

**Sensomotorische Unsicherheit im Sport:  
Bayes-Integration des Vorwissens in Wahrnehmungs- und  
Handlungsprozesse**

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vorgelegt von  
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Von der Philosophisch-humanwissenschaftlichen Fakultät der Universität Bern auf Antrag  
von Prof. Dr. Ernst-Joachim Hossner (Hauptgutachter) und Dr. Lisa Maurer  
(Zweitgutachterin) angenommen.

Dekan: Prof. Dr. Elmar Anhalt

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## Diese kumulative Dissertation umfasst folgende Zeitschriftenbeiträge

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### Artikel I

**Beck, D.**, Hossner, E.-J. & Zahno, S. (2023). Mechanisms for handling uncertainty in sensorimotor control in sports: A scoping review. *International Review of Sport and Exercise Psychology*, 1–35. <https://doi.org/10.1080/1750984X.2023.2280899>

### Artikel II

**Beck, D.**<sup>1</sup>, Zahno, S.<sup>1</sup>, Kredel, R. & Hossner, E.-J. (2024). From simple lab tasks to the virtual court: Bayesian integration in tennis. [Manuskript in Begutachtung im *Journal of Neurophysiology*].

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<sup>1</sup> Diese Autoren haben gleich viel zum Forschungsprojekt beigetragen und teilen sich die Erstautorenschaft der Beiträge.

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## Zusammenfassung

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Bei komplexem sensomotorischen Verhalten wie im Sport entsteht Unsicherheit durch die Mehrdeutigkeit der eingehenden sensorischen Informationen, durch zeitliche Verzögerungen bei der Informationsübertragung sowie durch Rauschen in sensomotorischen Signalen. Der Umgang mit dieser sensomotorischen Unsicherheit ist entscheidend, um beispielsweise einen Tennisrückschlag erfolgreich ins gegnerische Feld zu spielen. Normative Theorien wie die Bayes-Entscheidungstheorie (Körding & Wolpert, 2006) bieten einen vereinheitlichenden Erklärungsrahmen im Umgang mit sensomotorischer Unsicherheit in Wahrnehmungs- und Handlungsprozessen. Konkret sind aus der Grundlagenforschung fünf Mechanismen im Umgang mit sensomotorischer Unsicherheit bekannt und empirisch belegt: (1) *Multisensorische Integration*, (2) *Integration des Vorwissens*, (3) *Risiko-Optimierung*, (4) *Redundanz-Ausnutzung* und (5) *Impedanzkontrolle*. Es stellt sich jedoch die Frage, ob Ergebnisse, die auf einfachen Laboraufgaben beruhen, das Verhalten in komplexen Aufgaben erklären. Die Untersuchung dieses Transfers wird weit über die Sportwissenschaft hinaus zunehmend gefordert.

In einem ersten Schritt dieser Dissertation wurde daher eine Übersichtsarbeit (Artikel I) über den empirischen Literaturstand zum Umgang mit Unsicherheit im Sport erstellt. Dabei wurde gezeigt, dass die meisten Studien zum Umgang mit Unsicherheit mit komplexen sensomotorischen Bewegungsaufgaben in den Rahmen normativer Theorien passen. Bis auf wenige Ausnahmen werden in diesen Studien aber nicht systematisch die Vorhersagen überprüft, die aus normativen Theorien abgeleitet werden können. Somit wurde durch die Übersichtsarbeit aufgezeigt, dass weitere empirische Forschung notwendig ist, um die Gültigkeit dieser Mechanismen auf komplexe Bewegungsaufgaben übertragen zu können. Daher wurden in einem zweiten Schritt in dieser Dissertation mit Fokus auf dem Mechanismus der *Integration von Vorwissen* in einer dreiteiligen empirischen Studienreihe Vorhersagen aus der Bayes-Entscheidungstheorie abgeleitet und in den Sportkontext übersetzt (Artikel II, III und IV). Die Resultate bestätigen, dass der Mechanismus der Bayes-Integration des Vorwissens zur Reduktion von Unsicherheit auch in einer komplexen Aufgabe wie dem Tennisrückschlag folgendermassen wirkt: Verschiedene Wahrscheinlichkeitsverteilungen (auch komplexe bimodale) können erlernt werden und beeinflussen mit zunehmender Verlässlichkeit das prädiktive Blickverhalten (Artikel II), die Bewegungsausführung des Rückschlags (Artikel III) sowie in dessen Vorbereitung die Gewichtsverlagerung im Splitstep und optimieren dadurch

die resultierende Leistung (Artikel IV). Diese Ergebnisse untermauern somit die Generalisierbarkeit von normativen Theorien basierend auf zwei Jahrzehnten experimenteller Grundlagenforschung.

