation from the hit/miss boundary, as evidenced by a significant main effect of outcome uncertainty, $F(1,16) = 110.86$, $P < 0.001$, $\eta_p^2 = 0.87$ (Fig. 8*A*). Specifically, in trials with outcomes close to the hit/miss boundary, fixation durations were prolonged, resulting in the longest fixation durations in narrow misses (270.71 ± 62.44 ms), and the shortest durations in clear hits (173.61 ± 34.20 ms).

The more condensed analysis of *session 3*, which involved fewer trials comparing hits and misses, also revealed significantly longer durations in misses across all conditions, $F(1,11) = 57.55$, $P < 0.001$, $\eta_p^2 = 0.84$. In addition, longer durations in C_{noBall} and $C_{noBallnoTarget}$ compared with C_{full} gave rise to a main effect condition, $F(2,1.33) = 30.73$, $P < 0.001$, $\eta_p^2 = 0.74$ (Fig. 8*B*).

Outcome-dependent saccade latency differences.

We further analyzed saccade latencies contingent on action outcomes to investigate whether predictive valuation processes were considered when planning predictive saccades. Saccade latencies were significantly longer in misses than in hits in C_{full} in *sessions 1* and *2* [Difference: 56.42 ± 40.42 ms; $t(15) = 5.58$, $P < 0.001$, $d = 1.40$] as well as in *session 3*, $t(12) = 2.21$, $P = 0.02$, $d = 0.61$ (Difference: 27.86 ± 45.49 ms). No significant differences were found in C_{noBall}, $t(11) = 0.19$, $P = 0.43$, $d = 0.06$ (Difference: 5.70 ± 102.46 ms). Although mean latency was, on average, 45.75 ms longer in misses in $C_{noBallnoTarget}$, no significant differences were found due to lack of consistency across subjects (±122.73 ms), $t(11) = 1.29$, $P = 0.11$, $d = 0.37$ (Fig. 9*A*). Latencies in clear hits and misses across all subjects and conditions are depicted in Fig. 9*B*. Post hoc analyses, conducted to reveal influencing factors on latency differences, showed that participants executed a higher number of saccades during the timespan between $t_{Release}$ and t_{dmin} (*n* saccades) in misses compared with hits in C_{full} S1 + 2 (mean difference miss − hit: 0.23 ± 0.23), $t(15) = 4.01$, $P < 0.01$, $d = 1.00$, accompanied by smaller saccade amplitudes in misses than in hits (mean difference miss − hit: −0.66 ± 1.14°), $t(15) = -2.31$, $P = 0.04$, $d = -0.58$. Regression analyses, considering the influence of *n* saccades or saccade amplitudes on saccade latencies, show that the higher number of saccades and the smaller saccade amplitudes in misses than in hits in C_{full} S1 + 2 led to enlarged latencies in misses compared with hits of ~15 ms in this condition. In all other conditions (including C_{full} S3), we did not find significant differences regarding *n* saccades and saccade amplitudes when comparing hit-and-miss trials.

Post-Error adaptations.

Repeated-measures ANOVAs, with the within-subject factors outcome previous trial (hit vs. miss) and outcome current trial (hit vs. miss) were used to add another aspect to the relation between predictive saccades and (predictive) valuation processes. Saccade latencies were prolonged in trials in which the previous trial was a miss, $F(1,16) = 12.13$, $P < 0.01$, $\eta_p^2 = 0.43$ (Fig. 10*A*). The same effect was observed in the dependent variable fixation duration, i.e., fixation durations were prolonged in trials following a miss, $F(1,16) = 17.31$, $P < 0.001$, $\eta_p^2 = 0.52$ (Fig. 10*B*).

Table 1. *Mean minimum distances between fixation locations after predictive saccades and ball trajectories, and mean distances between these locations and the target across conditions*

	Full S1 + S2	Full S3	noBall	noBallnoTarget
$\overline{Demp}$	0.59 ± 0.20	0.46 ± 0.07	0.54 ± 0.12	0.81 ± 0.25
$\overline{Dgt}$	0.92 ± 0.23	0.88 ± 0.19	0.79 ± 0.21	1.36 ± 0.35

Values are means ± SD in degrees of visual angle; $n = 16–17$. S, session. $\overline{Demp}$, distances between fixation locations after predictive saccades and ball trajectories; $\overline{Dgt}$, distances between fixation locations after predictive saccades and the target.

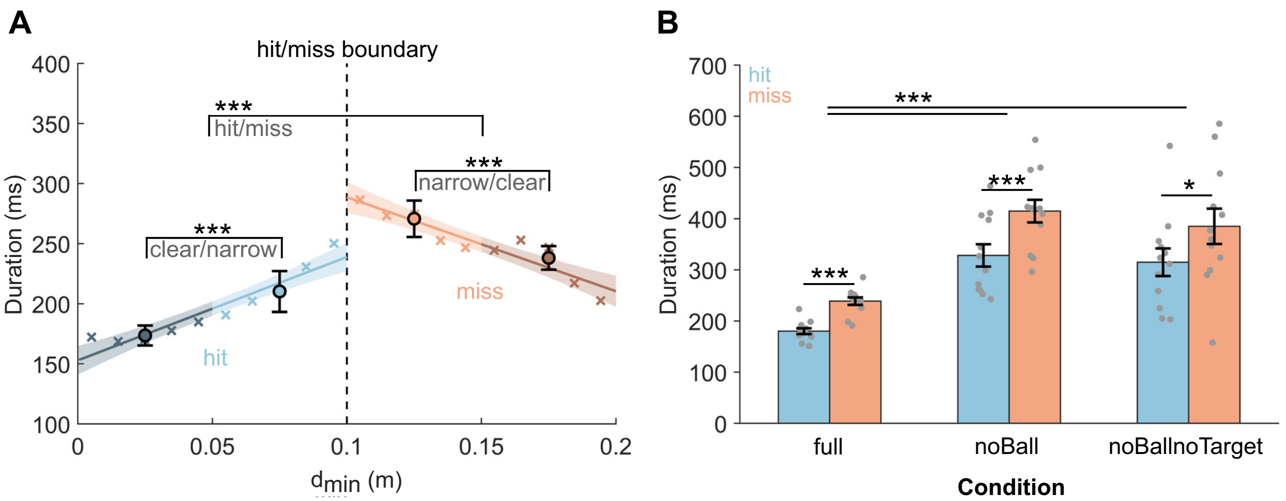


Figure 8. *A*: fixation durations after the time of minimum distance between ball and target (t_{dmin}) in trials with predictive saccades separated by outcomes (hit vs. miss) and sizes of the deviations from the hit/miss boundary, or outcome uncertainty (clear vs. narrow), respectively, including data from *sessions 1* and *2*. Regression lines (with 95% confidence intervals) show fixation durations depending on outcome distances from the target (d_{min}) in bins of 0.01 m. *B*: fixation durations after t_{dmin} in trials with predictive saccades in the three experimental conditions from *session 3*, separated by results (hit vs. miss). Values are means ± SE, gray dots represent participant means; $***P < 0.001$, $*P < 0.05$.

DISCUSSION

The main objective of this study was to investigate whether sensorimotor predictions are used to facilitate visual information uptake in the context of (error) feedback processing. For this purpose, we measured eye movements during the execution of a semivirtual throwing task that allowed participants to form predictions about future action effects, and that was suitable to disentangle possible functional mechanisms behind predictive eye movements. We found that predictively chosen fixation locations covaried with future action effects not only in trials in which visual information about the movement of the ball was available (which allowed for predictions based on learned internal models of the dynamic properties of the environment), but also in trials in which no ball flight information was accessible and the prediction of future action effects could only be based on internal information about the movement (efference copy and afferent proprioceptive information, i.e., sensorimotor information). This finding indicates that sensorimotor predictions were used to control visual information uptake.

Task Performance as Prerequisite for Successful Sensorimotor Predictions

Previous studies suggest that the accuracy of sensorimotor predictions is related to task performance (38, 51, 61). Therefore, we chose a comparatively simple task variant in the current study, in which subjects achieved a hit rate of ∼48% in the first block of 100 trials, and rapidly increased their throwing performance over the first two sessions. Manipulation of the visual feedback in *session 3* (by masking

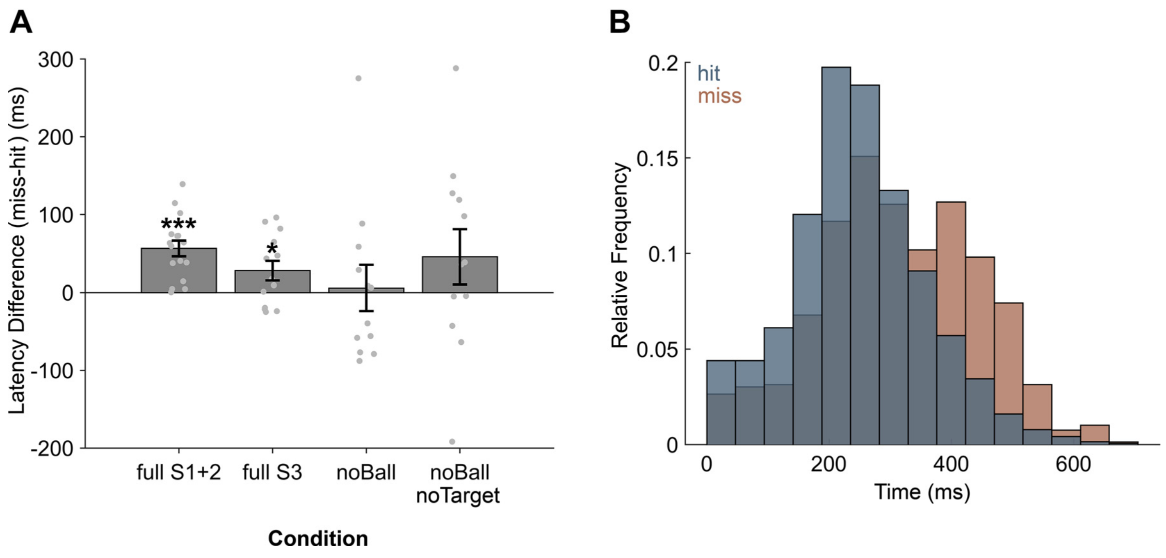


Figure 9. *A:* latency differences of predictive saccades in clear misses and hits (miss-hit) across conditions. Positive values represent longer latencies in misses. *B:* saccade latencies in clear hits and misses across all participants and conditions. S, Session. Values are means ± SE, gray dots represent participant means; $***P < 0.001$, $*P < 0.05$.

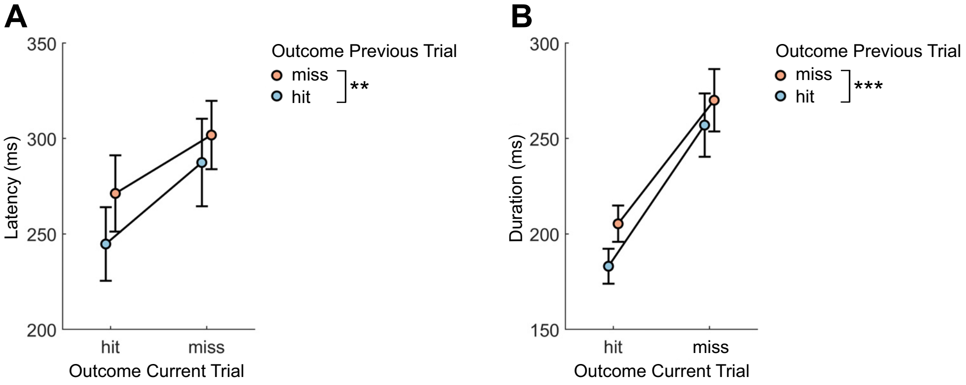


Figure 10. Saccade latencies (*A*) and fixation durations (*B*) depending on the action outcome (hit vs. miss) in the previous trial. Results are separated by the outcome of the current trial to reduce residual variance within this comparison. Values are means ± SE; $***P < 0.001$, $**P < 0.01$.

the ball flight after release) led to a slight drop in performance. However, this was compensated for over the course of the session, and following the parameters from previous studies using the same task, the prerequisites for successful sensorimotor predictions were met in all conditions of the current experiment (36, 51).

Locations of Predictive Saccades Covary with Future Action Effects

As described earlier, previous studies did not provide the ability to distinguish whether predictive eye movements toward the endpoints of own movements were related to action planning or outcome valuation of actions due to closed-loop control and spatial overlap between action and effect sites in the examined tasks (18–31). In an effort to disentangle possible functional mechanisms giving rise to predictive saccades in goal-directed actions, Pfeuffer et al. (33) used a task in which simple manual actions (key presses) produced simple distal action effects (predictable visual stimuli on the left or right side of a screen after a short delay). In this task, participants predictively directed their gaze toward the distal effects of their actions, and the predictive saccades occurred almost exclusively after the manual responses. These observations were seen as support for the idea that predictive saccades could serve the function of outcome valuation of actions rather than being related to action planning. However, in the task used, discrimination between intended and predicted action effects was not possible due to the dichotomous outcome. The aim of the present study was to further differentiate the potential link between predictive saccades and outcome valuation, in the expectation that gaze is directed to predicted action effects based on sensorimotor predictions. To do so, we used a task in which action effects could vary from trial to trial, while the intended action effect (the task goal, i.e., hitting a target with a ball) remained constant.

To test the extent to which sensorimotor predictions were actually used in predictive saccades, covariation between predictively chosen fixation locations and action effects was calculated. Results revealed covariation between fixation locations after predictive saccades and ball trajectories in C_{full}. However, as studies on predictive saccades in interception tasks have demonstrated (6–15), saccades toward predicted action effects can merely be based on learned internal models of the dynamic properties of the ball flight. To exclude this explanation for predictive eye movements, we introduced conditions without ball flight information (i.e., the ball was masked after release, and only static outcome feedback was presented). As expected, covariation between fixation locations after predictive saccades and action effects was also observed in the condition $C_{\mathrm{noBallnoTarget}}$. Here, predictions and resulting predictive saccades could only be based on internal information about the movement (efference copy and afferent proprioceptive information). This result supports the hypothesis that saccades are made to the predicted action effect based on sensorimotor predictions for the sake of outcome valuation. According to the theory of internal models (39, 40), the execution of these saccades carries the potential for precise quantification of deviations (in direction and amplitude) from a known target or intended action effect—which might be especially beneficial when outcome feedback is available only briefly and, therefore, easy to miss. Furthermore, the location of the predicted action effect should contain the most precise information on deviations of the actual from the predicted action effect, which is a critical aspect for error attribution or for updates of the forward model predictions in case predictions were not optimal. The facilitation of comparisons between predicted and actual outcomes was also reported as a not-yet-proven alternative hypothesis for predictive saccades toward future bouncing points in racket games (62). Thus, our results provide further evidence for an outcome valuation background of predictive saccades in both saccades toward self-generated action effects and toward future positions of moving objects one has to intercept. Furthermore, they show not only instructed eye movements can profit from efference copy information (2–5) but also spontaneous eye movements can access and use this information combined with the resulting forward model predictions to fine-tune chosen fixation locations.

In the condition without ball flight information, but with visible target after release (C_{noBall}), fixation locations after predictive saccades and action effects did not covary. Fixation locations after predictive saccades were centered on the target, and as a result, in miss trials, the gaze was farthest away from respective action effects in error trials compared with the other conditions. This finding, combined with the shorter saccade latencies in this condition, suggests that the subjects' gaze was attracted by the salient visual anchor "target," and that sensorimotor prediction was not used for planning these predictive saccades. Thus, if action effect prediction is nontrivial and a visual anchor provides a proper estimate for the future feedback location, thereby potentially enhancing the precision of saccade landing positions, sensorimotor prediction gets displaced. Even though saliency is only a weak predictor of eye movements (reviewed in Refs. 17 and 63), and it has been shown that top-down mechanisms can override salience (e.g., see Refs. 64 and 65), the force of attraction in the present experiment seemed to be strong enough to create this bias. However, this finding might be restricted to the specific throwing task used, in which action effects only differ slightly from each other and range only within a small field of vision. This task characteristic also explains the small effect sizes of *R* when randomization was applied.

Predictive Saccades Are Executed Consistently

Analyses of prevalence showed that predictive saccades were executed consistently across subjects and trials. Predictive saccades toward the target region (initiated after release) were executed as a function of the availability of visual information, with the lowest prevalence of around 54% being present in the condition with the least amount of visual guidance ($C_{\mathrm{noBallnoTarget}}$—ball flight and target masked after release). The lower prevalence in $C_{\mathrm{noBallnoTarget}}$ could have been caused by the difficulty to predict action effects without information about ball flight, as well as the absence of a visual anchor (i.e., the target). These challenges might also be represented by prolonged latencies before the initiation of predictive saccades in this condition. Still, prevalence was higher across all conditions than in the study by Pfeuffer et al. (33) in which predictive saccades were executed in 10–50% of the trials, depending on the specific experiment and condition. Those differences in prevalence could be due to the fact that the chosen gaze locations in our study might provide helpful information for movement adaptations in the subsequent trials and that predictive saccades are thus task-relevant. Previous studies showed that predictions are made about where task-relevant information is going to appear, and that saccades are naturally directed toward locations with high informational value (16, 54, 66–68).

In line with Pfeuffer et al. (33), only in rare cases were saccades toward the target region performed before the movement was completed. Since those saccades (referred to as anticipatory saccades) did not covary with action effects, they seem to represent saccades toward the intended action effect.

Latencies of Predictive Saccades Indicate a Relationship with Predictive Valuation Processes

Latencies of valid predictive saccades in conditions that revealed covariation between fixation locations after predictive saccades and action effects ranged from around 241 ms to around 316 ms. These latencies correspond to the effect window of the neural correlate for predictive error valuation (200–350 ms after release), the error-related negativity (ERN), in the task at hand (36), and might suggest that these saccades were executed as a result of predictive valuation processes (i.e., after internally rating a trial as a hit or a miss). This conjecture is further supported by latency differences between hit and miss trials in the respective conditions, where latencies were longer in misses than in hits. Different reasons could account for the observed latency differences. For example, according to Maurer et al. (69), it can be assumed that outcome estimates are produced continuously and their accuracy increases with accumulating input information as the action and its effects evolve. In cases of hits, the input information may have been clear and accurate relatively early, leading to relatively fast outcome estimates and faster saccade initiation. This explanation is supported by the post hoc results on post-error adaptations where saccade latencies were prolonged in trials following misses. However, it is also possible that in some trials, saccades toward predicted hits were expressed based on experiences and a resulting hit bias (70, 71) instead of waiting for accurate input information for sensorimotor predictions. In addition to these processing-related explanations, motivational aspects could have led to earlier gaze shifts in hits (56–58). The enlarged difference between latencies in hits and misses in C_{full} in *sessions 1* and *2* compared with C_{full} in *session 3*, can be explained by specific behavioral characteristics (higher number of saccades in misses accompanied by smaller saccade amplitudes of predictive saccades leading to longer saccade latencies in misses compared with hits) at the beginning of the experiment.

Predictive valuation processes expressed in eye movements were also found in a go versus no-go task, where a moving object was occluded for some time and had to be intercepted in case it would hit a distinct area (15). The earliest time point at which eye movements started to differentiate decision outcomes (go vs. no-go) coincided with the onset of hand movements. Based on those results, Fooken and Spering (15) stressed the potential of studying naturally occurring eye movements as a continuous readout of cognitive processes. In addition, research on value-dependent eye movements indicates that the control of saccadic eye movements is closely linked to the brain circuitry responsible for action valuation based on the fact that the consequences of eye movements are considered when selecting targets and planning eye movements to these targets (reviewed in Refs. 17, 67, and 72). However, to establish a direct link between predictive valuation processes and predictive saccades in self-generated movements, studies are needed that combine EEG measurements with eye movement recordings, or directly analyze gaze contingencies between targets with different values depending on predicted outcomes.

Fixation Durations Indicate Task-Relevance of the Predictively Chosen Fixation Locations

Fixation durations after feedback at chosen locations after predictive saccades depended on movement outcomes. In *sessions 1* and *2*, fixation durations were longer in misses than in hits, but also longer the closer results were to the hit/miss boundary. These patterns could have resulted from differences in processing demands (54), with fixations being terminated when the required information was acquired (73, 74). Processing demands are assumed to be higher in misses because adequate movement adaptations for the next trial have to be derived. They should also be higher at the hit/miss boundary for two possible reasons: first, predictions are potentially less successful in narrow trials, which could have led to higher feedback dependencies (61), or to surprise effects. Several studies show that unpredictable objects are fixated longer than predictable objects (45, 75, 76). According to Henderson (54), increased fixation durations in expectation violations in scene perception serve the purpose of updating knowledge representations to consider the unexpected information. In active movements, this extra time could be used for forward model updates. The second potentially complementary reason for prolonged durations in narrow hits and misses might be the inherent noisiness of perception and action (77), making it difficult to derive suitable marginal adjustments in those cases.

However, differences in processing demands could also be explained by specific task characteristics. For example, it might take less time to process a hit in the Skittles task since the information to be processed is available more quickly (through the sound of two colliding billiard balls) and more saliently (the ball bounces off the target at a specific angle instead of passing the target in misses) compared with misses. This would limit the generalization to other tasks. However, the observed post-error adaptations (i.e., the prolonged fixation durations in trials that follow errors) show that information processing during these fixations goes beyond the mere discrimination of specific outcomes and is about gaining information to optimize performance, as post-error adaptations are thought to serve performance improvements in the near future (60).