Darüber hinaus wurde mit der dreiteiligen empirischen Studienreihe zum Verständnis beigetragen, wie normative Theorien aus der Grundlagenforschung im Sport zu verstehen sind. Visuelle Unsicherheit tritt im Sport in der Regel durch hohen Zeitdruck auf und damit mit wenig akkumulierter visueller Information wie im Tennis beim Rückschlag schneller Bälle. Dies hat zur Konsequenz, dass das Vorwissen in der kontinuierlichen antizipativen Entscheidungsfindung unter hohem Zeitdruck frühe vorbereitende Bewegungen (Blickbewegungen und Gewichtsverlagerung im Splitstep) beeinflusst. Steht aber genügend Zeit zur Verfügung, können vorhergesagte Zustandsschätzungen durch eingehende sensorische Informationen überprüft und gegebenenfalls angepasst werden. Diese Erkenntnis im Kontext aktueller Sensomotoriktheorien trägt somit auch zur klassischen Anticipationsforschung in der Sportwissenschaft bei. So sind interne Vorhersagen im Umgang mit sensomotorischer Unsicherheit in der kontinuierlichen Entscheidungsfindung integraler Bestandteil für die Verhaltenskontrolle. Zudem konnte empirisch erklärt werden, dass Leistungsabnahmen bei unwahrscheinlichen Ereignissen nicht als ‹Fehler› des Systems angesehen werden sollten. Vielmehr sollten die Kosten für Fehlentscheidungen in seltenen Fällen als funktionale Strategie zur Verbesserung der Gesamtleistung betrachtet werden, wie es in der Bayes-Entscheidungstheorie vorhergesagt wird. Ferner konnte gezeigt werden, dass sich Effekte der Bayes-Integration in komplexen Bewegungen zwar mit beispielsweise biomechanischen Effekten überlagern, aber dennoch bedeutend für die Verhaltenskontrolle bleiben.

Diese Dissertation zeigt, wie durch den Einsatz virtueller Welten der Transfer von einfachen Laboraufgaben zu komplexem Bewegungsverhalten unter strengen experimentellen Bedingungen und gleichzeitiger hoher externer Validität konkret gelingen kann. Damit leistet diese Dissertation einen Beitrag zum Verständnis, wie Vorwissen in Wahrnehmungs- und Handlungsprozesse im Sport integriert wird und dadurch sensomotorische Unsicherheiten reduziert und komplexe Bewegungsaufgaben bewältigt werden können.

## **1 Einleitung und Problemstellung: Von der Unsicherheit in einfachen Laboraufgaben zum virtuellen Tennis**

Während unserer Interaktionen mit der Umwelt sind wir kontinuierlich sensomotorischer Unsicherheit ausgesetzt (Faisal et al., 2008; Kersten et al., 2004; Körding & Wolpert, 2006; van Beers et al., 2002; Witt & Riley, 2014). Besonders im Sport, wo die Grenzen motorischer Leistungsfähigkeit ausgelotet werden, spielt ein optimaler Umgang mit dieser Unsicherheit eine entscheidende Rolle. Im Tennis etwa treten bei der Ausführung eines Rückschlags vielfältige Unsicherheiten auf. So stellt sich die Frage, mit welcher Geschwindigkeit der Ball ankommt, welche Flugbahn er nimmt und welche zeitlich gegliederte Bewegungsabfolgen vonnöten sind, um den Ball erfolgreich zu erreichen und zurückzuspielen. Auch die Abwägung zwischen dem Risiko eines eigenen Fehlers und der taktischen Platzierung nahe der Linien, um den Gegner in Bedrängnis zu bringen, ist dabei essenziell. Während diese Unsicherheit das Tennisspiel herausfordernd und faszinierend macht, hat die Reduktion von Unsicherheit in anderen sportlichen Kontexten, etwa beim Überqueren eines schmalen Berggrats, existentielle Bedeutung – hier kann die präzise Einschätzung des nächsten Tritts über Leben und Tod entscheiden.

Die übergeordnete Frage, wie die sensomotorische Unsicherheit effektiv reduziert werden kann, um ein hohes Mass an Bewegungskontrolle zu erreichen, wird im ersten Artikel dieser Dissertation untersucht (Artikel I, Beck et al., 2023). Dieser Artikel I, ein *Scoping Review*, bietet eine umfassende Übersicht über die grundlegenden Quellen und Qualitäten der Unsicherheit in der sensomotorischen Kontrolle. Anschliessend werden in Artikel I fünf identifizierte Mechanismen zum Umgang mit Unsicherheit aus der Grundlagenforschung zusammengefasst und es wird in einer systematischen Literaturrecherche untersucht, inwieweit diese fünf Mechanismen auf komplexe sensomotorische Aufgaben, wie sie typischerweise im Sport auftreten, übertragbar sind. Abschliessend werden die fünf Mechanismen innerhalb des theoretischen Rahmens der optimalen Feedback-Kontrolle verankert. Gemäss dem *Scoping Review* (Artikel I, Beck et al., 2023) werden die drei nachfolgenden Abschnitte der Arbeit in drei zentrale Themenbereiche gegliedert. In Unterkapitel 1.1, *Unsicherheit in der Sensomotorik*, wird zunächst die grundlegende wissenschaftliche Problemstellung dargelegt, während in Unterkapitel 1.2, *Mechanismen im Umgang mit Unsicherheit in der sensomotorischen Kontrolle komplexer Bewegungen*, und in Unterkapitel 1.3, *Optimale*

*Feedback-Kontrolle*, theoretische Lösungsansätze sowie deren empirische Evidenz in komplexen sensomotorischen Aufgaben erläutert werden.

In Unterkapitel 1.4, *Bayes-Integration des Vorwissens*, wird anschliessend auf die theoretischen Grundlagen der empirischen Untersuchungsreihe eingegangen, bevor in Unterkapitel 1.5, *Ansatz optimaler Modelle in der experimentellen Verhaltensforschung*, diese theoretischen Grundlagen und deren Untersuchungen kritisch beleuchtet werden und das Vorgehen in der empirischen Untersuchungsreihe dieser Dissertation begründet wird. Schliesslich wird in Abschnitt 1.6, *Einsatz virtueller Welten zur Untersuchung von komplexen sensomotorischen Verhaltens*, aufgezeigt, welcher potenzielle Erkenntnisgewinn sich ergibt, wenn Mechanismen aus den Grundlagenwissenschaften auf Probleme komplexer Bewegungen übertragen werden, und wie der Einsatz virtueller Realität es ermöglicht, komplexe Bewegungen unter strengen experimentellen Bedingungen zu untersuchen.

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## Artikel I

**Beck, D., Hossner, E.-J. & Zahno, S. (2023).** Mechanisms for handling uncertainty in sensorimotor control in sports: A scoping review. *International Review of Sport and Exercise Psychology*, 1–35. <https://doi.org/10.1080/1750984X.2023.2280899>

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### 1.1 Unsicherheit in der Sensomotorik

Die Unsicherheit in der Sensomotorik ist ein vielschichtiges Problem. Sensorische Informationen sind häufig objektiv mehrdeutig (Kersten et al., 2004; Witt & Riley, 2014). Ein und dasselbe dreidimensionale Objekt kann beispielsweise unterschiedliche retinale Bilder erzeugen, während umgekehrt verschiedene dreidimensionale Objekte zu identischen retinalen Bildern führen können. Ein ähnliches Problem offenbart sich bei der Materialwahrnehmung: Ein Material (z. B. Silber) kann je nach Lichtverhältnissen aufgrund der Lichtreflexion unterschiedlich erscheinen, während ein identisches Erscheinungsbild von verschiedenen Materialien stammen kann (Kersten et al., 2004, S. 2).

Darüber hinaus werden sowohl sensorische als auch motorische Signale durch zufällige Fluktuationen und nicht zum Signal gehörende Störungen verrauscht (Faisal et al., 2008; Körding & Wolpert, 2006; van Beers et al., 2002). Dieses Rauschen ist in der motorischen Ausführung typischerweise zusätzlich von der Signalstärke abhängig (Harris & Wolpert, 1998).

Weiterhin entsteht Unsicherheit durch die unvermeidbare zeitliche Verzögerung, die alle sensomotorischen Prozesse begleitet und die zudem je nach Sinnesmodalität unterschiedlich lang ist. Ein Beispiel für diese zeitliche Verzögerung zwischen Sinnesmodalitäten ist das visuelle und das akustische Signal desselben Ereignisses: Das visuelle Signal trifft vor dem akustischen Signal ein. So erscheint beispielsweise der Blitz eines Gewitters, bevor der Donner ertönt, oder wir sehen den Aufprall eines Balls auf dem Boden, bevor das Geräusch zu hören ist. Folglich kann unser sensomotorisches Kontrollsyste nur auf Informationen zurückgreifen, die bereits unterschiedlich veraltet sind (Franklin & Wolpert, 2011).