We proposed specific advantages of directing gaze toward predicted action effects for the valuation of own actions. However, the simpler comparison between fixation durations in hits and misses in the three experimental conditions in *session 3* shows that regardless of whether the sensorimotor prediction was used for the selection of feedback locations or not (in C_{noBall}), result patterns were similar, i.e., durations were prolonged in misses compared with hits. Hence, in the current study, we could not differentiate whether fixation locations chosen with the inclusion of sensorimotor predictions outweigh other positions in terms of information gain for the valuation of actions. This can be explained by the only marginal differences in positions on the task space resulting from the two strategies [either looking to the target, i.e., intended action effect (in C_{noBall},), or to the predicted action effect (in $C_{\mathrm{noBallnoTarget}}$, C_{full})]. Detecting differences in the informational value of the chosen positions would require a more fine-grained analysis of the result patterns in all experimental conditions, which could have been possible with more trials per condition. A possible benefit of using sensorimotor prediction for selecting appropriate feedback locations could also have been tested by establishing a relationship between prediction accuracy and throwing performance. However, it is as yet unclear how prediction accuracy can be defined. The *R* value can be used to express that there is a systematic relationship between selected fixation locations after predictive saccades and ball flights. However, the magnitude of the *R* value cannot serve as a prediction performance measure, as it depends on movement variability and randomization of highly varying throws results in higher $\overline{\mathrm{D0}}$ values. Moreover, it is not clear whether participants aimed for a minimum distance between fixation locations and ball positions, so that a small $\overline{\mathrm{Demp}}$ value represents a good prediction, or whether a position between the target and the ball is the most suitable to be able to perform necessary comparisons for outcome valuation. The selection of such an intermediate position (between intended and predicted effects) would facilitate the comparison between intended and actual effects and might be the strategy chosen since participants did not completely disengage from the target in misses (see Supplemental Tables S1 and S2). External perturbations were not expectable in the current task, diminishing the importance of a comparison between predicted and actual effects. Finally, $\overline{\mathrm{Demp}}$ was also small in the condition without the inclusion of sensorimotor predictions (C_{noBall}), since fixating on the target serves as a valid estimate for the future effect in case of high hit rates. For now, we can therefore merely conclude that sensorimotor prediction is used to predictively direct eye movements to task-relevant locations, without specifying the precise spatial target and whether precise positioning yields a performance benefit.

Conclusions

The analysis of eye movements during the execution of a semivirtual throwing task revealed that humans are able to use internal outcome prediction of self-generated movements to direct their gaze toward predicted action effects. This phenomenon is observable when ball trajectories can be tracked, but is also present without any ball flight information when no target acting as a visual anchor attracts gaze. The informational value of predictively chosen fixation locations is indicated by differences in fixation durations after feedback depending on throwing performance. Thus, humans are able to use sensorimotor prediction to direct their gaze toward task-relevant feedback locations. Dependencies of saccade latencies on movement outcomes imply that predictive valuation processes are also involved in the planning of predictive saccades. However, exact result patterns are yet to be investigated. Likewise, the relationship between predictive abilities that drive gaze to a not yet known optimal position and performance needs to be further examined.

DATA AVAILABILITY

Source data for this study are openly available at https://doi.org/10.17605/OSF.IO/JT9AC.

SUPPLEMENTAL MATERIAL

Supplemental Tables S1–S3: https://doi.org/10.17605/OSF.IO/DPA2G.

GRANTS

This research was supported by the Collaborative Research Center “Cardinal Mechanisms of Perception,” funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation; SFB/TRR 135 TP B6 and B2) under Grant Number 222641018 and the Research Cluster “The Adaptive Mind,” funded by the Excellence Program of the Hessian Ministry of Higher Education, Science, Research and the Arts.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

T.K.B., A.C.S., H.M., M.H., and L.K.M. conceived and designed research; T.K.B. performed experiments; T.K.B. analyzed data; T.K.B., A.C.S., H.M., H.M., M.H., and L.K.M. interpreted results of experiments; T.K.B. prepared figures; T.K.B. drafted manuscript; T.K.B., A.C.S., H.M., H.M., M.H., and L.K.M. edited and revised manuscript; T.K.B., A.C.S., H.M., H.M., M.H., and L.K.M. approved final version of manuscript.

REFERENCES

1. **Brouwer A. D**, **Flanagan JR**, **Spering M.** Functional use of eye movements for an acting system. *Trends Cogn Sci* 25: 252–263, 2021. doi:10.1016/j.tics.2020.12.006.
2. **Chen J**, **Valsecchi M**, **Gegenfurtner KR.** Role of motor execution in the ocular tracking of self-generated movements. *J Neurophysiol* 116: 2586–2593, 2016. doi:10.1152/jn.00574.2016.
3. **Niehorster DC**, **Siu WW**, **Li L.** Manual tracking enhances smooth pursuit eye movements. *J Vis* 15: 11, 2015. doi:10.1167/15.15.11.
4. **Steinbach MJ**, **Held R.** Eye tracking of observer-generated target movements. *Science* 161: 187–188, 1968. doi:10.1126/science.161.3837.187.
5. **Vercher J-L**, **Quaccia D**, **Gauthier GM.** Oculo-manual coordination control: respective role of visual and non-visual information in ocular tracking of self-moved targets. *Exp Brain Res* 103: 311–322, 1995. doi:10.1007/BF00231717.
6. **de la Malla C**, **Smeets JB**, **Brenner E.** Potential systematic interception errors are avoided when tracking the target with one's eyes. *Sci Rep* 7: 10793, 2017. doi:10.1038/s41598-017-11200-5.
7. **Fooken J**, **Yeo S-H**, **Pai DK**, **Spering M.** Eye movement accuracy determines natural interception strategies. *J Vis* 16: 1, 2016. doi:10.1167/16.14.1.
8. **Fooken J**, **Spering M.** Eye movements as a readout of sensorimotor decision processes. *J Neurophysiol* 123: 1439–1447, 2020. doi:10.1152/jn.00622.2019.
9. **Diaz G**, **Cooper J**, **Rothkopf C**, **Hayhoe M.** Saccades to future ball location reveal memory-based prediction in a virtual-reality interception task. *J Vis* 13: 20, 2013. doi:10.1167/13.1.20.
10. **Hayhoe MM**, **McKinney T**, **Chajka K**, **Pelz JB.** Predictive eye movements in natural vision. *Exp Brain Res* 217: 125–136, 2012. doi:10.1007/s00221-011-2979-2.
11. **Kishita Y**, **Ueda H**, **Kashino M.** Eye and head movements of elite baseball players in real batting. *Front Sports Act Living* 2: 3, 2020. doi:10.3389/fspor.2020.00003.
12. **Land MF**, **Furneaux S.** The knowledge base of the oculomotor system. *Philos Trans R Soc Lond B Biol Sci* 352: 1231–1239, 1997. doi:10.1098/rstb.1997.0105.
13. **Land MF**, **McLeod P.** From eye movements to actions: how batsmen hit the ball. *Nat Neurosci* 3: 1340–1345, 2000. doi:10.1038/81887.
14. **Mann DL**, **Nakamoto H**, **Logt N**, **Sikkink L**, **Brenner E.** Predictive eye movements when hitting a bouncing ball. *J Vis* 19: 28, 2019. doi:10.1167/19.14.28.
15. **Fooken J**, **Spering M.** Decoding go/no-go decisions from eye movements. *J Vis* 19: 5, 2019. doi:10.1167/19.2.5.
16. **Fiehler K**, **Brenner E**, **Spering M.** Prediction in goal-directed action. *J Vis* 19: 10, 2019. doi:10.1167/19.9.10.
17. **Schütz AC**, **Braun DI**, **Gegenfurtner KR.** Eye movements and perception: a selective review. *J Vis* 11: 9, 2011. doi:10.1167/11.5.9.
18. **Land MF**, **Mennie N**, **Rusted J.** The roles of vision and eye movements in the control of activities of daily living. *Perception* 28: 1311–1328, 1999. doi:10.1068/p2935.
19. **Hayhoe MM.** Vision using routines: a functional account of vision. *Vis Cogn* 7: 43–64, 2000. doi:10.1080/135062800394676.
20. **Johansson RS**, **Westling G**, **Bäckström A**, **Flanagan JR.** Eye–hand coordination in object manipulation. *J Neurosci* 21: 6917–6932, 2001. doi:10.1523/JNEUROSCI.21-17-06917.2001.
21. **Ballard DH**, **Hayhoe MM**, **Li F**, **Whitehead SD.** Hand-eye coordination during sequential tasks. *Philos Trans R Soc Lond B Biol Sci* 337: 331–339, 1992. doi:10.1098/rstb.1992.0111.
22. **Ballard DH**, **Hayhoe MM**, **Pelz JB.** Memory representations in natural tasks. *J Cogn Neurosci* 7: 66–80, 1995. doi:10.1162/jocn.1995.7.1.66.
23. **Sailer U**, **Flanagan JR**, **Johansson RS.** Eye–hand coordination during learning of a novel visuomotor task. *J Neurosci* 25: 8833–8842, 2005. doi:10.1523/JNEUROSCI.2658-05.2005.
24. **Brouwer AM**, **Franz VH**, **Gegenfurtner KR.** Differences in fixations between grasping and viewing objects. *J Vis* 9: 18–1824, 2009. doi:10.1167/9.1.18.
25. **Mennie N**, **Hayhoe M**, **Sullivan B.** Look-ahead fixations: anticipatory eye movements in natural tasks. *Exp Brain Res* 179: 427–442, 2007. doi:10.1007/s00221-006-0804-0.
26. **Kurz J**, **Hegele M**, **Reiser M**, **Munzert J.** Impact of task difficulty on gaze behavior in a sequential object manipulation task. *Exp Brain Res* 235: 3479–3486, 2017. doi:10.1007/s00221-017-5062-9.
27. **Baldauf D**, **Wolf M**, **Deubel H.** Deployment of visual attention before sequences of goal-directed hand movements. *Vision Res* 46: 4355–4374, 2006. doi:10.1016/j.visres.2006.08.021.
28. **Epelboim J.** Gaze and retinal-image-stability in two kinds of sequential looking tasks. *Vision Res* 38: 3773–3784, 1998. doi:10.1016/S0042-6989(97)00450-1.
29. **Epelboim J**, **Steinman RM**, **Kowler E**, **Pizlo Z**, **Erkelens CJ**, **Collewijn H.** Gaze-shift dynamics in two kinds of sequential looking tasks. *Vision Res* 37: 2597–2607, 1997. doi:10.1016/S0042-6989(97)00075-8.
30. **Herst AN**, **Epelboim J**, **Steinman RM.** Temporal coordination of the human head and eye during a natural sequential tapping task. *Vision Res* 41: 3307–3319, 2001. doi:10.1016/S0042-6989(01)00158-4.
31. **Neggers SF**, **Bekkering H.** Ocular gaze is anchored to the target of an ongoing pointing movement. *J Neurophysiol* 83: 639–651, 2000. doi:10.1152/jn.2000.83.2.639.
32. **Land MF.** Eye movements and the control of actions in everyday life. *Prog Retin Eye Res* 25: 296–324, 2006. doi:10.1016/j.preteyeres.2006.01.002.
33. **Pfeuffer CU**, **Kiesel A**, **Huestegge L.** A look into the future: spontaneous anticipatory saccades reflect processes of anticipatory action control. *J Exp Psychol Gen* 145: 1530–1547, 2016. doi:10.1037/xge0000224.
34. **Anguera JA**, **Seidler RD**, **Gehring WJ.** Changes in performance monitoring during sensorimotor adaptation. *J Neurophysiol* 102: 1868–1879, 2009. doi:10.1152/jn.00063.2009.
35. **Flanagan JR**, **Wing AM.** The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. *J Neurosci* 17: 1519–1528, 1997. doi:10.1523/JNEUROSCI.17-04-01519.1997.
36. **Maurer LK**, **Maurer H**, **Müller H.** Neural correlates of error prediction in a complex motor task. *Front Behav Neurosci* 9: 209, 2015. doi:10.3389/fnbeh.2015.00209.
37. **Wolpert DM.** Computational approaches to motor control. *Trends Cogn Sci* 1: 209–216, 1997. doi:10.1016/S1364-6613(97)01070-X.
38. **Jordan MI**, **Rumelhart DE.** Forward models: supervised learning with a distal teacher. *Cogn Sci* 16: 307–354, 1992. doi:10.1207/s15516709cog1603_1.
39. **Kawato M.** Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9: 718–727, 1999. doi:10.1016/S0959-4388(99)00028-8.
40. **Miall RC**, **Wolpert DM.** Forward models for physiological motor control. *Neural Netw* 9: 1265–1279, 1996. doi:10.1016/S0893-6080(96)00035-4.
41. **Desmurget M**, **Grafton S.** Forward modeling allows feedback control for fast reaching movements. *Trends Cogn Sci* 4: 423–431, 2000. doi:10.1016/S1364-6613(00)01537-0.
42. **Wolpert DM**, **Ghahramani Z.** Computational principles of movement neuroscience. *Nat Neurosci* 3, Suppl: 1212–1217, 2000. doi:10.1038/81497.
43. **Holroyd CB**, **Coles MGH.** The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychol Rev* 109: 679–709, 2002. doi:10.1037/0033-295X.109.4.679.
44. **Maurer LK**, **Joch M**, **Hegele M**, **Maurer H**, **Müller H.** Predictive error processing distinguishes between relevant and irrelevant errors after visuomotor learning. *J Vis* 19: 18, 2019. doi:10.1167/19.4.18.
45. **Henderson JM**, **Weeks PA**, **Hollingworth A.** The effects of semantic consistency on eye movements during complex scene viewing. *J Exp Psychol Hum Percept Perform* 25: 210–228, 1999. doi:10.1037/0096-1523.25.1.210.

46. **Henderson JM**, **Hollingworth A.** Eye movements and visual memory: detecting changes to saccade targets in scenes. *Percept Psychophys* 65: 58–71, 2003. doi:10.3758/BF03194783.
47. **Reichle ED**, **Pollatsek A**, **Fisher DL**, **Rayner K.** Toward a model of eye movement control in reading. *Psychol Rev* 105: 125–157, 1998. doi:10.1037/0033-295X.105.1.125.
48. **Liversedge SP**, **Findlay JM.** Saccadic eye movements and cognition. *Trends Cogn Sci* 4: 6–14, 2000. doi:10.1016/S1364-6613(99)01418-7.
49. **Rayner K.** Eye movements in reading and information processing: 20 years of research. *Psychol Bull* 124: 372–422, 1998. doi:10.1037/0033-2909.124.3.372.
50. **Van Beers RJ.** Motor learning is optimally tuned to the properties of motor noise. *Neuron* 63: 406–417, 2009. doi:10.1016/j.neuron.2009.06.025.
51. **Joch M**, **Hegele M**, **Maurer H**, **Müller H**, **Maurer LK.** Brain negativity as an indicator of predictive error processing: the contribution of visual action effect monitoring. *J Neurophysiol* 118: 486–495, 2017. doi:10.1152/jn.00036.2017.
52. **Müller H**, **Sternad D.** Decomposition of variability in the execution of goal-oriented tasks: three components of skill improvement. *J Exp Psychol Hum Percept Perform* 30: 212–233, 2004. doi:10.1037/0096-1523.30.1.212.
53. **Brainard DH.** The psychophysics toolbox. *Spat Vis* 10: 433–436, 1997.
54. **Henderson JM.** Gaze control as prediction. *Trends Cogn Sci* 21: 15–23, 2017. doi:10.1016/j.tics.2016.11.003.
55. **Staub A.** The effect of lexical predictability on distributions of eye fixation durations. *Psychon Bull Rev* 18: 371–376, 2011. doi:10.3758/s13423-010-0046-9.
56. **Milstein DM**, **Dorris MC.** The influence of expected value on saccadic preparation. *J Neurosci* 27: 4810–4818, 2007. doi:10.1523/JNEUROSCI.0577-07.2007.
57. **Milstein DM**, **Dorris MC.** The relationship between saccadic choice and reaction times with manipulations of target value. *Front Neurosci* 5: 122, 2011. doi:10.3389/fnins.2011.00122.
58. **Takikawa Y**, **Kawagoe R**, **Itoh H**, **Nakahara H**, **Hikosaka O.** Modulation of saccadic eye movements by predicted reward outcome. *Exp Brain Res* 142: 284–291, 2002. doi:10.1007/s00221-001-0928-1.
59. **Müller H**, **Sternad D.** A randomization method for the calculation of covariation in multiple nonlinear relations: illustrated with the example of goal-directed movements. *Biol Cybern* 89: 22–33, 2003. doi:10.1007/s00422-003-0399-5.
60. **Danielmeier C**, **Ullsperger M.** Post-error adjustments. *Front Psychol* 2: 233, 2011. doi:10.3389/fpsyg.2011.00233.
61. **Maurer LK**, **Joch M**, **Hegele M**, **Maurer H**, **Müller H.** Relevance of predictive and postdictive error information in the course of motor learning. *Neuroscience* 486: 77–90, 2022. doi:10.1016/j.neuroscience.2021.05.007.
62. **Mann DL**, **Spratford W**, **Abernethy B.** The head tracks and gaze predicts: how the world's best batters hit a ball. *PLoS One* 8: e58289, 2013. doi:10.1371/journal.pone.0058289.
63. **Tatler BW**, **Hayhoe MM**, **Land MF**, **Ballard DH.** Eye guidance in natural vision: reinterpreting salience. *J Vis* 11: 5, 2011. doi:10.1167/11.5.5.
64. **Einhäuser W**, **Rutishauser U**, **Koch C.** Task-demands can immediately reverse the effects of sensory-driven saliency in complex visual stimuli. *J Vis* 8: 2.1–219, 2008. doi:10.1167/8.2.2.
65. **Henderson JM**, **Brockmole JR**, **Castelhano MS**, **Mack M**. Visual saliency does not account for eye movements during visual search in real-world scenes. In: *Eye Movements: A Window on Mind and Brain*, edited by Gompel RPGV, Fischer MH, Murray WS, Hill RL**.** Amsterdam: Elsevier, 2007, p. 537–562.
66. **Bray TJP**, **Carpenter RHS.** Saccadic foraging: reduced reaction time to informative targets. *Eur J Neurosci* 41: 908–913, 2015. doi:10.1111/ejn.12845.
67. **Gottlieb J**, **Hayhoe M**, **Hikosaka O**, **Rangel A.** Attention, reward, and information seeking. *J Neurosci* 34: 15497–15504, 2014. doi:10.1523/JNEUROSCI.3270-14.2014.
68. **Najemnik J**, **Geisler WS.** Eye movement statistics in humans are consistent with an optimal search strategy. *J Vis* 8: 4.1–414, 2008. doi:10.1167/8.3.4.
69. **Maurer LK**, **Maurer H**, **Hegele M**, **Müller H.** Can Stephen Curry really know?—Conscious access to outcome prediction of motor actions. *PLoS One* 17: e0250047, 2022. doi:10.1371/journal.pone.0250047.
70. **Cañal-Bruland R**, **Balch L**, **Niesert L.** Judgement bias in predicting the success of one's own basketball free throws but not those of others. *Psychol Res* 79: 548–555, 2015. doi:10.1007/s00426-014-0592-2.
71. **Maglott JC**, **Chiasson D**, **Shull PB.** Influence of skill level on predicting the success of one's own basketball free throws. *PLoS One* 14: e0214074, 2019. doi:10.1371/journal.pone.0214074.
72. **Bisley JW**, **Goldberg ME.** Attention, intention, and priority in the parietal lobe. *Annu Rev Neurosci* 33: 1–21, 2010. doi:10.1146/annurev-neuro-060909-152823.
73. **Hayhoe MM**, **Bensinger DG**, **Ballard DH.** Task constraints in visual working memory. *Vision Res* 38: 125–137, 1998. doi:10.1016/S0042-6989(97)00116-8.
74. **Henderson JM.** Human gaze control during real-world scene perception. *Trends Cogn Sci* 7: 498–504, 2003. doi:10.1016/j.tics.2003.09.006.
75. **Võ ML-H**, **Henderson JM.** Object–scene inconsistencies do not capture gaze: evidence from the flash-preview moving-window paradigm. *Atten Percept Psychophys* 73: 1742–1753, 2011. doi:10.3758/s13414-011-0150-6.
76. **Võ MLH**, **Henderson JM.** Does gravity matter? Effects of semantic and syntactic inconsistencies on the allocation of attention during scene perception. *J Vis* 9: 24.1–24.15, 2009. doi:10.1167/9.3.24.
77. **Wei K**, **Körding K.** Relevance of error: what drives motor adaptation? *J Neurophysiol* 101: 655–664, 2009. doi:10.1152/jn.90545.2008.

Study II

Published as: **Predicted task success and outcome history mediate eye movements toward locations with high informational or motivational value**

Brand, T. K.*, Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. (2025). Predicted task success and outcome history mediate eye movements toward locations with high informational or motivational value. Journal of Neurophysiology, 134(2), 568-579.*

J Neurophysiol 134: 568–579, 2025.
First published July 17, 2025; doi:10.1152/jn.00072.2025

american physiological society

JNP JOURNAL OF NEUROPHYSIOLOGY

RESEARCH ARTICLE

Control of Movement

Predicted task success and outcome history mediate eye movements toward locations with high informational or motivational value

Theresa K. Brand,[1,3] **Alexander C. Schütz,**[2] **Hermann Müller,**[1,3] **Heiko Maurer,**[1] **Mathias Hegele,**[1,3]* **and** **Lisa K. Maurer**[1,3]*

[1]*Neuromotor Behavior Laboratory, Department of Psychology and Sport Science, Justus Liebig University Giessen, Giessen, Germany;* [2]*General and Biological Psychology, Department of Psychology, Philipps University Marburg, Marburg, Germany; and* [3]*Center for Mind, Brain and Behavior (CMBB), Universities of Marburg and Giessen, Giessen, Germany*

Abstract

Previous research revealed that the action outcomes of self-generated movements can be predicted internally before outcome feedback becomes available. These sensorimotor predictions have been shown to guide gaze toward locations in the environment with high informational value for feedback processing. To test whether they can further be used to assign specific values to different parts of the visible space in the context of motor learning, we assessed systematic differences between gaze toward targets with high informational value (showing graded movement outcome feedback) and targets with high motivational value (showing the monetary reward in a current trial) as a function of (predicted) task success (hit vs. miss) in a goal-directed throwing task. We observed large interindividual differences in the proportion of fixations on each target, highlighting that stable individual tendencies strongly influence whether gaze is directed toward informational or motivational content. However, individual baseline proportions were fine-tuned by the throwing outcome of previous trials (e.g., a larger proportion of fixations on the informational target in trials that followed a miss in the previous trial) and the predicted outcome of a current trial (a larger proportion of fixations on the motivational target in predicted hits compared to misses). Thus, we conclude that, in the context of motor learning, humans combine outcome history with sensorimotor predictions, including the predictive valuation of outcome feedback, to assign value to different parts of the visible space and to guide gaze at highly valued locations, albeit modestly and subordinate to more stable individual preferences.