Schliesslich entsteht Unsicherheit auch durch Redundanz, da es in der Regel viele Möglichkeiten gibt, eine motorische Aufgabe zu lösen (Todorov & Jordan, 2002). So kann etwa die gleiche Wurfweite durch mehrere Kombinationen von Abwurfwinkel und -geschwindigkeit erreicht werden (Dupuy et al., 2000). Zusammenfassend ist zu konstatieren, dass sensomotorische Unsicherheit durch Mehrdeutigkeit, Rauschen, Verzögerungen und Redundanz entsteht.

Es existieren nicht nur verschiedene Quellen der Unsicherheit, sondern auch verschiedene Qualitäten von Unsicherheit, weshalb diese in drei Hauptkategorien unterteilt wird: erwartete Unsicherheit, unerwartete Unsicherheit sowie Volatilität (Bland & Schaefer, 2012). Dabei kann Unsicherheit durch Wahrscheinlichkeiten spezifiziert werden, indem jedem möglichen sensomotorischen Zustand eine Wahrscheinlichkeit zugeordnet wird (Sternad, 2018, S. 184). Erwartete Unsicherheit betrifft Fälle, in denen die Ergebniswahrscheinlichkeiten möglicher Zustände bekannt und stabil sind, beispielsweise die Ergebnisunsicherheit beim Würfeln oder beim Tennisspiel mit einer bekannten Gegner\*in. Unerwartete Unsicherheit tritt auf, wenn der Würfel plötzlich unbemerkt in einen Betrugswürfel mit ungewöhnlichen Wahrscheinlichkeiten ausgetauscht wird oder wenn unbemerkt andere Tennisbälle mit unbekannten Sprungeigenschaften verwendet werden, deren Wahrscheinlichkeiten nicht mehr durch frühere Erfahrungen vorhergesagt werden können. Volatilität beschreibt schliesslich eine häufige Änderung der Wahrscheinlichkeiten, z. B. durch häufiges Auswechseln verschiedener Würfel oder durch wechselhaften Wind beim Tennisspiel.

In Anbetracht der verschiedenen Qualitäten und Quellen von Unsicherheit stellt sich die übergeordnete Frage, wie die sensomotorische Unsicherheit effektiv reduziert werden kann, um ein hohes Mass an Bewegungskontrolle zu erreichen.

## **1.2 Mechanismen im Umgang mit Unsicherheit in der sensomotorischen Kontrolle komplexer Bewegungen**

In der Grundlagenforschung zur sensomotorischen Kontrolle wurden fünf Mechanismen nachgewiesen, die zur Reduktion von Unsicherheit in der Bewegungskontrolle beitragen (für Übersichtsarbeiten, siehe z. B. Franklin & Wolpert, 2011; Gallivan et al., 2018; Körding & Wolpert, 2006; Todorov, 2004):

- (1) *Multisensorische Integration*: Um die sensorische Mehrdeutigkeit zu reduzieren und eine robuste Zustandsschätzung zu erhalten, werden verschiedene sensorische Informationen miteinander kombiniert und entsprechend ihrer relativen Zuverlässigkeit nach den Prinzipien der Bayes-Statistik gewichtet (Ernst & Banks, 2002).
- (2) *Integration des Vorwissens*: Nach den gleichen Prinzipien der Bayes-Statistik im Fall der Integration verschiedener sensorischer Informationen wird die Unsicherheit über die Zustandsschätzung durch die zusätzliche Integration des Vorwissens reduziert (Körding & Wolpert, 2004).
- (3) *Risiko-Optimierung*: Da typischerweise mehrere Bewegungsvarianten zur Lösung einer bestimmten Bewegungsaufgabe existieren, müssen die damit verbundenen Risiken bei der Bewegungsausführung berücksichtigt werden. Um das Kosten-Nutzen-Verhältnis zu optimieren, wird daher das inhärente motorische Rauschen bei der motorischen Planung und Steuerung mit einbezogen (Trommershäuser et al., 2003).
- (4) *Redundanz-Ausnutzung*: Die Verhaltenssteuerung kann als Suche nach einer optimalen Variante in einem redundanten Lösungsraum aufgefasst werden. Dies impliziert, dass Unsicherheit durch motorisches Rauschen nur dann minimiert werden muss, wenn die zielrelevanten Variablen ausserhalb des Bereichs optimaler Lösungen variieren (Bernstein, 1987; Scholz & Schöner, 1999; Todorov & Jordan, 2002).
- (5) *Impedanzkontrolle*: Durch Kontraktion der Muskeln kann die Gelenksteifigkeit gezielt modifiziert werden. Dadurch lassen sich Störungen oder Schläge im Bereich des erwarteten Ausmasses unmittelbar dämpfen (Burdet et al., 2001; Hogan, 1984).