NEW & NOTEWORTHY We elucidate the potential benefits of internally generated action outcome predictions with respect to the optimization of information uptake in the context of motor learning. Here, we show that outcome predictions are used in combination with outcome history to weigh the value of different parts of the environment, albeit being subordinate to stable individual gaze preferences.

action monitoring; forward model; predictive eye movements; sensorimotor prediction; throwing task

INTRODUCTION

Over the past decades, extensive research has demonstrated that humans can internally predict action outcomes based on movement-related information (e.g., 1–5). So-called forward models simulate the input-output relationships of the musculoskeletal system, using sensory information about the current state of the body and the environment, along with copies of the motor commands (6–8). In the context of action monitoring, these sensorimotor predictions can be used by the central nervous system to assess deviations between predicted and intended sensory action effects before actual sensory feedback becomes available and thus to detect errors before they occur. This predictive valuation of outcome feedback has various benefits. First, it enables continuous adjustments to ongoing movements in closed-loop tasks more rapidly by bypassing processing delays in neural signal transduction (9, 10), and second disambiguates the

---

*M. Hegele and L. K. Maurer contributed equally to this work.

Correspondence: T. K. Brand (theresa.brand@sport.uni-giessen.de).

Submitted 12 February 2025 / Revised 22 April 2025 / Accepted 12 July 2025

source of performance errors; only predictable errors are one's own and require subsequent corrections of movement parameters, while external errors caused by unsystematic fluctuations in the environment are unpredictable and therefore ignored (11). The latter is especially relevant in motor learning as it helps to solve the credit assignment problem of error attribution (e.g., 12, 13).

To further justify the effort the central nervous system invests in sensorimotor predictions, we have recently proposed that they might also facilitate selective attention toward task-relevant locations in the environment over the course of motor learning (14). Such a mechanism could provide significant behavioral benefits, particularly when multiple stimuli dynamically compete for attention during the execution of a motor task. In this case, sensorimotor predictions, including the predictive valuation of outcome feedback, might be used to assign value to different parts of the visible space, thereby guiding gaze to locations with high informational value for trial-to-trial adaptations. In a recent study, we indeed found evidence supporting this hypothesis: we observed a direct link between sensorimotor predictions and predictive saccades landing on the predicted action effects of goal-directed throwing movements. Fixation durations at the predictively chosen locations were modulated by action outcome (longer durations for misses than for hits) and outcome uncertainty (longer fixation durations for narrow hits/misses than for clear hits/misses), suggesting the informational value of the predictively chosen locations for feedback processing (14). In the present study, we sought to put our hypothesis on the behavioral benefits of sensorimotor predictions, including the predictive valuation of outcome feedback, to further tests. To do so, we examined systematic differences in the selection of competing fixation targets as a function of (predicted) task success in a goal-directed throwing task. These targets either offered high informational value (graded movement outcome feedback) or high motivational value (monetary reward for a hit in the current trial).

Several studies highlight that saccades are specialized for selectively sampling information from the environment as described above (for a review, see Ref. 15). Already in 1935, Guy Thomas Buswell established that viewers tend to look at the regions in scenes likely to hold the most meaningful and relevant information to the observer (16). Since then, it has been repeatedly shown that saccades can maximize information gain under some visual search or discrimination paradigms (17–23). For example, Peterson and Eckstein (21) found that humans saccade to locations that maximize perceptual performance in determining the identity, sex, and emotional state of a face. In natural behavior, one of the most important roles of saccades is to sample information to assist ongoing actions. Despite multiple demands on attention, subjects manage to select gaze targets to sample the relevant information at the appropriate time (e.g., Refs. 24–27). According to Gottlieb et al. (15), the fact that saccades do so in a goal-directed fashion implies that the brain has mechanisms for assigning priority to sources of information based on the demands of the task.

Besides the prospective gain in task-relevant visual information via saccades, low-level features of scenes, such as visual saliency (e.g., Ref. 28), and motivational aspects of stimuli, such as a monetary reward linked to saccade targets (29, 30), influence decisions about target selection for saccades. These influencing factors of saccadic target selections have been studied extensively (for reviews, see Refs. 31–33). With respect to the competition of saliency and reward, for example, studies have shown that humans dynamically trade off saliency and reward in visual search displays to select saccade targets that maximize expected reward (34–36). Several studies show that task demands can suppress the influence of saliency completely (e.g., Refs. 37, 38). Daddaoua et al. (39) demonstrated that visual cues are most frequently attended via saccades when they combine positive feedback with a reduction of uncertainty compared with both aspects acting alone. These findings suggest that saccades are driven by an integrated value estimation, balancing the desire to close "information gaps" (reducing uncertainty or harvesting information) with the intrinsic attraction to rewarding stimuli (conditioned reinforcement from positive cues). In broader terms, Xu-Wilson et al. (40) proposed that the brain may continuously assign a dynamic value (integrating various cognitive factors) to every part of the visible space, forming a priority map (41). Each saccade is the brain's attempt to direct the fovea toward the region currently estimated to have the highest value.

In goal-directed actions, like targeted throws, the informational value of movement outcome feedback should depend on the (predicted) outcome of the action (hit vs. miss). Although it is particularly important to process feedback on erroneous trials to derive suitable adjustments (to succeed in the long term), it may be less crucial to guide gaze toward learning relevant information if one is sure that a trial is going to be a hit. This difference in the value of outcome feedback is theoretically reflected by longer fixation durations at the feedback location in erroneous throws (14). In practice, we observe that when popular basketball players expect to make the shot, they sometimes turn around immediately after releasing the ball and do not (need to) perceive the outcome feedback (see also Ref. 42). To hit a second time under the same circumstances, the same motor command can be used, and attending to spectators' reactions may provide a higher motivational value than looking at how the ball strikes the basket. Considering these observations, it is reasonable to assume that sensorimotor predictions serve to not only identify locations with high informational value for feedback processing (14) but also assign specific values to those locations based on the predicted action outcome. Such a mechanism could provide significant behavioral benefits when multiple stimuli dynamically compete for attention during the execution of a motor task. In addition to sensorimotor predictions of current action outcomes, previous action outcomes may influence the expected value of different locations. Following error trials, it becomes crucial to assess whether a movement correction led to the desired effect. Prolonged fixation durations at feedback locations following an error trial suggest an increased value of outcome feedback in these trials, regardless of the current trial outcome (14).

Although previous studies have demonstrated how value gets assigned to visual stimuli while passively viewing a scene (43), while executing visual search and discrimination tasks (44–47), or to assist ongoing movements (24–27, 48, 49), we aim to explain value assignment during the evaluation of one's own actions.

Thus, the goal of the present study was to investigate whether sensorimotor predictions, including the predictive valuation of outcome feedback, are used to assign value to possible fixation locations, thereby optimizing information uptake in the context of motor learning. To this end, we assessed systematic differences in the selection of competing fixation targets with either high informational value (providing graded movement outcome feedback) or high motivational value (displaying the monetary reward for a hit in the current trial), as a function of (predicted) task success in a goal-directed throwing task. The motivational target was designed to mimic real-time reinforcement for a successful throw, akin to spectators' reactions or glancing at a scoreboard in naturalistic settings. A third potential fixation target displayed the progress through the experiment, which we consider to be of neutral value and thus independent of the action outcome. We expected that predicted errors would increase the value of graded outcome feedback, leading to more fixations on the informational target in error trials. Conversely, we expected more fixations on the motivational target in predicted hits, as reward-related information would have a higher value in these cases. In addition, we explored how outcome history (outcome trial n−1) might influence the integration of sensorimotor predictions (of the outcome in a current trial) into saccadic programming.

MATERIALS AND METHODS

Participants

Twenty-two participants (10 females, 12 males; mean age: 21.95 ± 2.15 yr, range: 19–28) were recruited from the student population of the Justus Liebig University, Giessen, Germany. All participants were right-handed, had normal or corrected-to-normal vision, and reported no history of upper limb injuries. Each participant completed the study over 2 days, with sessions lasting approximately 1 h each. Compensation included either course credit or a monetary payment, along with an additional performance-based reward of up to €17.50 on the second day. The study adhered to the ethical standards outlined in the Declaration of Helsinki (2013, except §35, pre-registration) and was approved by the Ethical Review Board of the Justus Liebig University, Giessen. Written informed consent was obtained from all participants before the study.

Task and Setup

Participants performed a complex, goal-directed throwing task modeled after the British pub game "Skittles." In the traditional game, a ball attached to the top of a post by a string is swung around the post to hit target objects on the opposite side. The task is ballistic, meaning that no online corrections can be made during movement execution, and it involves a temporal separation between movement execution and the observation of its final outcome. Both aspects allow for internal predictions of future action outcomes before outcome feedback becomes naturally available. Skittles is a redundant task, meaning that specific action outcomes can be achieved through an infinite number of angle-velocity combinations at ball release. Furthermore, the relationship between execution variables (release angle and velocity) and resulting outcomes is nonlinear, making outcome prediction nontrivial and cognitively impenetrable.

In the semivirtual version of the task (see also Refs. 3, 4, 50), participants performed a physical, ballistic throw resembling a frisbee toss using a metal lever (manipulandum) while the resulting action effect (the ball moving around the post) was visible only on a computer screen (Dell Alienware AW2521HF; active screen size: 37.7 × 30.2 cm, full-screen size: 55 × 31 cm; resolution: 1,280 × 1,024 pixels; refresh rate: 120 Hz; Fig. 1*A*). The screen depicted a virtual representation of the metal lever (whose position continuously represented the position of the physical manipulandum), a green virtual ball (luminance: 93.81 dc/m^2; RGB: [25, 153, 0]), a gray center post (luminance: 2.49 dc/m^2; RGB: [30, 30, 30]), a red throwing target (luminance: 25.44 dc/m^2; RGB: [153, 25, 0]), and a predefined start position (Fig. 1*B*). The configuration on the screen displayed the original Skittles task from an overhead perspective. The participants' heads were not fixed with a chin or forehead rest, allowing slight variation in eye-to-screen distance. At a typical eye-to-screen distance of 70 cm, stimulus sizes corresponded to visual angles of 0.7° for the ball and the throwing target, 3.4° for the center post, and 0.9° for the start position.

To virtually pick up and release the ball, participants placed or removed their index finger from an electrical contact sensor at the tip of the lever. The angle and velocity of the manipulandum at the moment of ball release (t_{Release}), which determined the ball's trajectory, were recorded using a 12-bit (0.09° resolution) magnetic angle sensor integrated into the manipulandum, sampling at 1,000 Hz. The calculation of the elliptical ball trajectory around the center post in each trial was based on a physical model of the task (51). Task parameters were as follows: Center post – radius $r = 0.25$ m, position $x = 0.0$ m, $y = 0.0$ m; throwing target – radius $r = 0.05$ m, position $x = 0.8$ m, $y = 0.9$ m; ball – radius $r = 0.05$ m, mass $m = 0.25$ kg; lever – length $l = 0.26$ m, position $x = 0.0$ m, $y = -1.36$ m; spring constant $D = 1.0$ N/m. Depending on execution parameters (i.e., the angle and velocity at the moment of ball release), the time between release and outcome feedback varied across trials, averaging 995 ± 100 ms. We defined the time point of outcome feedback as the moment when the ball reached its minimum distance from the throwing target. In line with previous studies (e.g., Refs. 3, 11, 52), this time point is referred to as t_{dmin} in the following.

In the regular task version, participants could see the ball moving toward the throwing target after ball release. A collision (hit) occurred when the minimum distance ($d_{\min}$) between the ball's trajectory and the target center was equal to or less than twice the ball/target radius. In these cases, the target was pushed away from its position, and the sound of two colliding billiard balls was heard. Depending on the collision angle, the ball bounced off the target at an angle consistent with energy transmission laws for rigid objects (akin to billiard balls). In trials where $d_{\min}$ exceeded twice the radius of the ball/target ($d_{\min} >$ 0.1 m), the ball missed the target.

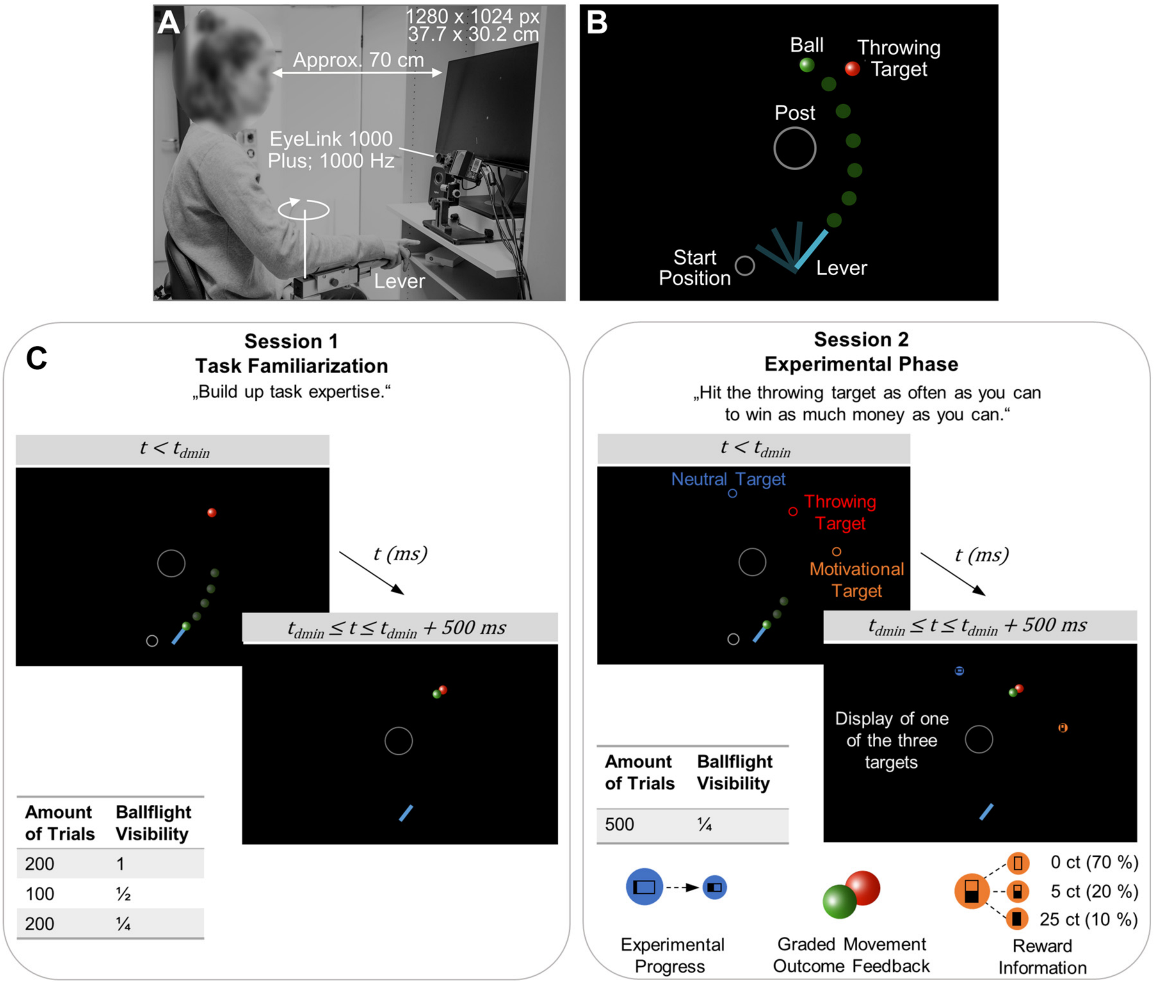


Figure 1. *A*: setup of the semi-virtual Skittles task. Participants performed throwing movements using a metal lever, resembling a frisbee toss. A virtual ball was released by lifting the index finger from an electrical contact sensor at the tip of the lever. The resulting action effects were displayed on a screen positioned in front of the participant. Eye movements were recorded throughout task execution using an Eyelink 1000 Plus with desktop mount running in remote mode. *B*: task space displayed on screen. The starting position for the throwing movements was located left of the lever's vertical axis. Upon release, a green ball followed an elliptical trajectory around a gray center post and toward a red throwing target. *C*: experimental schedule and design. The task was practiced over 500 trials in *session 1*, during which continuous visual feedback on the ball trajectory was gradually reduced (only proportions of the ball flight were visible on each trial) so that only static outcome feedback was provided for 500 ms at the time of the minimum distance between the ball and the throwing target (t_{dmin}). In *session 2*, only the first quarter of the ball trajectory was visible, and two additional visual targets were introduced alongside the primary throwing target. From trial start until t_{dmin}, the targets were displayed as equally salient and equally sized circles in distinct colors. The arrangement of the neutral and motivational targets was pseudorandomized across participants. Depending on the participants' gaze position at t_{dmin}, either the experimental progress (neutral target), graded movement outcome feedback (throwing or informational target), or reward information (motivational target) could be perceived for 500 ms. Participants were instructed to hit the throwing target as often as possible to maximize their monetary reward.

During task execution, eye position signals of the participants' right eye were recorded at 1,000 Hz using an EyeLink 1000 Plus (on a desktop mount; SR Research, Ottawa, Canada) running in remote mode. This mode allows for precise eye tracking without requiring physical head stabilization, supporting natural task engagement. The experimental software for task execution and data synchronization (eye tracking and throwing movements) was developed with MATLAB R2021b (The MathWorks, Inc., Natick, MA) and the Psychophysics Toolbox 3.0.18 (53).

Participants sat on a height-adjustable stool to align their horizontal line of vision with the center of the screen. The foam-padded manipulandum with a forearm rest was mounted on a height-adjustable stand, with its vertical rotation axis aligned below the participants' right elbow joint. Arm movements were restricted to the horizontal plane, specifically to rotations around this fixed vertical axis. Window blinds and artificial light ensured constant lighting conditions throughout data acquisition.

Although our study is framed within the motor learning literature, it differs from other often paradigms such as sensorimotor adaptation or sequence learning, which typically involve adjusting existing controllers or learning structured action sequences (54). In contrast, our semivirtual throwing task ("Skittles") requires participants to build a novel control policy de novo, as the mapping between movement and outcome is initially unfamiliar and nonlinear. Learning involves both discovering effective movement solutions and refining their execution with increasing precision. This combination of de novo controller formation and motor acuity development positions our task as a valuable model for studying attentional processes during real-world motor skill learning.

Procedure and Study Design

Participants performed the experimental task over 2 days, completing 500 throws each day. At the beginning of *session 1*, the task was explained to the participants using a miniature model of the real Skittles game. To familiarize participants with the semivirtual task, they completed 10 test trials before beginning the experimental schedule. Each session began with a 13-point calibration and validation procedure for eye tracking. Calibration was accepted only when average errors were below 0.5° and maximum errors were below 1°. Fixations on each calibration target were manually confirmed by the experimenter, and the calibration targets were displayed in random order.

To pick up the virtual ball at the beginning of each trial (the ball is visually attached to the virtual equivalent of the lever), participants placed their right index finger on the electrical contact sensor at the tip of the lever. They were instructed to initiate each trial by moving the tip of the virtual lever into the start position, left to the fixed end of the lever while simultaneously fixating on this point. When the lever reached the start position, the start position's color turned from red to yellow, and an online drift check was conducted. Data for the drift check were recorded for 100 ms after the lever remained inside the start position for 1 s. The start position turned green if the detected fixation deviated less than 2° from its center. After that, participants could begin with the throw at any time at their own rhythm. If drifts were detected, eye positions were recalibrated and revalidated using the 13-point procedure before continuing the experimental schedule.

Starting in front of their upper bodies, participants threw the virtual ball by moving the manipulandum outward, resembling a frisbee toss. Upon lifting their fingers from the contact sensor, the virtual ball was released from the virtual lever and traveled in a counter-clockwise trajectory around the center post. The drift check process prevented fast, rhythmic executions of subsequent trials, ensuring the task remained discrete. After every block of 100 trials, participants were given a short rest period, and the eye tracker was recalibrated.

Session 1 was designed to develop task expertise. During the initial 200 trials, continuous visual feedback was provided, showing the full ball trajectory. This feedback was then gradually reduced. For the next 100 trials, only the first half of the trajectory was displayed, and for the final 200 trials, only the first quarter was visible. On all trials in which only partial ball trajectories were visible, static outcome feedback was provided for 500 ms at the time of the minimum distance between the ball and the throwing target (t_{dmin}), showing the ball's position at that moment (Fig. 1*C*, *session 1*).

Session 2 served as the experimental phase, where participants performed the task under conditions similar to the final phase of *session 1*, with only the first quarter of the ball trajectory visible. In this session, two additional visual targets were introduced alongside the primary throwing target (in the following also denoted as the informational target, red, RGB: [175, 25, 0]): a motivational target (orange, RGB: [255, 125, 25]), and a neutral target (blue, RGB: [25, 125, 255]). The three targets were equidistant from the starting point (to control for oculomotor effort) and were displayed as equally sized unfilled circles at the start of each trial (Fig. 1*C*, *session 2*). The additional targets were positioned at an angular distance of 9.6° from the throwing target at a typical eye-to-screen distance of 70 cm, and their arrangement was pseudorandomized across participants to prevent positional biases.

Depending on the participants' gaze position at t_{dmin}, feedback at only one of the target locations could be perceived for 500 ms:

- The informational target showed the ball position relative to the throwing target position, providing graded visual feedback on the throwing outcome.
- The motivational target showed a vertical bar indicating the potential reward for the current trial. The bar could appear unfilled, half-filled, or filled in pseudorandom order, representing rewards of 0 cents (in 70% of all trials), 5 cents (20%), or 25 cents (10%) in case of a hit. Reward information was displayed regardless of the actual outcome of the current trial if the target was fixated at t_{dmin} and rewards were granted for hits regardless of whether the target was fixated (see also Ref. 39).
- The neutral target displayed a horizontal bar showing the participants' progress within a block of 100 trials (nonfilled at the start of a block, filled by the end).

Participants were briefed on the targets and their meanings at the beginning of *session 2*. To familiarize them with the appearance of the targets, they completed 10 further test trials. Before starting, the following specific instruction was given to the participants:

> "Your goal is to hit the throwing target as often as possible to maximize your monetary reward. In each trial, depending on the target you look at, you can either view your progress in a block of 100 trials, the potential reward for that trial, or feedback about the accuracy of your throw."

Acoustic feedback (the sound of two colliding billiard balls at t_{dmin} in cases of hits and its absence in cases of misses) was consistent across trials regardless of the fixated target. Thus, participants received outcome feedback even when fixating on the neutral or motivational target.

Data Processing and Analysis

Data processing and analyses were conducted using MATLAB R2021a. As a measure of task performance, we calculated the participants' hit rates (in blocks of 100 trials) throughout the experiment.

For the analysis of the eye-tracking data, we excluded trials, in which *a*) the center post was hit, *b*) the ball release trigger was not registered in the eye data so that t_{dmin} could not be defined, and *c*) in cases of recording problems that caused gaze data to remain centered around the start position throughout a whole trial. These exclusion criteria resulted in a data loss of 2.07%. In the remaining trials, target fixations were analyzed both over the course of the trial to examine participants' dynamic behavior and specifically at t_{dmin} to evaluate their predictive target selections across trials.

Continuous analysis.

Trials were time-normalized, with t_{Release} serving as the starting point and t_{dmin} as the end point. At each time stamp, the proportional selection of targets was calculated across all trials and participants. Fixations at each time point could fall into one of four categories—informational target, motivational target, neutral target, or no target—based on whether participants' gaze was within a 3° window around the center of the respective target.

Additional analyses at the participant level examined how different throwing outcomes (hit vs. miss) and the outcome history (outcome trial *n*-1) modulated dynamic target selection. Specifically, the relative frequency of fixations on each target over the trial course was compared for: *a*) hits following a hit versus misses following a hit, to evaluate the influence of the (predicted) outcome in the current trial, and *b*) hits following a hit versus hits following a miss, to assess the influence of the previous trial outcome on target selection. Hits were chosen as the default outcome because they occurred more frequently than misses, which increased statistical power for detecting meaningful differences. Moreover, this approach enhances the clarity of the results section. A supplemental figure offers an additional descriptive overview of the 2×2 dynamic sequence effects. Outcomes were classified based on d_{min}, with hits defined as $d_{\mathrm{min}} \leq 0.1$ m, and misses as $d_{\mathrm{min}} > 0.1$.

Analysis at t_{dmin}.

An exhaustive analysis of proportional target choices across different outcome(s) (histories) was conducted specifically at t_{dmin}. To improve the precision of predictive target selection analyses, a distinction was made between target fixations initiated before and after ball release. To only include target selections that could be based on sensorimotor predictions, target fixations were considered only if initiated after release. Fixations initiated before release ("early fixations") contain little or no movement-related (efferent and proprioceptive) information (14).

To assess general interindividual differences in target preferences, the proportional selection of targets at t_{dmin} was calculated across all trials for each participant, including the differentiation between early fixations and those made after release.

Statistical Analysis

The relative frequency of target fixations under varying outcomes, focusing on both the influence of current and previous trial outcomes, was analyzed using inferential statistics. For the continuous data representing the proportional selection of a target under a specific outcome (history) over the trial course, difference curves were calculated for each participant and each target for both planned comparisons: *a*) hits following a hit versus misses following a hit, to evaluate the influence of the (predicted) outcome in the current trial, and *b*) hits following a hit versus hits following a miss, to assess the influence of the previous trial outcome on target selection. A nonparametric point-based resampling technique (PBRT; 55) was applied to generate 95% confidence bands for the mean difference curve. This method is particularly suited for non-normally distributed continuous data that cannot be adequately modeled using basic mathematical functions.

For the analysis of the proportional target selection at t_{dmin}, we used (binomial) logistic regressions, common generalized linear models (GLMs), suitable for proportions that are computed as the ratio of the number of target events to the total number of trials, "n_y out of n" (56). These models naturally handle non-normality and heterogeneity issues, and the use of a logit link function guarantees that the fitted values will be exactly within the range [0, 1]. To account for the repeated-measures design, mixed-effects models (GLMMs) were estimated using the "glmer" function of the "lme4" package (57) for R 4.4.1 (R Foundation for Statistical Computing, Vienna, Austria). Four GLMMs were run to analyze the effects of current and previous trial outcomes (hit vs. miss) on the frequency (n_y out of n) of fixations for each target (the informational, the motivational, the neutral, or no target). Subject-level variability was included as a random effect. In line with recommendations for confirmatory hypothesis testing (58, 59), models initially included the maximal random-effects structure justified by the experimental design. Terms were iteratively removed to achieve model convergence and avoid singular fits. Model diagnostics were conducted using the DHARMa package in R (60). This tool simulates new values from the fitted models for each observation and provides readily interpretable standardized residuals that can be intuitively interpreted as residuals from linear regression. Diagnostic results confirmed the regression models were well-suited to the data, with robust statistical estimates. Detailed diagnostics, including model formulae, are available in the Supplemental material. To facilitate the interpretation of model terms as main effects, contrast coding was applied in all regression models (61). The significance of fixed effects was assessed using Wald statistics. Four participants were excluded from this analysis as they consistently fixated on the informational target across all trials at t_{dmin}. To evaluate whether the conclusions drawn from the GLMMs are robust when using an alternative statistical approach that, while less suited to the data, involves fewer "researcher degrees of freedom," we conducted repeated-measures ANOVAs as complementary analyses. Results of these ANOVAs, with the within-subject factors outcome current trial (hit vs. miss) and outcome previous trial (hit vs. miss), are presented in the Supplemental material and confirm the GLMM results.

Task performance, measured as hit rate (percentage), was analyzed across blocks of 100 trials using repeated-measures ANOVA. The normality of residuals was checked using Q-Q plots, and sphericity was tested using Mauchly's W. To address violations of the sphericity assumption, the Greenhouse–Geisser correction was applied. For post hoc tests, the Holm correction was used. The ANOVA analyses, including all assumption checks, were performed in JASP (v.0.18.3.0, The JASP Team, Amsterdam, The Netherlands). The significance level for all statistical tests was set at $\alpha = 0.05$, and all reported *P* values correspond to two-sided testing.

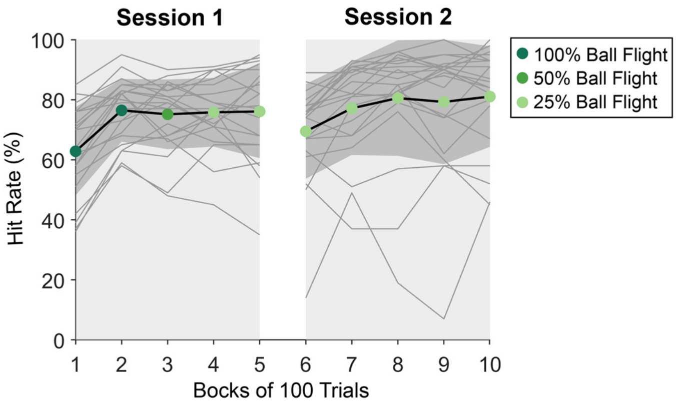


Figure 2. Development of task performance across the experiment for individual participants (gray lines) and the sample as a whole (black line). Shaded areas represent standard deviations highlighting interindividual differences in hit rate trajectories. Over the course of the experiment, continuous visual feedback was reduced, and only partial ball trajectories were visible, indicated by dots in shades of green. $n = 22$ subjects.

RESULTS

Task Performance

The analysis of hit rates across blocks of 100 trials throughout the experiment revealed significant performance changes, $F(9,189) = 8.15$, $P < 0.001$, $\eta_p{}^2 = 0.28$ (Fig. 2). After a significant improvement in hit rates from block 1 (62.82 ± 14.70%) to block 2 (76.46 ± 10.46%), task performance stabilized as the proportion of visible ball trajectory was gradually reduced over the rest of *session 1*. In *session 2*, during which only the first quarter of the ball trajectory was visible, participants exhibited further improvements (block 6 vs. 8: $P < 0.01$, block 6 vs. 9: $P < 0.05$, block 6 vs. 10: $P < 0.01$) after a small nonsignificant warm-up decrement (block 5 vs. 6: $P = 0.50$). Overall, participants achieved an average hit rate of 76.45 ± 10.46% in *session 2*.

Target Fixations

Figure 3A illustrates the temporal dynamics of gaze behavior across all trials and participants. In ∼20% of the trials, targets were fixated before the ball release ("early fixations"). Generally, participants made saccades to one of the targets ∼250 ms to 500 ms after ball release. The informational target was most frequently fixated. Fixations on the motivational and neutral targets, as well as no target fixations, occurred less often. However, as shown in Fig. 3B, illustrating the proportional target selections at t_{dmin} across individual participants, participants used diverse strategies. Four participants did not fixate on the neutral and motivational targets at all. Neither the hit rate of the participants in *session 2* (shown in increasing order from the leftmost to the rightmost subject in Fig. 3B) nor the arrangement of the additional targets seemed responsible for a specific behavioral pattern emerging. Only the neutral target was fixated less frequently (relative frequency) when it was positioned on the left versus right side of the target ($W = 67.00$, $n_1 = 11$, $n_2 = 11$; $P = 0.04$, $r = 0.25$).

To examine how the current trial outcome influenced target selection, we analyzed the temporal dynamics of proportional target fixations separately for hits and misses when the previous trial was a hit (Fig. 4A). The difference curves revealed a higher relative frequency of fixations on the motivational and neutral targets in upcoming hits compared with upcoming misses (indicating a hit bias), alongside a tendency toward fixations on the informational target in upcoming misses. The significant miss bias for the informational target toward the end of the trial indicates longer fixation durations on this target after feedback at t_{dmin} in misses compared with hits, a pattern not observed for the motivational or neutral target. Proportional fixations on no target represent the residual variance.

When considering the influence of the previous trial outcome (Fig. 4B), we observed a significant miss bias in the selection of the informational target. In addition, the previous trial outcome influenced fixations on the motivational and neutral targets: both targets were fixated more frequently when the previous trial was a hit.

The GLMMs analyzing target selections specifically at t_{dmin} (Fig. 5A), focusing on decisions made after release, analogously revealed a significant main effect of the

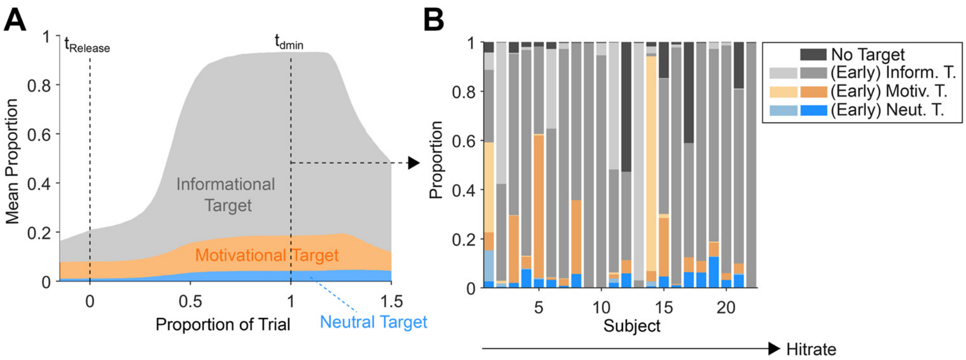


Figure 3. *A:* general behavior. Proportional target selection across all trials and participants over the trial course. Trials were time-normalized with ball release (t_{Release}) as the starting point and the time of minimum distance between the ball and the throwing target (t_{dmin}), i.e., feedback time point, as the endpoint. *B*: interindividual differences. Proportional target selection at t_{dmin} for each participant. "Early fixations" refer to trials in which a target was already fixated before t_{Release}. Participants are ordered from left to right by their individual hit rate (from lowest to highest). No systematic relationship was observed between performance (or performance improvements over time) and fixation behavior. $n = 22$ subjects.

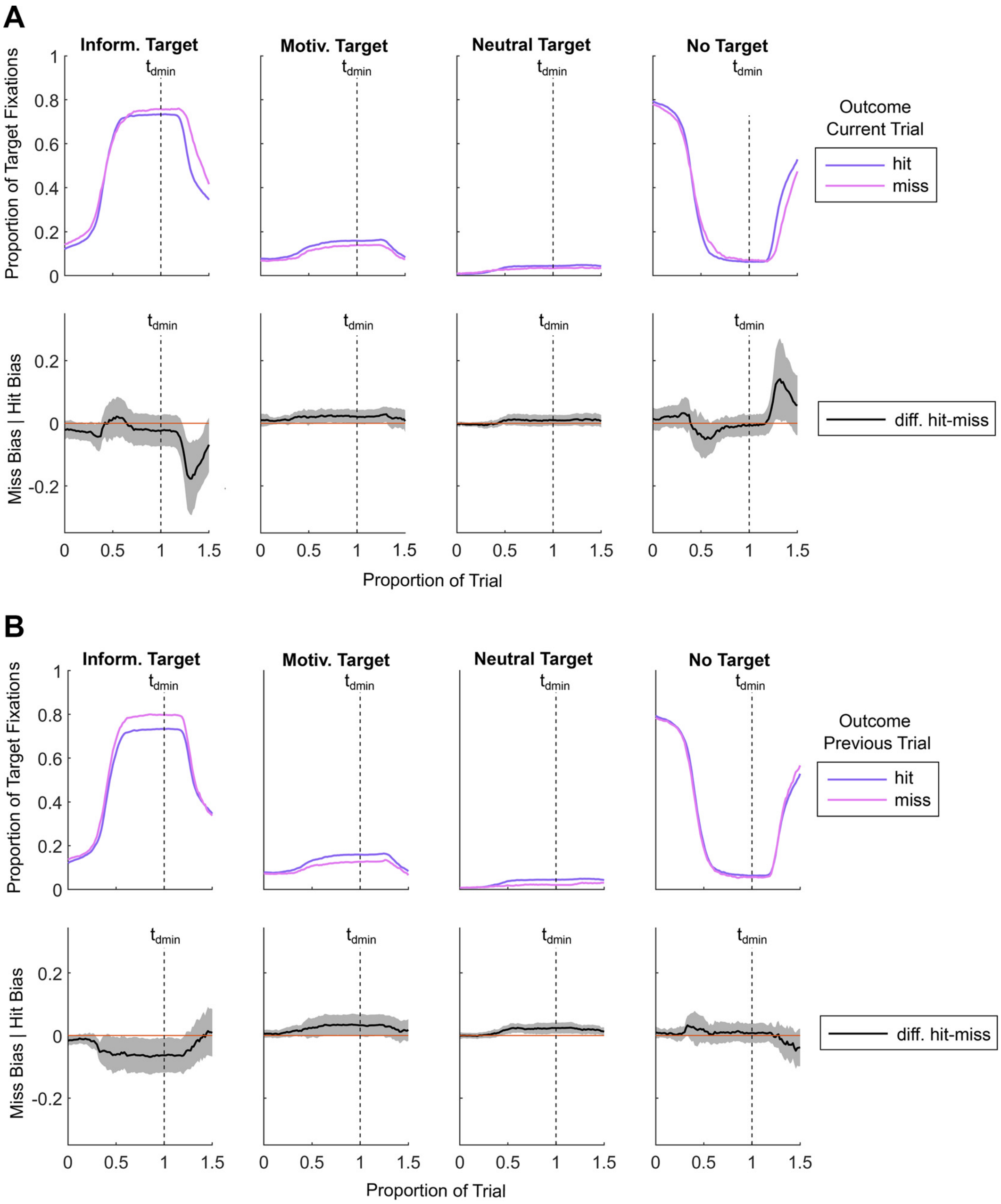


Figure 4. *A:* mean relative frequencies of fixations on each target throughout the trial course for hits following hits versus misses following hits, depicting the influence of the current trial outcome on target fixations. *B*: mean relative frequencies of fixations on each target throughout the trial course for hits following misses versus hits following hits depicting the influence of the previous trial outcome on target fixations. The second rows in *A* and *B* depict the mean difference curves for each target with 95% confidence bands calculated using the PBRT by Joch et al. (55). A "hit bias" reflects a higher relative frequency of target fixations in/after hits compared with misses, whereas a "miss bias" denotes the opposite pattern. Significant differences: 95% confidence bands exclude 0 (red line); trials were time-normalized with ball release as the starting point and the time of minimum distance between the ball and the throwing target (t_{dmin}), i.e., feedback time point, as the endpoint; $n = 22$ subjects.

previous trial outcome indicating a bias toward the informational target when the previous trial was a miss (Wald $z = 2.67$, $P < 0.01$), and the opposite for the motivational (Wald $z = -2.84$, $P < 0.01$) and the neutral targets (Wald $z = -3.59$, $P < 0.001$). In addition, a significant main effect of the current trial outcome was found for the motivational target, with more frequent fixations in upcoming hits (Wald $z = -3.68$, $P < 0.001$). The GLMM for fixations on no target was nonsignificant.

DISCUSSION

Previous research has shown that the outcomes of self-generated movements can be internally predicted and used to guide gaze (and presumably attention) toward locations with high informational value for feedback processing (14). Building on the concept proposed by Xu-Wilson et al. (40) that the brain continuously assigns dynamic value to every part of the visible space, the current study investigated whether these sensorimotor predictions, including the

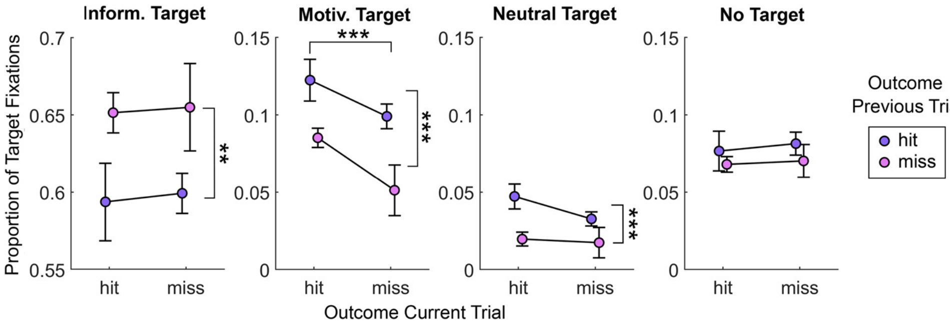


Figure 5. Relative frequencies of target fixations at the time of minimum distance between the ball and the throwing target (t_{dmin}) across different outcome(s) (histories). Values are means ± bootstrapped SE; Data were analyzed with GLMMs; $n = 18$ subjects; ***$P < 0.001$, **$P < 0.01$.

predictive valuation of outcome feedback, are used more specifically for dynamically assigning value to different parts of the visible space, with the potential to maximize information gain during motor learning. To this end, we assessed systematic differences in the selection of competing fixation locations, characterized by either high informational value (providing graded movement outcome feedback), high motivational value (displaying the monetary reward for a hit in the current trial), or neutral value (showing the experimental progress) as a function of (predicted) task success in a goal-directed throwing task.

With a focus on mechanisms for assigning priority to sources of information in the evaluation of own movements, we extend previous research that has demonstrated how value is assigned to visual stimuli while passively looking at a scene (43), while executing visual search or discrimination tasks (44–47), or to assist ongoing movements (24–27, 48, 49). Our findings provide evidence that previous action outcomes and current outcome predictions interact to fine-tune fixation proportions toward targets with distinct values in the evaluation of own actions. These results offer a deeper understanding of how gaze behavior is adaptively regulated in real-time during motor performance and learning.

Task Performance as Prerequisite for Successful Sensorimotor Predictions

Previous studies suggest that the accuracy of sensorimotor predictions is related to task performance (3, 6, 52). To facilitate prediction abilities, we chose a task in which subjects achieved an average hit rate of 63% in the first block of 100 trials. Participants maintained a stable performance level even under conditions with reduced ball-flight visibility and further improved performance in *session 2*. The observed level of task performance should have met the prerequisites for generating reliable sensorimotor predictions, consistent with prior findings using similar task designs (3, 4, 14).

General Gaze Behavior

The analysis of the temporal dynamics of gaze behavior revealed that saccades to one of the competing targets occurred ∼250–500 ms after ball release in ∼80% of the trials. These latencies and the prevalence of predictive saccades after release align with the saccadic behavior in the study by Brand et al. (14) using the same experimental task. The observed latencies correspond to the effect window of the neural correlate for predictive error valuation, the error-related negativity (ERN), in this task (200–350 ms after ball release; 4). This temporal alignment raises the possibility that these saccades were informed by movement-related information and could have been executed as a result of predictive valuation processes (i.e., after internally rating a trial outcome as an upcoming hit or miss).