Dabei stellt sich die Frage, inwieweit die einzelnen Mechanismen – die häufig in einfachen Bewegungsaufgaben wie typischerweise Zeige- oder Greifbewegungen untersucht wurden – auf komplexe sensomotorische Aufgaben im Sport übertragbar sind.

Im *Scoping Review* (Beck et al., 2023) wurde genau dieser Frage nachgegangen, indem untersucht wurde, ob eine entsprechende empirische Evidenz vorliegt. Die systematische

Literaturrecherche hat ergeben, dass zahlreiche empirische Befunde zu einer (1) *multisensorischen Integration* in einen ‹Bayes-Rahmen› passen. Es gibt jedoch nur empirische Evidenz aus zwei Studien, die spezifisch die Gewichtung sensorischer Informationen basierend auf ihrer Zuverlässigkeit untersucht haben (Gray, 2009; Kennel et al., 2015).

In Bezug auf den Mechanismus (2) *Integration des Vorwissens* liegt eine klare Evidenz dahin gehend vor, dass die Zuverlässigkeitsgewichtung des Vorwissens sowohl die Leistung verbessert als auch Rauschen und Mehrdeutigkeit in der Wahrnehmung und Handlung reduziert. Aus mehreren Studien geht hervor, dass diese Integration in vielen Fällen nahezu optimal ist (Arthur & Harris, 2021; Harris, Arthur, Vine, et al., 2022; Helm et al., 2020; Whittier et al., 2022).

Zu (3) *Risiko-Optimierung* in komplexen sensomotorischen Aufgaben wurde lediglich eine Studie gefunden, der zu entnehmen ist, dass das Bewegungsergebnis unter Berücksichtigung des motorischen Rauschens maximiert wird (Bertucco et al., 2020).

Hinsichtlich des Mechanismus der (4) *Redundanz-Ausnutzung* unterscheiden sowohl Expert\*innen als auch Anfänger\*innen zwischen aufgabenrelevanten und irrelevanten Variablen. Dupuy et al. (2000) konnten sogar zeigen, dass Menschen in einer Präzisionswurfaufgabe die Variabilität der Wurfweite minimieren, indem sie sowohl den Abwurfwinkel als auch die Abwurfgeschwindigkeit nahe am vorhergesagten mechanischen Optimum anpassen.

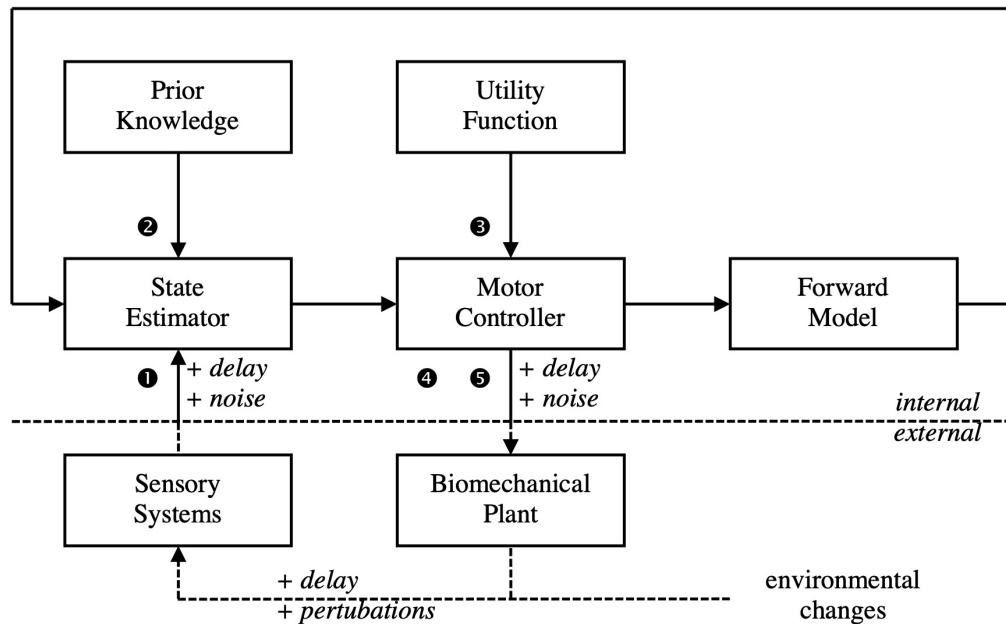
Zum Mechanismus (5) *Impedanzkontrolle* liegen nur drei Studien vor, die sich mit komplexen sensomotorischen Aufgaben befassen. Aus diesen geht hervor, dass die Impedanz aktiv durch Muskelkontraktion moderiert wird (Blenkinsop et al., 2016; Reeves et al., 2013; Reeves et al., 2016), indem beispielsweise stärkere Vibrationen beim Handstand durch erhöhte Handgelenkssteifigkeit unmittelbar gedämpft wurden (Blenkinsop et al., 2016).