Fixation durations on the informational target after feedback were longer for misses than hits, supporting the assumption that this target provided high informational value for feedback processing (14). The informational value and task relevance are further supported by the high proportion of fixations at this target (approximately 85%). Several studies demonstrated the importance of visual feedback about movement accuracy for maintaining or improving task performance (e.g., Ref. 62), which is the primary goal of this task. Achieving task success facilitates the secondary goal of monetary reward acquisition. In contrast, the motivational target had less immediate task relevance, as the reward was given for a hit irrespective of whether the target was fixated. Instead, the motivational target provided additional information about the amount of reward for a current trial, providing the opportunity for positive reinforcement in the case of a hit (39). Recent findings suggest that neurons in the lateral intraparietal cortex (LIP) integrate signals of prior reward probability, prior reward uncertainty, and posterior expected value to mediate active information-seeking behavior (63). As, in the current study, rewards were only provided in 30% of the trials, reward probability was rather low, which could have led to the low proportion (approximately 15%) of fixations on the motivational target. The neutral target, which simply displayed the progress within the experiment, was fixated least often (approximately 3%).

This general behavioral gaze pattern aligns with the observation that task relevance is the primary driver of attention in natural tasks (24, 64, 65). In decision-making contexts, Orquin and Mueller Loose (66) similarly proposed that decision-makers preferentially attend to stimuli with higher task relevance while largely ignoring stimuli with little or no task relevance.

However, participants in the present study used diverse strategies in their proportional target selections (see also Refs. 67–69), leading to individual baseline fixation proportions for each target that were not predictive of task performance. In particular, some participants regularly fixated on the motivational target while most did so only rarely. These differences likely reflect stable baseline tendencies shaped by person-specific factors. For example, Daddaoua et al. (39) attributed such individual differences to variations in the factors that drive intrinsic motivation, which may relate to an individual's learning style and the cognitive costs associated with processing information. However, it has also been shown that individuals' strategies can be task-specific (70). In the current study, we deliberately opted for ecologically valid competing targets by selecting a motivational target that resembled real-time reinforcement for a hit, comparable to spectators' reactions or to looking at the score board in naturalistic settings.

Systematic Modulation of Target Fixations by Previous and Current Trial Outcomes

To investigate whether sensorimotor predictions, including the predictive valuation of outcome feedback, were used additionally to dynamically assign value to the different targets for maximizing information gain during motor learning, we analyzed how the individual baseline proportions were modulated by the outcome of the current trial (hit vs. miss). As outcome feedback of a current trial was not yet available when participants decided to fixate on a specific target, any systematic modulations with respect to the current trial's outcome must have relied on predictive valuations of the upcoming result. Given that the previous trial outcome might influence the perceived value of different targets and the role of sensorimotor predictions for value assignment, we also examined modulations of baseline proportions by previous trial outcomes (outcome trial $n-1$).

Consistent with our hypothesis, we observed a higher relative frequency of fixations on the informational target in (predicted) errors, suggesting the assignment of increased value for graded movement outcome feedback when error correction was likely needed. However, this effect was not statistically significant. One reason for this may be that the informational target also retained informational value in hits, as precise movement outcome feedback reduces performance uncertainty in general. According to Sprague et al. (71), if a state is not updated, it is assumed that uncertainty about that state grows. Second, the informational target also had a motivational component in hits, as viewing the ball "colliding" with the target should act as positive reinforcement. This dual role of the informational target, providing positive feedback in hits and reducing uncertainty in both hits and misses, may have attenuated the difference in the relative fixation frequency between predicted hits and misses, as individuals assign value to both of these aspects (71, 72; for reviews, see Refs. 15, 31, 73, 74).

The relative frequency of fixations on the informational target was predominantly modulated by the outcome in a previous trial. Specifically, the informational target was fixated significantly more often after a miss in the previous trial. This finding suggests an intuitive assignment of high value to graded outcome feedback when individuals need to assess whether movement corrections led to the desired corrective effect after an error. In such cases, the informational target addresses an evident information gap, closure of which has high task relevance for learning and long-term task performance. This pattern of fixation on the informational target indicates an integration of recent experiences (i.e., outcome history) with sensorimotor predictions for value assignment, with the more reliable value-predictive cue "outcome history" playing a dominant role in guiding selective attention to learning-relevant information.

Fixations on the motivational target were also influenced by the previous trial outcome. Specifically, this target was fixated significantly more often following a hit in the previous trial, indicating the capacity for extracting extra information about reward magnitude in the current trial. A similar increase in fixations was observed for the neutral target, indicating that task-irrelevant information also received greater attentional allocation after a successful previous trial. However, it remains unclear whether the saccadic target selection was primarily driven by the assignment of value to the informational target after a miss, to the motivational target after a hit, or a combination of both factors, because the proportion of fixations on the different types of targets was not independent of each other in our paradigm.

The motivational target was furthermore fixated significantly more often in predicted hits compared with misses. This finding aligns with anecdotal behaviors observed in sports, such as the basketball players turning away from the hoop directly after a shot to perceive the spectators' reactions to their predicted hit instead of focusing on the outcome feedback. However, it remains unclear whether this value assignment is specifically driven by predicted hits or whether it reflects occasional shifts of attention toward motivational (or also neutral) stimuli in the absence of predicted errors.

Overall, within the bounds of stable individual preferences, the current findings highlight an integration of reliable previous outcome information with sensorimotor predictions of current outcomes to prioritize movement outcome feedback. In addition, sensorimotor predictions may also serve to indicate available attentional capacity, enabling the allocation of gaze to positive reinforcement cues when multiple stimuli compete for attention.

Conclusions

We studied information sampling in a goal-directed throwing task when targets with informational and motivational values were present in the scene. Targets were reliably fixated shortly after ball release but before outcome feedback. Our findings highlight that individual strategies and preferences play a central role in the prioritization of competing targets (other words), resulting in large interindividual differences in proportional target selection. Nevertheless, the analysis of the selection of fixation locations as a function of (predicted) task success revealed that individual baseline target choices were fine-tuned by both the outcome of the previous trial and the predicted outcome of the current trial. Our findings suggest that individuals primarily rely on outcome history to guide attention toward learning-relevant information while dynamically integrating sensorimotor predictions of current outcomes. In addition, sensorimotor predictions allow for shifts of selective attention to motivational cues when task demands are reduced. These findings contribute to a broader understanding of how previous action outcomes and sensorimotor predictions interact to allocate perceptual resources in the context of motor learning.

DATA AVAILABILITY

Source data are openly available at: https://doi.org/10.17605/OSF.IO/2AS9C.

SUPPLEMENTAL MATERIAL

Supplemental Material: https://doi.org/10.17605/OSF.IO/7XF8Z.

GRANTS

This research was supported by the Collaborative Research Center "Cardinal Mechanisms of Perception," funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation; SFB/TRR 135 TP B6 and B2) under Grant Number 222641018 and the Research Cluster "The Adaptive Mind," funded by the Excellence Program of the Hessian Ministry of Higher Education, Science, Research and the Arts.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

T.K.B., A.C.S., H. Müller, M.H., and L.K.M. conceived and designed research; T.K.B. performed experiments; T.K.B. analyzed data; T.K.B., A.C.S., and L.K.M. interpreted results of experiments; T.K.B. prepared figures; T.K.B. drafted manuscript; T.K.B., A.C.S., H. Müller, H. Maurer, M.H., and L.K.M. edited and revised manuscript; T.K.B., A.C.S., H. Müller, H. Maurer, M.H., and L.K.M. approved final version of manuscript.

REFERENCES

1. **Anguera JA**, **Seidler RD**, **Gehring WJ.** Changes in performance monitoring during sensorimotor adaptation. *J Neurophysiol* 102: 1868–1879, 2009. doi:10.1152/jn.00063.2009.
2. **Flanagan JR**, **Wing AM.** The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. *J Neurosci* 17: 1519–1528, 1997. doi:10.1523/JNEUROSCI.17-04-01519.1997.
3. **Joch M**, **Hegele M**, **Maurer H**, **Müller H**, **Maurer LK.** Brain negativity as an indicator of predictive error processing: the contribution of visual action effect monitoring. *J Neurophysiol* 118: 486–495, 2017. doi:10.1152/jn.00036.2017.
4. **Maurer LK**, **Maurer H**, **Müller H.** Neural correlates of error prediction in a complex motor task. *Front Behav Neurosci* 9: 209, 2015. doi:10.3389/fnbeh.2015.00209.
5. **Wolpert DM.** Computational approaches to motor control. *Trends Cogn Sci* 1: 209–216, 1997. doi:10.1016/S1364-6613(97)01070-X.
6. **Jordan MI**, **Rumelhart DE.** Forward models: supervised learning with a distal teacher. *Cognitive Science* 16: 307–354, 1992. doi:10.1207/s15516709cog1603_1.
7. **Kawato M.** Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9: 718–727, 1999. doi:10.1016/S0959-4388(99)00028-8.
8. **Miall RC**, **Wolpert DM.** Forward models for physiological motor control. *Neural Netw* 9: 1265–1279, 1996. doi:10.1016/S0893-6080(96)00035-4.
9. **Desmurget M**, **Grafton S.** Forward modeling allows feedback control for fast reaching movements. *Trends Cogn Sci* 4: 423–431, 2000. doi:10.1016/S1364-6613(00)01537-0.
10. **Wolpert DM**, **Ghahramani Z.** Computational principles of movement neuroscience. *Nat Neurosci* 3: 1212–1217, 2000. doi:10.1038/81497.
11. **Maurer LK**, **Joch M**, **Hegele M**, **Maurer H**, **Müller H.** Predictive error processing distinguishes between relevant and irrelevant errors after visuomotor learning. *J Vis* 19: 18, 2019. doi:10.1167/19.4.18.
12. **McDougle SD**, **Boggess MJ**, **Crossley MJ**, **Parvin D**, **Ivry RB**, **Taylor JA.** Credit assignment in movement-dependent reinforcement learning. *Proc Natl Acad Sci USA* 113: 6797–6802, 2016. doi:10.1073/pnas.1523669113.
13. **Parvin DE**, **McDougle SD**, **Taylor JA**, **Ivry RB.** Credit assignment in a motor decision making task is influenced by agency and not sensory prediction errors. *J Neurosci* 38: 4521–4530, 2018. doi:10.1523/JNEUROSCI.3601-17.2018.
14. **Brand TK**, **Schütz AC**, **Müller H**, **Maurer H**, **Hegele M**, **Maurer LK.** Sensorimotor prediction is used to direct gaze toward task-relevant locations in a goal-directed throwing task. *J Neurophysiol* 132: 485–500, 2024. doi:10.1152/jn.00052.2024.
15. **Gottlieb J**, **Hayhoe M**, **Hikosaka O**, **Rangel A.** Attention, reward, and information seeking. *J Neurosci* 34: 15497–15504, 2014. doi:10.1523/JNEUROSCI.3270-14.2014.
16. **Buswell GT.** *How people look at pictures: a study of the psychology and perception in art*. Chicago Press, 1935.
17. **Hoppe D**, **Rothkopf CA.** Multi-step planning of eye movements in visual search. *Sci Rep* 9: 144, 2019. doi:10.1038/s41598-018-37536-0.
18. **Najemnik J**, **Geisler WS.** Optimal eye movement strategies in visual search. *Nature* 434: 387–391, 2005. doi:10.1038/nature03390.
19. **Najemnik J**, **Geisler WS.** Eye movement statistics in humans are consistent with an optimal search strategy. *J Vis* 8: 4, 2008. doi:10.1167/8.3.4.
20. **Paulun VC**, **Schütz AC**, **Michel MM**, **Geisler WS**, **Gegenfurtner KR.** Visual search under scotopic lighting conditions. *Vision Res* 113: 155–168, 2015. doi:10.1016/j.visres.2015.05.004.
21. **Peterson MF**, **Eckstein MP.** Looking just below the eyes is optimal across face recognition tasks. *Proc Natl Acad Sci USA* 109: E3314–E3323, 2012. doi:10.1073/pnas.1214269109.
22. **Renninger LW**, **Verghese P**, **Coughlan J.** Where to look next? Eye movements reduce local uncertainty. *J Vis* 7: 6, 2007. doi:10.1167/7.3.6.
23. **Yang SC-H**, **Lengyel M**, **Wolpert DM.** Active sensing in the categorization of visual patterns. *eLife* 5: e12215, 2016 [Erratum in *eLife* 6: e25660, 2017]. doi:10.7554/eLife.12215.
24. **Land MF**, **Mennie N**, **Rusted J.** The roles of vision and eye movements in the control of activities of daily living. *Perception* 28: 1311–1328, 1999. doi:10.1068/p2935.
25. **Land MF**, **McLeod P.** From eye movements to actions: how batsmen hit the ball. *Nat Neurosci* 3: 1340–1345, 2000. doi:10.1038/81887.
26. **Triesch J**, **Ballard DH**, **Hayhoe MM**, **Sullivan BT.** What you see is what you need. *J Vis* 3: 86–94, 2003. doi:10.1167/3.1.9.
27. **Droll JA**, **Hayhoe MM**, **Triesch J**, **Sullivan BT.** Task demands control acquisition and storage of visual information. *J Exp Psychol Hum Percept Perform* 31: 1416–1438, 2005. doi:10.1037/0096-1523.31.6.1416.
28. **Itti L**, **Koch C.** A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Res* 40: 1489–1506, 2000. doi:10.1016/S0042-6989(99)00163-7.
29. **Liston DB**, **Stone LS.** Effects of prior information and reward on oculomotor and perceptual choices. *J Neurosci* 28: 13866–13875, 2008. doi:10.1523/JNEUROSCI.3120-08.2008.
30. **Sohn J**, **Lee D.** Effects of reward expectancy on sequential eye movements in monkeys. *Neural Netw* 19: 1181–1191, 2006. doi:10.1016/j.neunet.2006.04.005.
31. **Hayhoe MM.** Vision and action. *Annu Rev Vis Sci* 3: 389–413, 2017. doi:10.1146/annurev-vision-102016-061437.
32. **Schütz AC**, **Braun DI**, **Gegenfurtner KR.** Eye movements and perception: a selective review. *J Vis* 11: 9, 2011. doi:10.1167/11.5.9.
33. **Tatler BW**, **Hayhoe MM**, **Land MF**, **Ballard DH.** Eye guidance in natural vision: reinterpreting salience. *J Vis* 11: 5, 2011. doi:10.1167/11.5.5.
34. **Navalpakkam V**, **Koch C**, **Rangel A**, **Perona P.** Understanding how reward and saliency affect overt attention and decisions. *J Vis* 10: 32, 2010. doi:10.1167/10.7.32.
35. **Schütz AC**, **Trommershäuser J**, **Gegenfurtner KR.** Dynamic integration of information about salience and value for saccadic eye movements. *Proc Natl Acad Sci USA* 109: 7547–7552, 2012. doi:10.1073/pnas.1115638109.
36. **Stritzke M**, **Trommershäuser J**, **Gegenfurtner KR.** Effects of salience and reward information during saccadic decisions under risk. *J Opt Soc Am A Opt Image Sci Vis* 26: B1–B13, 2009. doi:10.1364/JOSAA.26.0000B1.
37. **Einhäuser W**, **Rutishauser U**, **Koch C.** Task-demands can immediately reverse the effects of sensory-driven saliency in complex visual stimuli. *J Vis* 8: 4, 2008. doi:10.1167/8.2.2.
38. **Henderson JM**, **Brockmole JR**, **Castelhano MS**, **Mack M**, **Gompel RPGV.** Visual saliency does not account for eye movements during visual search in real-world scenes. In: *Eye Movements*. Elsevier, 2007, p. 537–562.

39. **Daddaoua N**, **Lopes M**, **Gottlieb J.** Intrinsically motivated oculomotor exploration guided by uncertainty reduction and conditioned reinforcement in non-human primates. *Sci Rep* 6: 20202, 2016. doi:10.1038/srep20202.
40. **Xu-Wilson M**, **Zee DS**, **Shadmehr R.** The intrinsic value of visual information affects saccade velocities. *Exp Brain Res* 196: 475–481, 2009. doi:10.1007/s00221-009-1879-1.
41. **Fecteau J**, **Munoz D.** Salience, relevance, and firing: a priority map for target selection. *Trends Cogn Sci* 10: 382–390, 2006. doi:10.1016/j.tics.2006.06.011.
42. **Maurer LK**, **Maurer H**, **Hegele M**, **Müller H.** Can Stephen Curry really know? - Conscious access to outcome prediction of motor actions. *PLoS One* 17: e0250047, 2022. doi:10.1371/journal.pone.0250047.
43. **Cerf M**, **Frady EP**, **Koch C.** Faces and text attract gaze independent of the task: Experimental data and computer model. *J Vis* 9: 10, 2009. doi:10.1167/9.12.10.
44. **Takikawa Y**, **Kawagoe R**, **Itoh H**, **Nakahara H**, **Hikosaka O.** Modulation of saccadic eye movements by predicted reward outcome. *Exp Brain Res* 142: 284–291, 2002. doi:10.1007/s00221-001-0928-1.
45. **Horan M**, **Daddaoua N**, **Gottlieb J.** Parietal neurons encode information sampling based on decision uncertainty. *Nat Neurosci* 22: 1327–1335, 2019. doi:10.1038/s41593-019-0440-1.
46. **Ludwig CJH**, **Evens DR.** Information foraging for perceptual decisions. *J Exp Psychol Hum Percept Perform* 43: 245–264, 2017. doi:10.1037/xhp0000299.
47. **Stewart EEM**, **Ludwig CJH**, **Schütz AC.** Humans represent the precision and utility of information acquired across fixations. *Sci Rep* 12: 2411, 2022. doi:10.1038/s41598-022-06357-7.
48. **Land MF**, **Lee DN.** Where we look when we steer. *Nature* 369: 742–744, 1994. doi:10.1038/369742a0.
49. **Droll JA**, **Hayhoe MM.** Trade-offs between gaze and working memory use. *J Exp Psychol Hum Percept Perform* 33: 1352–1365, 2007. doi:10.1037/0096-1523.33.6.1352.
50. **Joch M**, **Hegele M**, **Maurer H**, **Müller H**, **Maurer LK.** Accuracy of motor error predictions for different sensory signals. *Front Psychol* 9: 1376, 2018. doi:10.3389/fpsyg.2018.01376.
51. **Müller H**, **Sternad D.** Decomposition of variability in the execution of goal-oriented tasks: three components of skill improvement. *J Exp Psychol Hum Percept Perform* 30: 212–233, 2004. doi:10.1037/0096-1523.30.1.212.
52. **Maurer LK**, **Joch M**, **Hegele M**, **Maurer H**, **Müller H.** Relevance of predictive and postdictive error information in the course of motor learning. *Neuroscience* 486: 77–90, 2022. doi:10.1016/j.neuroscience.2021.05.007.
53. **Brainard DH.** The psychophysics toolbox. *Spat Vis* 10: 433–436, 1997.
54. **Krakauer JW**, **Hadjiosif AM**, **Xu J**, **Wong AL**, **Haith AM.** Motor learning. *Compr Physiol* 9: 613–663, 2019 [Erratum in *Compr Physiol* 9: 1279, 2019]. doi:10.1002/cphy.c170043.
55. **Joch M**, **Döhring FR**, **Maurer LK**, **Müller H.** Inference statistical analysis of continuous data based on confidence bands—Traditional and new approaches. *Behav Res Methods* 51: 1244–1257, 2019. doi:10.3758/s13428-018-1060-5.
56. **Chen K**, **Cheng Y**, **Berkout O**, **Lindhiem O.** Analyzing proportion scores as outcomes for prevention trials: a statistical primer. *Prev Sci* 18: 312–321, 2017. doi:10.1007/s11121-016-0643-6.
57. **Bates D**, **Mächler M**, **Bolker B**, **Walker S.** Fitting linear mixed-effects models using lme4. *J Stat Soft* 67: 1–48, 2015. doi:10.18637/jss.v067.i01.
58. **Barr DJ**, **Levy R**, **Scheepers C**, **Tily HJ.** Random effects structure for confirmatory hypothesis testing: keep it maximal. *J Mem Lang* 68: 10.1016/j.jml.2012.11.001–278, 2013. doi:10.1016/j.jml.2012.11.001.
59. **Brauer M**, **Curtin JJ.** Linear mixed-effects models and the analysis of nonindependent data: a unified framework to analyze categorical and continuous independent variables that vary within-subjects and/or within-items. *Psychol Methods* 23: 389–411, 2018. doi:10.1037/met0000159.
60. **Hartig F.** DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models (Online). https://github.com/florianhartig/dharma [2025 Jan 13].
61. **Brehm L**, **Alday PM.** Contrast coding choices in a decade of mixed models. *J Mem Lang* 125: 104334, 2022. doi:10.1016/j.jml.2022.104334.
62. **Vaillancourt DE**, **Russell DM.** Temporal capacity of short-term visuomotor memory in continuous force production. *Exp Brain Res* 145: 275–285, 2002. doi:10.1007/s00221-002-1081-1.
63. **Foley NC**, **Kelly SP**, **Mhatre H**, **Lopes M**, **Gottlieb J.** Parietal neurons encode expected gains in instrumental information. *Proc Natl Acad Sci USA* 114: E3315–E3323, 2017. doi:10.1073/pnas.1613844114.
64. **Hayhoe MM.** Vision using routines: a functional account of vision. *Visual Cognition* 7: 43–64, 2000. doi:10.1080/135062800394676.
65. **Hayhoe MM**, **Shrivastava A**, **Mruczek R**, **Pelz JB.** Visual memory and motor planning in a natural task. *J Vis* 3: 49–63, 2003. doi:10.1167/3.1.6.
66. **Orquin JL**, **Mueller Loose S.** Attention and choice: a review on eye movements in decision making. *Acta Psychol (Amst)* 144: 190–206, 2013. doi:10.1016/j.actpsy.2013.06.003.
67. **Goh AX-A**, **Bennett D**, **Bode S**, **Chong TT-J.** Neurocomputational mechanisms underlying the subjective value of information. *Commun Biol* 4: 1346, 2021. doi:10.1038/s42003-021-02850-3.
68. **Brydevall M**, **Bennett D**, **Murawski C**, **Bode S.** The neural encoding of information prediction errors during non-instrumental information seeking. *Sci Rep* 8: 6134, 2018. doi:10.1038/s41598-018-24566-x.
69. **Bennett D**, **Bode S**, **Brydevall M**, **Warren H**, **Murawski C.** Intrinsic valuation of information in decision making under uncertainty. *PLoS Comput Biol* 12: e1005020, 2016. doi:10.1371/journal.pcbi.1005020.
70. **Clarke AD**, **Irons JL**, **James W**, **Leber AB**, **Hunt AR.** Stable individual differences in strategies within, but not between, visual search tasks. *Q J Exp Psychol (Hove)* 75: 289–296, 2022. doi:10.1177/1747021820929190.
71. **Sprague N**, **Ballard D**, **Robinson A.** Modeling embodied visual behaviors. *ACM Trans Appl Percept* 4: 11, 2007. doi:10.1145/1265957.1265960.
72. **Sullivan BT**, **Johnson L**, **Rothkopf CA**, **Ballard D**, **Hayhoe M.** The role of uncertainty and reward on eye movements in a virtual driving task. *J Vis* 12: 19, 2012. doi:10.1167/12.13.19.
73. **Gottlieb J.** Understanding active sampling strategies: empirical approaches and implications for attention and decision research. *Cortex* 102: 150–160, 2018. doi:10.1016/j.cortex.2017.08.019.
74. **Hayhoe MM**, **Matthis JS.** Control of gaze in natural environments: effects of rewards and costs, uncertainty and memory in target selection. *Interface Focus* 8: 20180009, 2018. doi:10.1098/rsfs.2018.0009.

Study III

Prepared as: **Do sensorimotor predictions provide top-down guidance of visual attention against bottom-up distraction?**

***Brand, T. K.**, Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. Do sensorimotor predictions provide top-down guidance of visual attention against bottom-up distraction? (prepared for submission)*

Do sensorimotor predictions provide top-down guidance of visual attention against bottom-up distraction?

Theresa K. Brand[a,c], Alexander C. Schütz[b,c], Hermann Müller[a,c], Heiko Maurer[a], Mathias Hegele[a,c] & Lisa K. Maurer[a,c]

[a] Neuromotor Behavior Laboratory, Department of Psychology and Sport Science,
Justus-Liebig-University Giessen, Germany

[b] Allgemeine und Biologische Psychologie, Philipps-Universität Marburg, Marburg, Germany

[c] Center for Mind, Brain, and Behavior, Universities of Marburg and Giessen, Germany

Correspondence concerning this article should be addressed to Theresa K. Brand,
Neuromotor Behavior Laboratory, Department of Psychology and Sport Science,
Justus-Liebig-Universität Giessen, Kugelberg 62, 35394 Giessen, Germany.
Email: theresa.brand@sport.uni-giessen.de.

Abstract

Previous research has extensively examined factors that guide gaze behavior in natural scenes and dynamic tasks (Hayhoe, 2017; Schütz et al., 2011; Tatler et al., 2011). While visual saliency plays a role in attracting visual attention (Itti & Koch, 2000), its influence can be overridden by task demands and top-down goals (Einhäuser et al., 2008; Henderson et al., 2007). In motor tasks, visual attention is thought to be guided in part by sensorimotor predictions — internal estimates of action outcomes of self-generated movements before external feedback is available — that help prioritize feedback-relevant information (Brand et al., 2024, 2025). The present study investigated how such predictions ("top-down") guide attention in competition with salient ("bottom-up") distractors in a semi-virtual goal-directed throwing task. Specifically, we assessed whether predicted task success (hit vs. miss) modulated the likelihood of fixating salient distractors during feedback-critical moments (i.e., between ball release and the arrival of outcome feedback). At the group level, (predicted) outcomes did not affect distractor fixations. However, a critical interaction emerged when accounting for performance level: high-performing participants fixated salient distractors less frequently in (predicted) misses than in hits, suggesting that motor expertise enables the contingent shielding of attention from salient distractors to prioritize action outcome feedback. In contrast, low performers showed no such modulation, likely due to lower predictive precision. Notably, this predictive modulation was modest compared to a robust, generalized suppression of distractors triggered by the presence of explicit task-relevant visual information (i.e., when ball trajectory information was still available at distractor onset).

Keywords: action monitoring, forward model, eye movements, sensorimotor prediction, throwing task

Significance Statement

We elucidate the potential benefits of internally generated action outcome predictions with respect to the optimization of information uptake in the context of motor learning. We demonstrate that, provided there is sufficient predictive precision as seen in high-performing individuals, outcome predictions can modulate saliency-driven attentional capture in feedback-critical situations. This modulation seems to be modest in comparison with the suppression of bottom-up influences triggered by the presence of explicit task-relevant visual input, though.

1 Introduction

Everyday behavior requires us to navigate a continuous stream of sensory information, particularly visual input, of which only a fraction is relevant to our current goals (Cosman & Vecera, 2014). To act efficiently, the visual system must therefore select where to look, prioritizing information that is useful for ongoing tasks while filtering out irrelevant input. Research on gaze target selection has shown that saccadic decisions arise from an interaction between top-down factors such as task goals and bottom-up saliency (for reviews, see Hayhoe, 2017; Schütz et al., 2011; Tatler et al., 2011). Visual saliency is sometimes solely described as a physical property of a visual stimulus. Contrasts in luminance, color, or orientation make objects stand out from their surroundings (Itti & Koch, 2000). Beyond these static features, however, the most potent attractors of attention are stimuli that pop out temporally, like the abrupt onset of a stimulus in an otherwise static display (Yantis & Jonides, 1984). That the sudden onset or motion changes of stimuli typically capture attention is indicated by interference with ongoing tasks (e.g., Folk & Remington, 2015; Jonides & Yantis, 1988; Schreij et al., 2008). Jonides and Yantis (1988) showed that in a visual search task, a letter with an abrupt onset was always selected first, even when there was no benefit for the observer in allocating attention to the onsetting item.

Yet the influence of salient stimuli is not obligatory. According to Priority Map Theory, attentional selection is governed by the dynamic weighting of goal-related and stimulus-driven signals (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Folk et al., 1992). This process assigns priority values to potential gaze locations, and the site with the highest integrated value becomes the next gaze target. For instance, during free viewing of natural scenes, where observers scan an image without a specific goal, gaze is guided primarily by the physical prominence of objects. This behavior stands in stark contrast to active search, where observers look for a particular target. Here, visual saliency fails to explain eye movements (Einhäuser et al., 2008). During such purposeful behavior, task demands can greatly diminish or even eliminate saliency-driven capture (Einhäuser et al., 2008; Henderson et al., 2007).

Such top-down suppression is critically important in naturalistic motor tasks in the context of motor learning. Successful action control depends on precisely timed acquisition of feedback about the outcome of one’s movements — for example, observing whether and how a basketball strikes the hoop after a free throw. In these moments, salient but irrelevant events (e.g., spectators waving their arms, or a flashing advertisement) have the potential to draw attention away from the action outcome, disrupting information uptake and impairing motor learning. Especially in the case of motor errors, the ability to resist (bottom-up) distraction becomes a functional necessity as outcome feedback is crucial for deriving suitable adjustments for future actions. Thus, beyond general goal-directed gaze control, efficient motor performance often requires shielding attention from bottom-up saliency in situations where feedback is critical.

Initial evidence suggests that sensorimotor predictions may contribute to such top-down control. Sensorimotor predictions arise from internal forward models that estimate the sensory consequences of actions based on employed motor commands and sensory information about the current state of the body and the environment (Flanagan & Wing, 1997; Kawato, 1999; Wolpert, 1997). They enable the central nervous system to assess deviations between predicted and intended sensory action effects before actual sensory feedback becomes available, allowing it to detect errors before they occur. Recent research suggests that sensorimotor predictions play a crucial role not only in internal error monitoring but also in guiding gaze allocation during goal-directed movements. These predictions guide predictive saccades toward expected action effect locations, with chosen positions providing high informational value for feedback processing (Brand et al., 2024). Moreover, when multiple potential gaze targets compete for attention, outcome predictions help assign value to gaze locations, prioritizing feedback-relevant targets in unsuccessful trials, while predicted success allows gaze to shift toward reward-associated cues (Brand et al., 2025).

These observations raise an important question that has not yet been addressed: Can sensorimotor predictions not only guide gaze toward informative locations but also suppress bottom-up attentional capture when it threatens the processing of feedback-critical information? In terms of priority-map theory, this would mean that prediction-based value signals can dynamically (depending on predicted task success) reduce the weight of saliency-driven inputs when they conflict with the need to process movement feedback.

The present study examined this possibility in a semi-virtual throwing task in which salient distractors occasionally appeared during the critical feedback interval after ball release. Because participants should have learned to predict the outcome of their throws in a training session (Jordan & Rumelhart, 1992), each trial in the experimental sessions was assumed to be informed by an internal estimate of success or failure. We tested whether the frequency of distractor fixations differed between predicted hits and predicted misses. Building on the findings from Brand et al. (2025), we hypothesized that predicted errors would increase the value of outcome feedback, strengthening top-down control and thereby reducing the likelihood of saliency-driven gaze shifts toward distractors. Predicted hits, by contrast, were expected to yield weaker top-down weighting of the feedback location and hence greater susceptibility to distraction.

2 Materials and Methods

2.1 Participants

We recruited 45 participants (29 females, 16 males; mean age: 26.62 ± 4.21 years, range: 19–36) from the student population of the Justus Liebig University, Giessen, Germany. All participants were right-handed, had normal or corrected-to-normal vision, and reported no history of upper limb injuries. Each participant completed the study over three days, with sessions lasting approximately one hour each. Compensation included either course credit or a monetary payment. The study adhered to the ethical standards outlined in the Declaration of Helsinki (2013, except §35, pre-registration) and was approved by the Ethical Review Board of the Justus Liebig University, Giessen. Written informed consent was obtained from all participants before the study.

We excluded two participants due to their strategy to only look at the ball release point and not perceive any other visual feedback (exclusion criteria precisely defined in the chapter *2.4 Data Processing and Analysis*), resulting in a sample size of 43 participants for the analyses.

2.2 Task and Setup

Participants performed a complex, goal-directed throwing task inspired by the British pub game "Skittles". Traditionally, Skittles involves swinging a ball attached to the top of a post by a string to knock over target objects positioned on the opposite side (Fig. 1*C*). The task requires a ballistic movement, preventing online corrections during execution, and features a temporal gap between movement completion and feedback about the action outcome. This structure allows participants to form internal predictions about their performance before receiving outcome feedback. Skittles also represents a redundant motor task in which the same result can be achieved with infinitely many combinations of release angle and velocity. Moreover, the nonlinear mapping between execution parameters and outcomes makes accurate predictions challenging and resistant to explicit cognitive calculation.

In the semi-virtual version of the task (see also Joch et al., 2017; Maurer et al., 2015), participants performed physical, ballistic throws using a metal lever (manipulandum) in a movement similar to a frisbee toss. However, the resulting action effect — the ball's trajectory around the post — was displayed only on a computer monitor (Dell Alienware AW2521HF; active screen size: 37.7 × 30.2 cm, full-screen size: 55 x 31 cm; resolution: 1280 x 1024 pixels; refresh rate: 120 Hz; RGB background: [130, 130, 130]; Fig. 1*A*). The monitor presented a virtual environment including a real-time representation of the manipulandum's position, a green virtual ball (RGB: [25, 153, 0]), a gray center post (RGB: [180, 180, 180]), a gray target (RGB: [180, 180, 180]), and a designated start position (Fig. 1*B*), providing an overhead view of the task environment. The participants' heads were not fixed with a chin- or forehead rest, allowing slight variation in eye-to-screen distance. At a typical eye-to-screen distance of 70 cm, stimuli subtended visual angles of 0.7° for the ball and the target, 3.4° for the center post, and 0.9° for the start position.

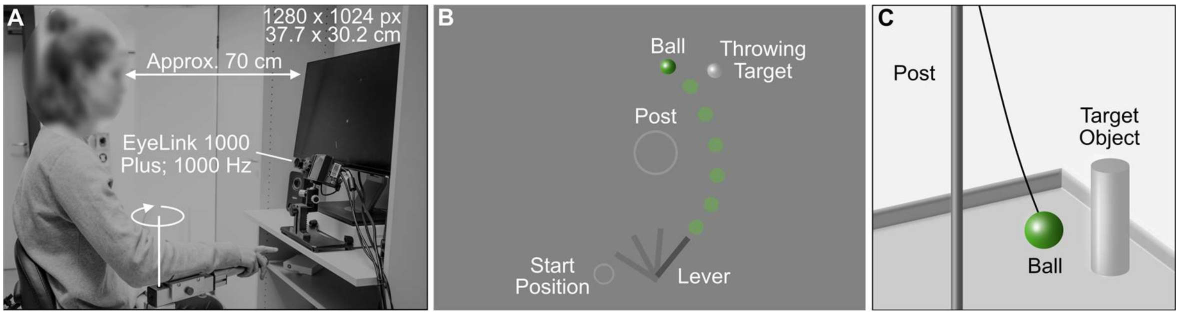


Figure 1. *A*: setup of the semi-virtual Skittles task. Participants performed throwing movements using a metal lever, resembling a frisbee toss. The virtual ball was released by lifting the index finger from an electrical contact sensor at the tip of the lever. The resulting action effects were displayed on a screen positioned in front of the participant. Eye movements were recorded throughout task execution using an Eyelink 1000 Plus with a desktop mount running in remote mode. *B*: task space displayed on-screen. The starting position for the throwing movements was located left of the lever's vertical axis. Upon release, a green ball followed an elliptical trajectory around a gray center post and toward a gray throwing target. *C*: sketch of the original Skittles game, where a ball attached to a post by a string is swung around the post, aiming to hit (a) target object(s) positioned on the opposite side.

Ball pickup and release were controlled by placing or lifting the index finger on or off a contact sensor at the tip of the lever. The manipulandum’s angle and velocity at the moment of ball release (t_{Release}), which defined the ball’s trajectory, were measured using a 12-bit (0.09° resolution) magnetic angle sensor integrated into the manipulandum, sampling at 1000 Hz. Trajectories were computed for each throw using a physical model of the Skittles task (Müller & Sternad, 2004), with the following parameters: Center post – radius $r = 0.25$ m, position $x = 0.0$ m, $y = 0.0$ m; throwing target – radius $r = 0.05$ m, position $x = 0.8$ m, $y = 0.9$ m; ball – radius $r = 0.05$ m, mass $m = 0.25$ kg; lever – length $l = 0.26$ m, position $x = 0.0$ m, $y = -1.36$ m; spring constant $D = 1.0$ N/m. To ensure an appropriate level of challenge with regard to task completion over the course of the experiment, the discrepancy between the actual and optimal release velocity for a given release angle was slightly increased in every trial. As a result, participants had to execute the movement with greater precision. The time between ball release and outcome feedback (time of minimum distance between the ball and the throwing target – t_{dmin}) varied across trials, averaging 981 ms (*SD* = 107 ms).

In the regular task version, participants could see the ball moving toward the throwing target after ball release. A collision (hit) occurred when the minimum distance (d_{min}) between the ball's trajectory and the target center was equal to or less than twice the ball/target radius. In these cases, the target was pushed away from its position, and the sound of two colliding billiard balls was heard. Depending on the collision angle, the ball bounced off the target at an angle consistent with energy transmission laws for rigid objects (akin to billiard balls). In trials where d_{min} exceeded twice the radius of the ball/target ($d_{\text{min}} > 0.1$ m), the ball missed the target.

During task execution, eye position signals of the participants' right eye were recorded at 1000 Hz using an EyeLink 1000 Plus (on a desktop mount; SR Research, Ottawa, Canada) running in remote mode. This mode allows for precise eye tracking without requiring physical head stabilization, supporting natural task engagement. The experimental software for task execution and data synchronization (eye tracking and throwing movements) was developed with MATLAB R2021b (The Mathworks, Inc., Natick, MA, USA) and the Psychophysics Toolbox 3.0.18 (Brainard, 1997).

Participants sat on a height-adjustable stool to align their horizontal line of vision with the screen center. The manipulandum, cushioned with foam and equipped with a forearm rest, was mounted on an adjustable stand with its vertical axis aligned with the participant's right elbow, allowing arm movements restricted to horizontal-plane rotations around this fixed axis. The laboratory lighting was controlled with blinds and artificial lights to maintain consistent illumination throughout the experiment.

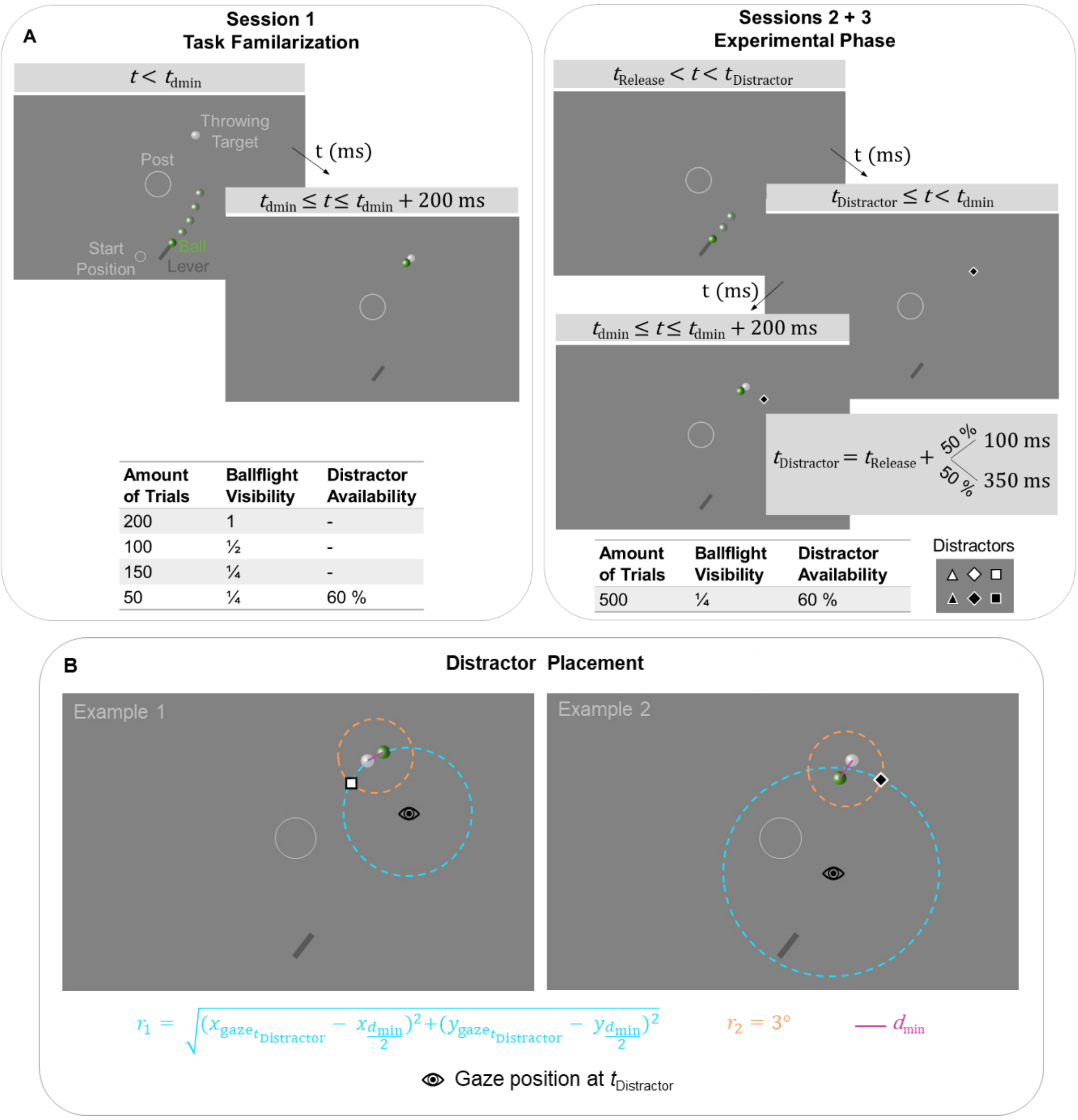
2.3 Procedure and Study Design

Participants executed the experimental task over three days, completing 500 throws per day. At the start of *session 1*, the task was explained using a miniature model of the original Skittles game. To familiarize participants with the semi-virtual task, they completed ten test trials before beginning the experimental schedule. Each session began with a 13-point eye-tracker calibration and validation procedure. Calibration was accepted only if the average error remained below 0.5° and the maximum error below 1°. Fixations on each calibration target were manually confirmed by the experimenter, and the calibration targets were displayed in random order.

At the beginning of each trial, participants placed their right index finger on the electrical contact sensor at the tip of the lever to pick up the virtual ball (the ball is visually attached to the virtual equivalent of the lever). They initiated each trial by moving the tip of the virtual lever into the start position left of its fixed end, while simultaneously fixating on this point. A traffic light-like sequence at the start position — red, then yellow, then green — indicated when the throw could begin. Starting in front of their upper bodies, participants threw the virtual ball by moving the manipulandum outward in a motion resembling a Frisbee toss. Lifting the finger from the contact sensor triggered the ball's release, launching it in a counter-clockwise path around the center post. The traffic light sequence at the start position prevented fast, rhythmic execution of subsequent trials, preserving the discrete nature of each trial. After every block of 100 trials, participants were given a short rest, and the eye tracker was recalibrated.