### **1.3 Optimale Feedback-Kontrolle**

Im *Scoping Review* (Beck et al., 2023) wurde ein theoretischer Rahmen gefunden, der die fünf Mechanismen (1)–(5) integriert. Obwohl die einzelnen Mechanismen unterschiedlichen theoretischen Strömungen entstammen, können alle Mechanismen innerhalb der Rahmentheorie der optimalen Feedback-Kontrolle (Kording & Wolpert, 2006; Todorov & Jordan, 2002) verordnet werden (siehe Abbildung 1).

**Abbildung 1**

*Optimaler Feedback-Regelkreis*



Anmerkung. Optimaler Feedback-Regelkreis (Kording & Wolpert, 2006, S. 323; Todorov, 2004, S. 910); kombiniert und modifiziert mit Angabe der Mechanismen (1)–(5) für den Umgang mit Unsicherheit in der sensomotorischen Steuerung: (1) *multisensorische Integration*, (2) *Integration des Vorwissens*, (3) *Risiko-Optimierung*, (4) *Redundanz-Ausnutzung* und (5) *Impedanzkontrolle*.

Die Kernelemente des Modells in Abbildung 1 sind auch in anderen führenden Theorien der motorischen Kontrolle zu finden, wie der Theorie interner Modelle (Wolpert et al., 1995), der Theorie der aktiven Inferenz (Friston, 2010) oder der Affordanz-Wettbewerbs-Hypothese (Cisek, 2007). Es existieren zwar Unterschiede zwischen diesen Theorien (siehe, z. B. Friston, 2011), aber der vereinende Kern dieser Theorien liegt in ihrer grundlegend probabilistischen Betrachtung der Wahrnehmung und Handlung, die auf Online-Vorhersagen und der Integration von Informationen nach den Bayes-Prinzipien basieren. Genauer formuliert teilen die Ansätze drei theoretische Schlüsselkonzepte, indem sie (1) die Notwendigkeit eines internen Vorwärtsmodells, (2) einer Bayes-Integration von sensorischen Informationen und Vorwissen sowie (3) einer kostenbasierten Optimierung der Verhaltenssteuerung geltend machen.

Diese drei Schlüsselkonzepte werden im Folgenden weiter ausgeführt:

- (1) Externale Veränderungen werden im Vorwärtsmodell auf Basis der aktuellen Zustandsschätzung, der herausgegebenen motorischen Befehle sowie unter Berücksichtigung intern simulierter physikalischer Gesetze online prädiziert. Die Notwendigkeit eines internen

Modells ergibt sich auf einer kurzen Zeitskala aus der durch zeitliche Verzögerungen generierten Unsicherheit bei der Informationsübertragung (Vorwärtsmodell) sowie auf einer längeren Zeitskala für die Bewegungsplanung (Kontrollmodell) unter Berücksichtigung der vorhergesagten Zustandsschätzung (McNamee & Wolpert, 2019). Darüber hinaus ermöglichen interne Vorwärtsmodelle die Unterscheidung dahin gehend, ob eintreffende reafferente sensorische Informationen die Folge unserer eigenen Handlungen sind oder von anderen Ereignissen aus der Umwelt stammen (McNamee & Wolpert, 2019), was für die sensomotorische Adaptation und das sensomotorische Lernen zentral ist.

(2) Da die Bayes-Integration im Fokus dieser Arbeit liegt, wird in Unterkapitel 1.5 ausführlich darauf eingegangen.

(3) Mehrere Handlungsoptionen werden online nach ihrem Nutzen evaluiert, während der Entscheidungsprozess selbst als ein Online-Prozess der Verhaltenskoordination und -kontrolle verstanden wird (Cisek, 2007). Dabei werden nicht nur interne Vorhersagen auf erwartete Veränderungen in der äusseren Umgebung in die Kosten-Nutzen-Abwägung einbezogen, sondern auch sensorische Konsequenzen des eigenen Handelns. Zusammengefasst ist Verhaltenskontrolle als ein fortlaufender Prozess antizipativer Online-Entscheidungen unter Unsicherheit auf Basis einer Kosten-Nutzen-Abwägung verschiedener Handlungsoptionen zu verstehen (Gallivan et al., 2018; Gordon et al., 2021).

#### **1.4 Bayes-Integration des Vorwissens**

Ausgehend von der Theorie interner Modelle (Wolpert et al., 1995) ist die gesamte sensomotorische Kontrollarchitektur internal verordnet und allein über das sensorische System sowie über motorische Befehle zum biomechanischen System mit der Aussenwelt verbunden (Abbildung 1). Das sensorische System ist somit die einzige Quelle neuer Informationen über die Aussenwelt. Diese sensorischen Informationen können jedoch mit bereits bestehendem Vorwissen über die Aussenwelt kombiniert werden.

Aus der Bayes-Inferenzstatistik, deren Ursprung auf die Arbeit von Bayes (1763) zurückgeht, lässt sich ableiten, wie Vorwissen mit sensorischen Informationen optimal verrechnet werden kann, oder genauer formuliert, wie wahrscheinlich ein latenter Zustand  $z$  bei gegebener sensorischer Information  $sens$  ist (siehe, z. B. Ma, 2023):

$$p(z|sens) = \frac{p(sens|z)p(z)}{p(sens)}$$

Dabei stellt  $p(z)$  die *Prior*-Wahrscheinlichkeitsverteilung dar, während  $p(sens|z)$  für die *Likelihood*-Wahrscheinlichkeitsverteilung steht und  $p(z|sens)$  die *Posterior*-Wahrscheinlichkeitsverteilung wiedergibt;  $p(sens) = \sum_z p(sens|z)(z)$  dient der Normierung. Der *Prior* entspricht in diesem Zusammenhang also der subjektiv angenommenen A-priori-Wahrscheinlichkeitsverteilung für das Auftreten möglicher latenter Zustände. Die *Likelihood* veranschaulicht die Wahrscheinlichkeitsverteilung für die beobachtete sensorische Information bei gegebenen möglichen Zuständen und wird als internes generatives Modell bezeichnet (McNamee & Wolpert, 2019, S. 341). Der *Posterior* gibt sonach die entsprechende A-posteriori-Wahrscheinlichkeitsverteilung für die möglichen Zustände bei beobachteter sensorischer Information wieder. Es gilt folglich:

$$Posterior \propto Likelihood * Prior.$$

Ohne verstrt auf die Mathematik einzugehen (fr die Mathematik, siehe, Ma, 2023), hngt der *Posterior* also direkt vom Produkt aus *Likelihood* und *Prior* ab. Wird angenommen, dass der Mittelwert des *Postriors* der Zustandsschtzung entspricht (z. B. der wahrgenommenen Position eines Objekts), ist diese Zustandsschtzung umso unsicherer, desto breiter der *Posterior* ist. Gleches gilt fr die *Likelihood*- und die *Prior*-Wahrscheinlichkeitsverteilung: Je breiter die Verteilung ist, desto unsicherer sind sowohl die sensorische Information als auch das Vorwissen, und desto weniger tragen sie jeweils zur Genauigkeit der Zustandsschtzung bei. Die Breite der Verteilung kann daher als ein Reliabilitsmass verstanden werden. Der Einfluss des *Priors* sowie der *Likelihood* auf den *Posterior* hngt demnach direkt von ihrer Reliabilitt ab. Im Extremfall eines *Priors*, bei dem jeder mgliche Zustand gleich wahrscheinlich ist (auch als neutraler *Prior* bezeichnet), entspricht der *Posterior* daher genau der *Likelihood*. Im anderen Extremfall, wenn keinerlei sensorische Informationen vorliegen, entspricht der *Posterior* genau dem *Prior*.

Mithin beschreibt die Bayes-Inferenzstatistik, wie eine interne Kontrollarchitektur auf statistisch optimale Weise Vorwissen und sensorische Informationen zu einem wahrgenommenen Zustand verrechnen kann.

### **1.5 Ansatz optimaler Modelle in der experimentellen Verhaltensforschung**

Normative Theorien ermglichen es, Verhalten zu verstehen (Krding, 2007). Die optimale Feedback-Kontrolle, auch synonym als Bayes-Entscheidungstheorie bezeichnet (Krding &

Wolpert, 2006, S. 323-324), ist eine normative Theorie. Daraus abgeleitete optimale Bayes-Modelle ermöglichen die Beantwortung der «Wozu?»-Frage (Körding, 2007) auf der rechenbasierten Erklärungsebene nach Marr (1982).

Der grosse Vorteil solcher Bayes-Modelle besteht darin, dass wir verstehen, wie die Modelle entstehen, um das tatsächliche menschliche Verhalten daran abgleichen zu können (Griffiths et al., 2012; Maloney & Mamassian, 2009). Für die experimentelle Forschung lassen sich daher aus Bayes-Modellen klare Vorhersagen ableiten, die auch im sportwissenschaftlichen Kontext überprüft werden können (Beck et al., 2023; Gredin et al., 2020; Harris, Arthur, Broadbent, et al., 2022). In eben diesem Sinne der Ableitung klarer Vorhersagen sollten auch optimale Modelle verwendet werden (Griffiths et al., 2012). Denn auch wenn menschliches Verhalten oft nahe an optimalen Lösungen liegt (Körding, 2007), impliziert der Vergleich mit optimalen Modellen nicht, dass Menschen auf der Implementierungsebene im Sinne von Marr (1982) genau solche optimalen Rechenprozesse durchführen (Griffiths et al., 2012).