Session 1 was designed to develop task expertise. During the first 200 trials, participants received continuous visual feedback showing the full trajectory of the virtual ball. This visual feedback was then progressively reduced: In the next 100 trials, only the first half of the trajectory was shown, and in the final 200 trials of *session 1*, only the first quarter was visible. On all trials in which only partial ball trajectories were visible, participants received static outcome feedback for 200 ms at the time of the minimum distance between the ball and the throwing target (t_{dmin}), showing the ball's position at that moment (Fig. 2*A*, left panel). Across all trials, participants received additional acoustic feedback (the sound of two colliding billiard balls at t_{dmin} for hits and its absence for misses). To prepare participants for the conditions in the experimental sessions (*sessions 2 and 3*), the final 50 trials of *session 1* introduced additional visual manipulations. In 60% of these trials, a salient distractor appeared. Additionally, the target was masked immediately after ball release and reappeared only at t_{dmin}, together with the ball's current position to provide outcome feedback (see Fig. 2*A*, right panel). This temporary absence of the target reduced fixation stability and facilitated oculomotor capture by distractors, thereby mimicking the classic gap paradigm (Saslow, 1967). The distractor appeared pseudo-randomly either 100 or 350 ms after release (with a ±30 ms jitter) and remained visible until the end of the static feedback display. These two time points were chosen to probe different stages of the prediction process: at 100 ms, predictions were unlikely to have formed, whereas at 350 ms, prediction-related effects were expected to emerge. This temporal distinction is supported by previous studies using the same task and EEG measurements (e.g., Joch et al., 2017; Maurer et al., 2015). Specifically, these studies report that predictive error perception is indexed by a negative deflection in fronto-central brain regions, termed the Error-Related Negativity (ERN; Gehring et al., 1993), peaking approximately 250 ms after ball release in erroneous throws. The late distractor onset, therefore, systematically follows the critical time window in which this neural signature of predictive outcome valuation is typically manifest (200-350 ms after ball release in Maurer et al., 2015).

The distractor pseudo-randomly took one of three shapes (square, diamond, or triangle) and one of two colors (black with white border or white with black border – equal luminance contrast from background), to avoid habituation. For the same reason, distractors were shown only in 60% of the trials. The distractor's surface area matched that of the ball and the target. Distractor location was determined relative to the feedback location. Specifically, a circle was constructed around the current gaze position at distractor onset, passing through the midpoint between the ball and the target at t_{dmin} ($\frac{d_{\text{min}}}{2}$), which served as an approximation of the feedback location. The distractor was then placed pseudo-randomly at one of the two intersection points between this circle and a second circle centered on $\frac{d_{\text{min}}}{2}$ with a radius of 3° (Fig. 2*B*). In cases where the current gaze position at $t_{\text{Distractor}}$ was closer than 3° to $\frac{d_{\text{min}}}{2}$, the two constructed circles did not intersect. In such cases, the distractor was displayed at a fixed horizontal distance of 3° to the left or right of $\frac{d_{\text{min}}}{2}$. The chosen method ensured that the angular distance between the distractor and the approximated feedback point was constant. The distance between the distractor and the current gaze position at distractor onset varied across trials.



Amount of Trials	Ballflight Visibility	Distractor Availability
200	1	-
100	½	-
150	¼	-
50	¼	60 %

Amount of Trials	Ballflight Visibility	Distractor Availability
500	¼	60 %

Figure 2. *A:* experimental schedule and design. Participants practiced the task over 500 trials in *session 1*, during which continuous visual feedback on the ball trajectory was gradually reduced

(only proportions of the ball flight were visible on each trial) so that only static outcome feedback was provided for 200 ms at the time of the minimum distance between the ball and the throwing target (t_{dmin}). In the final 50 trials of session 1, salient distractors were introduced in 60% of the trials to prepare participants for the conditions of the experimental phase. In *sessions 2 and 3*, distractors appeared in 60%, pseudo-randomly, either 100 or 350 ms after ball release (with a ±30 ms jitter). Distractors further varied pseudo-randomly in shape (square, diamond, triangle) and color (black with white border or white with black border), to prevent habituation. Participants were instructed to hit the throwing target as often as possible. *B:* distractor placement. Distractor location was determined relative to the feedback location. Specifically, a circle was constructed around the current gaze position at distractor onset ($t_{\text{Distractor}}$), passing through the midpoint between the ball and the target at t_{dmin} ($\frac{d_{\text{min}}}{2}$), which served as an approximation of the feedback location. The distractor was then placed at one of the two intersection points between this circle and a second circle centered on $\frac{d_{\text{min}}}{2}$ with a radius of 3°. This method ensured that the angular distance between the distractor and the approximated feedback point was constant. The distance between the distractor and the current gaze position at distractor onset varied across trials.

Sessions 2 and 3 constituted the experimental phase, where participants performed the task under the same conditions as in the final phase of *session 1*. Before starting *session 2*, participants again completed 10 test trials to reacquaint themselves with the task dynamics. Throughout the experiment, participants were instructed to aim for the target in every trial and to beat their previous high score in each new block of 100 trials. Additionally, they were informed about the appearance of the distractors before each session as follows: "In some (*sessions 2 and 3*)/the last 50 trials (*session 1*), additional visual stimuli might appear that are not relevant to task completion".

2.4 Data Processing and Analysis

Data processing and analyses were conducted using MATLAB R2021a. As a measure of task performance, we calculated the participants' hit rates across blocks of 100 trials throughout the experiment.

For the analysis of the eye-tracking data, we excluded trials, in which (a) the center post was hit, (b) the ball release trigger was missing in the eye-tracking data, preventing synchronization with the ball trajectory in the respective trials, and (c) in in cases of poor eye-tracking data quality (i.e., precision or accuracy >2°, track loss, or artifacts). Additionally (d), we excluded trials in which participants' gaze remained centered around the start position throughout the entire trial, reflecting a special strategy used by some participants who relied on proprioceptive as well as auditory rather than visual feedback. These exclusion criteria led to an overall data loss of 14.07%, including 2.87% post hits, 2.43% due to technical issues, and 8.78% due to participant strategy. Following the subsequent exclusion of two participants who consistently employed the gaze-centered strategy (criterion d), the final data loss within the remaining sample was 10.96%. The decomposition of the eye tracking data into saccades and fixations was carried out with the built-in EyeLink algorithm with thresholds set to: velocity (> 30 °/s), motion (0.1°), and acceleration (> 8,000 $°/s^2$).

To examine the prevalence of distractor fixations for each participant *(sessions 2 and 3)*, we searched for trials in which a saccade was made into a 1.5° target window around the distractor center, in the time window between $t_{\text{Distractor}}$ and t_{dmin}. Note that the radius of 1.5° represents the midpoint between the estimated feedback location at $\frac{d_{\text{min}}}{2}$ and the distractor center. Thus, only if the gaze was closer to the distractor than to the feedback location in a trial, a distractor was registered as being fixated. To validate the 1.5° criterion for distractor fixations, we computed the relative position of each detected distractor fixation along the distractor–feedback axis. Specifically, we calculated the proportion of the distance between the fixation and the distractor relative to the distance between the fixation and the midpoint between the distractor and the feedback ($\frac{\overline{FD}}{\overline{Fd}}$, where *F* represents the fixation location, *D* the location of the distractor, and d the location of $\frac{d_{\text{min}}}{2}$, i.e., the feedback location). The results of this sanity check are presented in Figure S1 in the Supplemental Material. A value of 1 indicates equidistance; values < 1 indicate gaze was closer to the distractor. We expected left-skewed histograms with values clustered toward zero, indicating reliable fixation on the distractor and not on predicted feedback locations.

As the main dependent measure, we calculated the difference in distractor fixation rates between hits and misses. Action outcomes were categorized based on d_{min}, with hits defined as $d_{\text{min}} \leq 0.1$ m and misses as $d_{\text{min}} > 0.1$ m.

2.4.1 Post Hoc Analyses

Due to the overall absence of overt differences in proportional distractor fixations between hits and misses across both distractor timings ($t_{\text{Distractor}}$), we conducted a more fine-grained post hoc analysis. We hypothesized that trials resulting in narrow outcomes—throws close to the hit–miss boundary—are inherently more difficult to predict (consistent with fixation-duration patterns after feedback seen in Brand et al., 2025), potentially obscuring effects that would otherwise emerge for clear outcomes. To address this, hit and miss trials were further separated into clear and narrow outcomes according to d_{min} in m (clear hits = [0; 0.05], narrow hits =]0.05; 0.1], narrow misses =]0.1; 0.15], clear misses =]0.15; 0.2]). Given the well-documented dependency of predictive abilities on task expertise (Jordan & Rumelhart, 1992; Maurer et al., 2015), participants' throwing performance was included as a critical factor. Participants were divided into two performance groups based on the median hit rate across experimental sessions 2 and 3 (59.80%): low performers (hit rate < 60%, $n = 22$) and high performers (hit rate ≥ 60%, $n = 21$). To more clearly isolate potential effects of sensorimotor expertise, the first 100 trials of *session 2* were treated as a warm-up phase and excluded from analysis. Only thereafter did mean hit rates across the sample exceed 50 % in every subsequent block of 100 trials. Proportional distractor fixation rates were then compared across the four outcome bins, separately for the two distractor onset timings (100 and 350 ms after release), and for both performance groups.

To more precisely disentangle behavior as a function of within-trial timing, we conducted an additional analysis that categorized distractor fixations by saccadic latency relative to distractor onset: reactive (< 150 ms) versus delayed (≥ 150 ms).

2.5 Statistical Analysis

Task performance, measured as hit rate (%), was analyzed across blocks of 100 trials using a repeated-measures ANOVA. Normality of residuals was checked with Q–Q plots, and sphericity was tested using Mauchly's W. To address violations of the sphericity assumption, the Greenhouse-Geisser correction was applied. Post hoc comparisons were Holm-corrected.

To examine whether overall distractor fixation rates were related to task performance (hit rate across *sessions 2 and 3*), a Pearson correlation was computed. To examine differences in fixation rates between successful and unsuccessful trials separately for both distractor timings, individual mean hit–miss differences were tested against zero using one-sample *t*-tests. Assumptions of normality were checked with Q–Q plots. Analyses, including assumption checks, were conducted in JASP (v.0.18.3.0, The JASP Team, Amsterdam, The Netherlands).

For a more fine-grained analysis of proportional distractor fixations, we fitted binomial logistic mixed-effects models (GLMMs) using the glmer function from the lme4 package (Bates et al., 2015) in R 4.4.1 (R Foundation for Statistical Computing, Vienna, Austria). These models are appropriate for proportion data (number of fixations out of total trials), handle non-normality and heterogeneity, and ensure predicted values fall within [0,1] via the logit link. Subject-level variability was modeled as a random intercept, with maximal random-effects structures specified initially and simplified as needed to achieve convergence and avoid singular fits. Two GLMMs were run: (1) a model examining the effects of action outcome (clear/narrow hit, clear/narrow miss), $t_{\text{Distractor}}$ (early vs. late), and group (high vs. low performers), including their interactions; and (2) a model in which saccade type (reactive vs. delayed) was further included. This second model included all main effects and interactions up to the three-way level for all four factors. The four-way interactions were excluded.

Model diagnostics were conducted using the DHARMa package (Hartig, 2024), which simulates residuals to assess model fit. Diagnostics confirmed that all models were well-suited to the data. To aid interpretation of main effects, contrast coding was applied for two-level factors (Brehm & Alday, 2022). For multi-level factors, estimated marginal means and pairwise contrasts were computed with the emmeans package (Lenth, 2023). Post hoc contrasts were corrected for multiple testing using Tukey adjustment. The significance of fixed effects was assessed using Wald *z*-statistics.

The alpha level for all statistical tests was set at $\alpha = 0.05$, and all reported *P* values correspond to two-sided testing.

3 Results

3.1 Task Performance

Analysis of hit rates across blocks of 100 trials revealed significant performance changes throughout the experiment, $F(7.07,297.12) = 34.61$, $P < 0.001$, $\eta_p^2 = 0.45$ (Fig. 3). After a significant improvement in hit rates from block 1 (33.81 ± 16.18%) to block 2 (49.60 ± 15.29%), task performance stabilized as the proportion of visible ball trajectory was gradually reduced over the rest of *session 1*. The introduction of distractors in 60% of the final 50 trials of *session 1* led to a small, non-significant performance decline. In *session 2*, conducted under the same conditions as the final trials of *session 1*, participants showed continued improvement (e.g., block 6 vs. 8: $P < .001$). After a small warm-up decrement (block 10 vs. 11: $P = 0.01$), participants showed further performance gains in *session 3* (e.g., block 11 vs. 13: $P < 0.001$). Across the experimental *sessions 2 and 3*, participants achieved an average hit rate of 59.01 ± 13.38%.

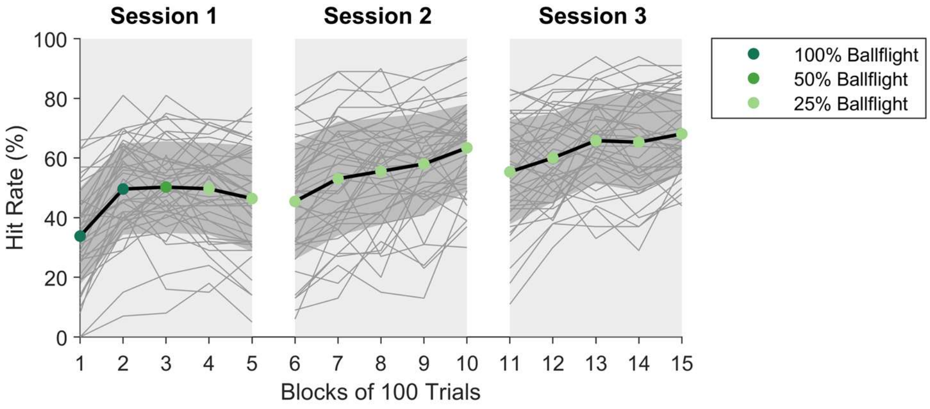


Figure 3. Development of task performance across the experiment for individual participants (gray lines) and the overall sample (black line). Shaded areas represent standard deviations, illustrating interindividual variability in hit rate trajectories. Throughout the experiment, continuous visual feedback was reduced, and only partial ball trajectories were visible, indicated by dots in shades of green. Distractors were introduced in 60% of trials starting from the final 50 trials of *session 1*.

3.2 Distractor Fixations

Distractors were fixated in 31.51% of trials on average, with substantial inter-individual variability (SD = 22.68%). This fixation rate did not correlate with overall task performance (hit rate in *sessions 2 and 3*; $r = -0.04$, $P = 0.78$; Fig. 4). One-sample *t*-tests revealed no significant deviation of the mean difference in distractor fixation rates between hits and misses from zero for both distractor onset timings (early distractor: $M = 0.00 \pm 0.08$, $t(42) = 0.09$, $P = 0.93$, $d = 0.01$; late distractor: $M = 0.00 \pm 0.07$, $t(42) = -.38$, $P = 0.71$, $d = -0.06$). Analyses of saccade latencies showed that the early distractor was fixated on average 301.23 ± 82.02 ms after onset, whereas the late distractor was fixated 244.17 ± 70.21 ms after onset.

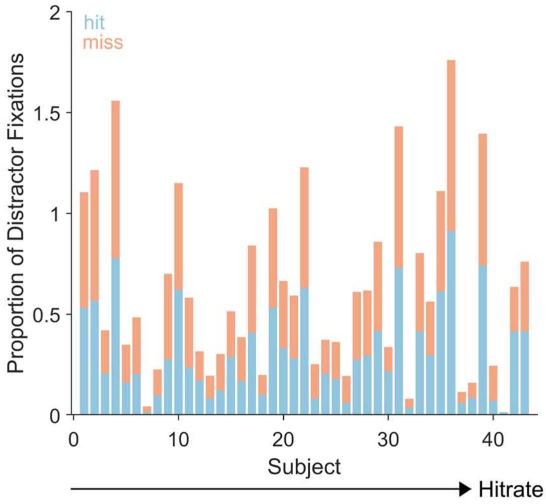


Figure 4. Proportion of distractor fixations in hits and misses for each participant, ordered by increasing hit rate. Proportions can sum to a maximum of two, indicating that the distractor was fixated in every trial a distractor appeared.

A more fine-grained analysis using a GLMM with group (low vs. high performers), $t_{\text{Distractor}}$ (early vs. late) and action outcome (clear hit, narrow hit, narrow miss, clear miss) as factors revealed no significant overall effects of group (Wald $z = -0.26$, $P = 0.80$), $t_{\text{Distractor}}$ (Wald $z = -0.24$, $P = 0.81$), or action outcome on distractor fixation rates (reference condition: clear hit; narrow hit: Wald $z = 1.26$, $P = 0.21$, narrow miss: Wald $z = -1.64$, $P = 0.10$, clear miss: Wald $z = -0.51$, $P = 0.61$). A significant group × action outcome interaction for clear miss trials indicates that high performers exhibited fewer distractor fixations than low performers in clear misses (Wald $z = -2.44$, $P = 0.02$). Post Hoc comparisons confirmed that only high performers fixated the distractor significantly less in clear misses compared to clear hits (Wald $z = 3.49$, $P < 0.01$) and narrow hits (Wald $z = 3.23$, $P = 0.01$; Fig. 5).

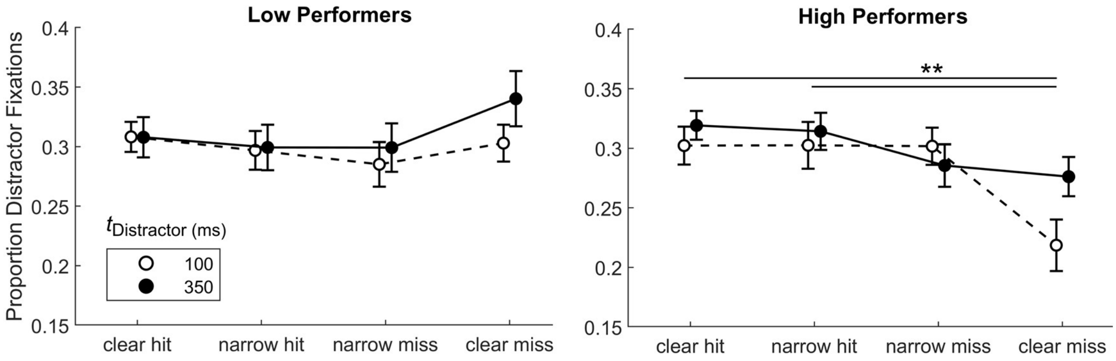


Figure 5. Proportion of distractor fixations across action outcomes (clear hit, narrow hit, narrow miss, clear miss) separately for early and late distractors ($t_{\text{Distractor}}$; appearance either 100 or 350 ms after ball release) as well as low and high performers. Values are means ± bootstrapped SE; $^{**}P < .01$.

Adding saccade type (reactive vs. delayed) as an additional factor to the GLMM to focus on within-trial timing revealed a strong interaction between saccade type and $t_{\text{Distractor}}$ (Wald $z = -18.53$, $P < .001$). This interaction indicates that the difference in probabilities between delayed and reactive responses depends critically on when the distractor appears (Fig. 6*A*). For the late distractor onset, the difference between delayed and reactive saccades was relatively small: reactive saccades toward the distractor were only slightly less likely than delayed ones (model-predicted fixation probability $P_{\text{Fixation}} = 0.09$ vs. 0.13). For the early distractor onset, however, this difference was highly pronounced. Reactive saccades got strongly suppressed, while delayed saccades became considerably more likely ($P_{\text{Fixation}} = 0.02$ vs. $P_{\text{Fixation}} = 0.23$). Taken together, the combination of an early-onset distractor and a reactive response was the least frequently observed behavior. Figure 6*B* illustrates the spatial distribution of gaze positions at the moments when early and late distractors appeared. Looking at the right panels of Figure 6*A*, it is descriptively evident that action outcome modulated distractor fixation rate only for delayed, but not reactive, saccades within the high-performance group.

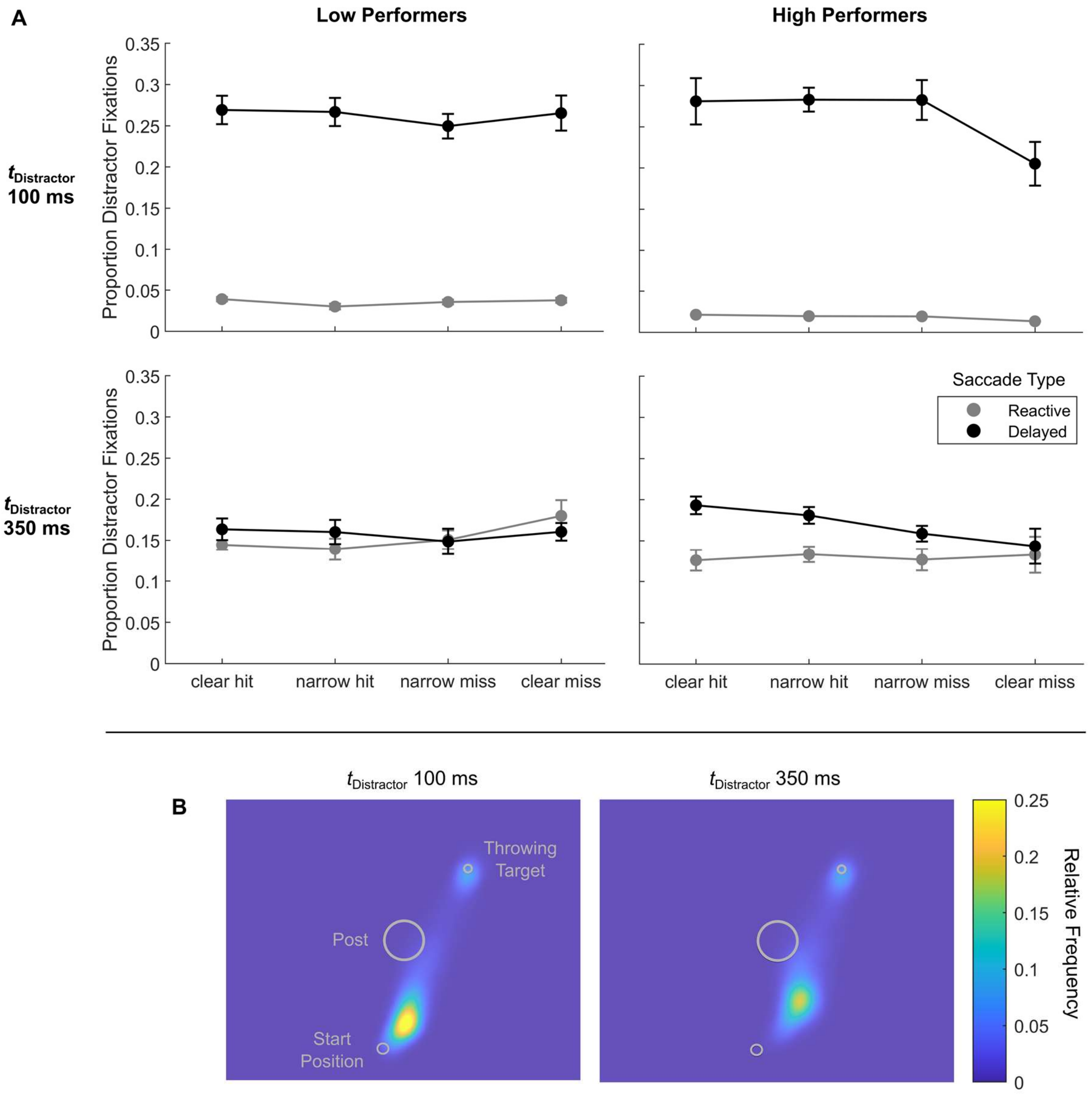


Figure 6. *A:* proportion of distractor fixations across action outcomes (clear hit, narrow hit, narrow miss, clear miss) separately for early and late distractors ($t_{\text{Distractor}}$; appearance either 100 or 350 ms after ball release), low and high performers, as well as reactive and delayed saccades. Values are means ± bootstrapped SE. *B:* heatmaps showing gaze positions at distractor onsets.

4 Discussion

Previous research has shown that the influence of saliency on gaze target selection can be suppressed when task demands require it (e.g., Einhäuser et al., 2008; Henderson et al., 2007). We hypothesized that this suppression is modulated dynamically by sensorimotor predictions, whereby predicted movement errors would strengthen top-down control to prioritize task-critical outcome feedback, consequently suppressing attentional capture by irrelevant distractors. Predicted hits, by contrast, were expected to yield weaker top-down weighting of outcome feedback and hence greater susceptibility to distraction. To test this, we examined whether predicted task success (hit vs. miss) modulates the frequency of fixating salient distractors presented during feedback-critical moments (i.e., after ball release) in a goal-directed throwing task.

4.1 Sensorimotor Predictions Modulate Saliency-driven Attentional Capture, but Only for Higher Skilled Individuals

Contrary to expectations, the overall proportion of distractor fixations did not differ between predicted hits and predicted misses at the group level, irrespective of the distractor onset timing (100 vs. 350 ms after release). This initial finding suggested that there is no influence of sensorimotor predictions on bottom-up attraction to salient stimuli. Across participants, distractors were fixated in approximately one-third of trials, with substantial interindividual variability that was unrelated to overall task performance. Stable individual differences in gaze target selection are well documented (e.g., de Haas et al., 2019). Li and Chen (2018) specifically demonstrated that individuals differ not only in their sensitivity to semantic content but also in their attraction to low-level visual features, such as color or luminance, which fits with the observed person-specific baseline preferences toward salient distractors.

However, a fine-grained analysis accounting for expertise and outcome prediction difficulty revealed a critical interaction: High performers (those with higher overall hit rates in the experimental sessions according to a median split) showed selectively reduced distractor fixations in clear miss trials compared to clear and narrow hit trials, whereas low performers showed no such systematic differentiation between outcomes. Thus, with sufficient task expertise, individuals can shield attention from salient, task-irrelevant stimuli, specifically when sensorimotor predictions signal a high need for action outcome feedback to derive suitable movement adjustments for the next trial. This result aligns with the idea that experts possess more accurate and reliable internal forward models (Jordan & Rumelhart, 1992; Maurer et al., 2015). Low performers, presumably lacking sufficient predictive accuracy, were unable to contingently modulate saliency-driven attentional capture based on trial outcome.

4.2 Temporal Dynamics of Top-Down Control

In the present study, distractors were presented at two different time points during the interval between ball release and action outcome feedback. We hypothesized that modulation of distractor fixation frequency as a function of trial outcome would occur primarily for late distractor onsets (350 ms after release), as outcome predictions were expected to be incomplete at the earlier time point (100 ms after release). However, outcome-related modulation of distractor fixations in high performers was observed for both early and late distractor onsets, which initially appears at odds with the assumption that sensorimotor predictions are only available at later time points. Analyses of saccade latencies revealed that distractor fixations were initiated, on average, around 300 ms after the appearance of an early distractor (i.e., around 400 ms after ball release, Fig. 7). Thus, even when distractors appeared early, fixations typically occurred late enough to allow predictive processes to influence attentional selection. In the task at hand, EEG studies have identified a pronounced negative deflection in fronto-central brain regions associated with the predictive valuation of action outcomes (hit vs. miss) emerging approximately 200-350 ms after ball release (Error Related Negativity (ERN); Joch et al., 2017; Maurer et al., 2015).

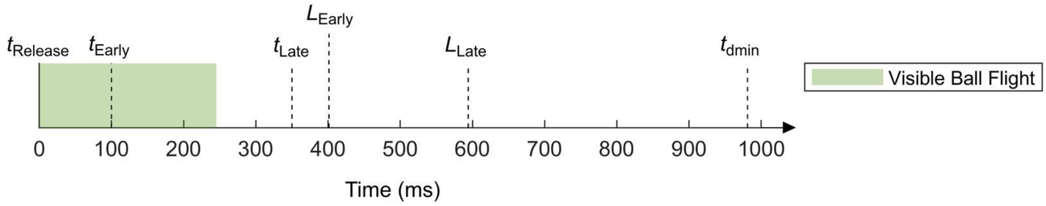


Figure 7. Average chronology of events within a trial. Time points denote: t_{Release}, moment of ball release; t_{Early} and t_{Late}, mean onset times of early or late distractors; L_{Early} and L_{Late}, mean latencies of saccades toward an early or late distractor; t_{dmin}, mean feedback onset. The green shaded area indicates the mean interval during which ball-flight information was available.

To further disentangle within-trial timing effects, distractor fixations were classified as reactive (<150 ms) or delayed (≥150 ms) based on saccadic latency relative to distractor onset. This analysis revealed a strong interaction between distractor timing and saccade type. When the distractor appeared early, both high and low performers were substantially less likely to execute reactive saccades toward the distractor. At early distractor onset, the ball flight was still visible (until about 250 ms after release, see Fig. 7), providing ongoing task-relevant visual information that could compete effectively with the distractor for attentional selection. Indeed, the heatmap depicting gaze positions at early distractor onset (Fig. 6*B*) shows that gaze was centered near the release position, consistent with monitoring of the ball's initial flight. This generalized suppression indicates that participants were aware of when task-relevant visual information remained available and exploited this knowledge to override saliency-driven gaze allocation. This finding aligns with the signal suppression hypothesis, which suggests that salient stimuli automatically generate an attentional priority signal, but that signal can be actively suppressed by an inhibitory control process before attention is captured (Gaspelin & Luck, 2018; Sawaki & Luck, 2010). A growing body of behavioral, eye-tracking, and electrophysiological research supports the existence of such proactive suppression, particularly when task demands are stable and predictable (Chang & Egeth, 2019; Feldmann-Wüstefeld et al., 2021; Gaspelin & Luck, 2018, 2019; Sawaki & Luck, 2010; Zhao et al., 2024). An alternative, though not mutually exclusive, explanation for the low frequency of reactive saccades toward early distractors is that the ball flight itself constituted a highly salient stimulus. According to Itti and Koch (2000), the most salient object is chosen in a winner-take-all fashion. However, the slightly stronger suppression of reactive saccades after early distractors observed descriptively in high performers compared to low performers favors an interpretation in terms of at least partially informed top-down prioritization rather than purely stimulus-driven competition. Together, this pattern indicates that knowledge about the temporal availability of task-relevant information is shared across performance levels, as both performance groups suppressed reactive saccades to early distractors.

Most likely, distractor fixations were initiated delayed after an early distractor onset. Participants may have waited until task-relevant information (ball flight) was exhausted before allowing gaze to shift toward the distractor. A delayed saccade to the early distractor still allowed enough time, in principle, to orient the gaze to the outcome feedback location. Therefore, a general suppression (in terms of delayed responses) of an early distractor was not as critical as when a distractor appeared later in the trial, closer to the feedback time point. In case of misses, however, it seems a safer strategy (adopted by skilled individuals) to suppress distractors in either way so as not to miss important feedback information.

In late distractor trials, reactive and delayed saccades occurred with comparable likelihood, in contrast to early distractor trials. At this point in the trial, distractors appeared against an otherwise empty display, rendering them salient from a bottom-up perspective (Fecteau & Munoz, 2006). Taken together, these time-dependent results highlight the importance of task constraints in shaping the relative contributions of top-down and bottom-up processes to gaze allocation (Bonev et al., 2013).

Crucially, at a descriptive level, the top-down modulation of distractor fixations by sensorimotor predictions observed in high performers was evident only for delayed saccades. This observation aligns with previous work demonstrating that visual saliency and value-related information are processed with different temporal dynamics (Schütz et al., 2012; Stritzke et al., 2009). Fast eye movements are dominated by stimulus saliency, whereas longer-latency saccades increasingly incorporate value- and goal-related information. The initial, rapid processing of saliency appears to be largely immune to the prediction-based value signal, which only exerts its control over the later, cognitively influenced saccades.

4.3 Limitations and Future Directions

The overall effects of the predicted outcome on distractor fixation rates were relatively small. This minor modulation may stem from the fact that participants had sufficient time after distractor onset to shift their gaze toward the distractor and still return to the feedback location in time, regardless of distractor onset timing. Stronger effects may therefore emerge in paradigms with tighter temporal overlap between distractors and feedback. Conversely, if the competition between the distractor and the feedback is too strong, it may lead to complete top-down suppression of all distractor fixations, thereby masking any subtle modulation effects, similar to the strong suppression observed for reactive saccades at the early distractor onset. In the current study, a balance between attentional capture by salient distractors and top-down suppression was necessary to uncover differences in distractor fixation rates in (predicted) hits and misses. To elicit reliable distractor fixations, the present study mimicked the classic gap paradigm by temporarily removing the target, thereby reducing fixation stability and facilitating oculomotor capture by distractors (Saslow, 1967). Pilots showed that when the task-relevant target remained visible throughout the trial, saliency-driven attentional capture by distractors was strongly reduced due to robust top-down anchoring of gaze. Consequently, the findings exhibit greater ecological validity for situations in which a clear visual anchor for guiding gaze is absent (e.g., in a Tennis setting, compared to a fixed-target task like Basketball).

A further reason for the small modulation of distractor fixations by sensorimotor predictions may be the overall low hit rates in the present experiment compared with previous work that focused on the influence of sensorimotor predictions on gaze allocation (Brand et al., 2024, 2025). With weaker performance, sensorimotor predictions may have lacked the precision needed (Jordan & Rumelhart, 1992) to reliably bias gaze away from salient but task-irrelevant stimuli in pending errors.

To better disentangle the contribution of sensorimotor predictions in the top-down modulation of attentional capture by salient distractors, future work should consider: (1) extended practice to ensure high motor expertise and adequate predictive skills, and (2) paradigms with stronger temporal competition between the distractor and the outcome feedback.

5 Conclusions

In summary, the findings demonstrate that sensorimotor predictions can modulate the extent to which gaze is captured by salient distractors during critical phases of action feedback. High-performing participants were able to suppress saliency-driven fixations when predictions signaled an error, highlighting the role of sensorimotor predictions in prioritizing feedback-relevant information. However, a more robust, generalized suppression of bottom-up influence was observed when explicit task-relevant information (i.e., the visible ball trajectory) was present. This result suggests that prior knowledge about the availability of relevant visual input may lead to stronger, general top-down suppression than the dynamic, trial-by-trial value signal. Additionally, the modulation of saliency-driven gaze allocation by sensorimotor predictions acts among stable person-specific susceptibility toward salient stimuli.

Data Availability

Source data will be openly available.

Supplemental Material

Supplemental material available at: https://doi.org/10.17605/OSF.IO/32JFX.

Grants

This research was supported by the Collaborative Research Center "Cardinal Mechanisms of Perception," funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation; SFB/TRR 135 TP B6 and B2) under Grant Number 222641018 and the Research Cluster "The Adaptive Mind," funded by the Excellence Program of the Hessian Ministry of Higher Education, Science, Research and the Arts.

Disclosures

No conflicts of interest, financial or otherwise, are declared by the authors.

Author Contributions

T.K.B., A.C.S., H. Müller, H. Maurer, M.H., and L.K.M. conceived and designed research; T.K.B. performed experiments; T.K.B. analyzed data; T.K.B, A.C.S., and L.K.M. interpreted results of experiments; T.K.B. prepared figures; T.K.B. drafted manuscript; T.K.B., and L.K.M. edited and revised manuscript.

References

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bisley, J. W., & Goldberg, M. E. (2010). Attention, Intention, and Priority in the Parietal Lobe. *Annual Review of Neuroscience*, *33*(1), 1–21. https://doi.org/10.1146/annurev-neuro-060909-152823

Bonev, B., Chuang, L. L., & Escolano, F. (2013). How do image complexity, task demands and looking biases influence human gaze behavior? *Pattern Recognition Letters*, *34*(7), 723–730. https://doi.org/10.1016/j.patrec.2012.05.007

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433–436.

Brand, T. K., Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. (2024). Sensorimotor prediction is used to direct gaze toward task-relevant locations in a goal-directed throwing task. *Journal of Neurophysiology*, *132*(2), 485–500. https://doi.org/10.1152/jn.00052.2024

Brand, T. K., Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. (2025). Predicted task success and outcome history mediate eye movements toward locations with high informational or motivational value. *Journal of Neurophysiology*, *134*(2), 568–579. https://doi.org/10.1152/jn.00072.2025

Brehm, L., & Alday, P. M. (2022). Contrast coding choices in a decade of mixed models. *Journal of Memory and Language*, *125*, 104334. https://doi.org/10.1016/j.jml.2022.104334

Chang, S., & Egeth, H. E. (2019). Enhancement and Suppression Flexibly Guide Attention. *Psychological Science*, *30*(12), 1724–1732. https://doi.org/10.1177/0956797619878813

Einhäuser, W., Rutishauser, U., & Koch, C. (2008). Task-demands can immediately reverse the effects of sensory-driven saliency in complex visual stimuli. *Journal of Vision*, *8*(2), 2. https://doi.org/10.1167/8.2.2

Fecteau, J., & Munoz, D. (2006). Salience, relevance, and firing: A priority map for target selection. *Trends in Cognitive Sciences*, *10*(8), 382–390. https://doi.org/10.1016/j.tics.2006.06.011

Feldmann-Wüstefeld, T., Weinberger, M., & Awh, E. (2021). Spatially Guided Distractor Suppression during Visual Search. *The Journal of Neuroscience*, *41*(14), 3180–3191. https://doi.org/10.1523/JNEUROSCI.2418-20.2021

Flanagan, J. R., & Wing, A. M. (1997). The Role of Internal Models in Motion Planning and Control: Evidence from Grip Force Adjustments during Movements of Hand-Held Loads. *The Journal of Neuroscience*, *17*(4), 1519–1528. https://doi.org/10.1523/JNEUROSCI.17-04-01519.1997

Folk, C. L., & Remington, R. W. (2015). Unexpected abrupt onsets can override a top-down set for color. *Journal of Experimental Psychology: Human Perception and Performance*, *41*(4), 1153–1165. https://doi.org/10.1037/xhp0000084

Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology. Human Perception and Performance*, *18*(4), 1030–1044.

Gaspelin, N., & Luck, S. J. (2018). The Role of Inhibition in Avoiding Distraction by Salient Stimuli. *Trends in Cognitive Sciences*, *22*(1), 79–92. https://doi.org/10.1016/j.tics.2017.11.001

Gaspelin, N., & Luck, S. J. (2019). Inhibition as a potential resolution to the attentional capture debate. *Current Opinion in Psychology*, *29*, 12–18. https://doi.org/10.1016/j.copsyc.2018.10.013

Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A Neural System for Error Detection and Compensation. *Psychological Science*, *4*(6), 385–390. https://doi.org/10.1111/j.1467-9280.1993.tb00586.x

Hartig, F. (2024). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.* (Version R package version 0.4.7) [Computer software]. https://github.com/florianhartig/dharma

Hayhoe, M. M. (2017). Vision and Action. *Annual Review of Vision Science*, *3*(1), 389–413. https://doi.org/10.1146/annurev-vision-102016-061437

Henderson, J. M., Brockmole, J. R., Castelhano, M. S., & Mack, M. (2007). Visual saliency does not account for eye movements during visual search in real-world scenes. In R. P. G. V. Gompel, M. H. Fischer, W. S. Murray, & R. L. Hill (Eds.), *Eye Movements* (pp. 537–562). Elsevier. https://doi.org/10.1016/B978-008044980-7/50027-6

Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, *40*(10–12), 1489–1506. https://doi.org/10.1016/S0042-6989(99)00163-7

Joch, M., Hegele, M., Maurer, H., Müller, H., & Maurer, L. K. (2017). Brain negativity as an indicator of predictive error processing: The contribution of visual action effect monitoring. *Journal of Neurophysiology*, *118*(1), 486–495. https://doi.org/10.1152/jn.00036.2017

Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & Psychophysics*, *43*(4), 346–354. https://doi.org/10.3758/BF03208805

Jordan, M. I., & Rumelhart, D. E. (1992). Forward Models: Supervised Learning with a Distal Teacher. *Cognitive Science*, *16*(3), 307–354. https://doi.org/10.1207/s15516709cog1603_1

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, *9*(6), 718–727. https://doi.org/10.1016/S0959-4388(99)00028-8

Lenth, R. (2023). *Emmeans: Estimated Marginal Means, aka Least-Squares Means* (Version R package version 2.0.1) [Computer software]. https://CRAN.R-project.org/package=emmeans

Li, A., & Chen, Z. (2018). Personalized Visual Saliency: Individuality Affects Image Perception. *IEEE Access*, *6*, 16099–16109. https://doi.org/10.1109/ACCESS.2018.2800294

Maurer, L. K., Maurer, H., & Müller, H. (2015). Neural correlates of error prediction in a complex motor task. *Frontiers in Behavioral Neuroscience*, *9*, 209. https://doi.org/10.3389/fnbeh.2015.00209

Müller, H., & Sternad, D. (2004). Decomposition of Variability in the Execution of Goal-Oriented Tasks: Three Components of Skill Improvement. *Journal of Experimental Psychology: Human Perception and Performance*, *30*(1), 212–233. https://doi.org/10.1037/0096-1523.30.1.212

Saslow, M. G. (1967). Effects of Components of Displacement-Step Stimuli Upon Latency for Saccadic Eye Movement. *Journal of the Optical Society of America*, *57*(8), 1024. https://doi.org/10.1364/JOSA.57.001024

Sawaki, R., & Luck, S. (2010). Control of memory-driven attentional bias in selective attention: Electrophysiological evidence. *Journal of Vision*, *10*(7), 101–101. https://doi.org/10.1167/10.7.101

Schreij, D., Owens, C., & Theeuwes, J. (2008). Abrupt onsets capture attention independent of top-down control settings. *Perception & Psychophysics*, *70*(2), 208–218. https://doi.org/10.3758/PP.70.2.208

Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Eye movements and perception: A selective review. *Journal of Vision*, *11*(5), 9. https://doi.org/10.1167/11.5.9

Schütz, A. C., Trommershäuser, J., & Gegenfurtner, K. R. (2012). Dynamic integration of information about salience and value for saccadic eye movements. *Proceedings of the National Academy of Sciences*, *109*(19), 7547–7552. https://doi.org/10.1073/pnas.1115638109

Stritzke, M., Trommershäuser, J., & Gegenfurtner, K. R. (2009). Effects of salience and reward information during saccadic decisions under risk. *Journal of the Optical Society of America A*, *26*(11), B1. https://doi.org/10.1364/JOSAA.26.0000B1

Tatler, B. W., Hayhoe, M. M., Land, M. F., & Ballard, D. H. (2011). Eye guidance in natural vision: Reinterpreting salience. *Journal of Vision*, *11*(5), 5–5. https://doi.org/10.1167/11.5.5

Wolpert, D. M. (1997). Computational approaches to motor control. *Trends in Cognitive Sciences*, *1*(6), 209–216. https://doi.org/10.1016/S1364-6613(97)01070-X

Yantis, S., & Jonides, J. (1984). Abrupt visual onsets and selective attention: Evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *10*(5), 601–621. https://doi.org/10.1037/0096-1523.10.5.601

Zhao, G., Chen, J., Duan, Y., Li, S., Wang, Q., & Li, D. (2024). The proactive and reactive mechanisms of learned spatial suppression. *Cerebral Cortex*, *34*(8), bhae333. https://doi.org/10.1093/cercor/bhae333

III

Appendix

List of Publications

Brand, T. K., Maurer, L. K., Müller, H., Döhring, F. R., & Joch, M. (2022). Predictability shapes movement kinematics and grip force regulation in human object handovers. *Human movement science*, *85*, 102976.

Brand, T. K., Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. (2024). Sensorimotor prediction is used to direct gaze toward task-relevant locations in a goal-directed throwing task. *Journal of Neurophysiology*, *132*(2), 485-500.

Brand, T. K., Schütz, A. C., Müller, H., Maurer, H., Hegele, M., & Maurer, L. K. (2025). Predicted task success and outcome history mediate eye movements toward locations with high informational or motivational value. *Journal of Neurophysiology*, *134*(2), 568-579.

Declaration of Authorship

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

Gießen, 6 January 2026

(Theresa Karoline Brand)