Dies wird von Kritiker\*innen oftmals missverstanden. So beziehen sich solche Kritiker\*innen zur Erklärung menschlicher Verhaltenskontrolle statt auf die «komplizierten» Rechenprozesse der Bayes-Entscheidungstheorie auf «einfache» Heuristiken, die dann zu Schlagworten wie «less is more» führen (Bowers & Davis, 2012; Gigerenzer & Gaissmaier, 2011, S. 453; Vertreter\*innen aus der Sportwissenschaft, z. B. Raab, 2012, S. 105). Wie die Heuristiken gefunden werden, lassen sie indes offen.

Belousov et al. (2016) konnten anhand der Aufgabe, einen Ball aus der Luft zu fangen, zeigen, dass vier der am häufigsten genannten Heuristiken rechnerisch optimale Lösungen unter Unsicherheit sind. Damit leisteten sie einen bedeutenden Beitrag zur Lösung dieses Diskurses, da sie darlegen konnten, wie Heuristiken aus «komplizierten» Rechenprozessen entspringen. Damit veranschaulichen sie exemplarisch den Zweck solcher rechnerisch optimalen Modelle, nämlich zu verstehen, wozu Menschen z. B. nach diesen Heuristiken in Bezug auf das Ballfangen handeln. In ebendiesem Sinne ist auch der Verweis auf die normative Bayes-Entscheidungstheorie in der empirischen Untersuchungsreihe dieser Dissertation zu verstehen, um klare Vorhersagen abzuleiten, die experimentell überprüft und verstanden werden können. Dieser Ansatz wurde in der Sportwissenschaft bisher in nur wenigen Studien zum Einfluss des Vorwissens auf das sensomotorische Verhalten im Sport verfolgt (Beck et al., 2023), was aber zunehmend gefordert wird (Gredin et al., 2020; Harris, Arthur, Broadbent, et al., 2022).

## ***1.6 Einsatz virtueller Welten zur Untersuchung des komplexen sensomotorischen Verhaltens***

Das Erforschen komplexer Bewegungen bildet eine Kernaufgabe der Sportwissenschaft. Während in der Grundlagenforschung oft Beispiele aus dem Sport in der Einleitung verwendet werden (wie z. B. Bayes-Integration im Tennisrückschlag bei Kording & Wolpert, 2004), ermöglicht die Technik der virtuellen Realität (VR) heute eine realistischere Untersuchung dieser Konzepte. Durch den Einsatz von VR können diese komplexen Bewegungsaufgaben nicht mehr nur vereinfacht anhand von Zeige- oder Greifbewegungen untersucht werden, sondern tatsächlich in der vollen Komplexität der zeitlichen und räumlichen Dynamik, etwa eines echten Tennisrückschlags, erforscht werden.

Einerseits gibt es keinen Grund, daran zu zweifeln, dass die gleichen Mechanismen auch bei komplexeren Bewegungen wirken. Andererseits ist die externe Validität der Ergebnisse der Grundlagenforschung nicht immer gegeben. So betonen etwa Wolpert et al. (2011, S. 748) in ihrer Übersichtsarbeit zu rechenbasierten Mechanismen motorischen Lernens: «It is not clear whether the learning models that are developed will generalize to tasks such as tying shoelaces or learning to skateboard.»

Dieser Gedanke kann in dreierlei Hinsicht vertieft werden. Erstens kann ein Mechanismus aus der Grundlagenforschung auch bei komplexen Aufgaben wirken, jedoch von anderen Effekten überlagert werden. Ein Beispiel hierfür zeigen Bar-Eli et al. (2007), die nachweisen konnten, dass Fussballtorhüter\*innen in Elfmetersituationen häufiger, als es optimal wäre, zur Seite springen, anstatt in der Mitte des Tores zu bleiben. Dies lässt vermuten, dass die Kostenfunktionen der Handlungsoptionen nicht immer eindeutig sind. In diesem Fall spielen möglicherweise die sozialen Kosten des Nichthandelns (z. B. das Risiko, von den Zuschauer\*innen negativ beurteilt zu werden) eine mitentscheidende Rolle.

Zweitens müssen die Mechanismen erweitert werden, um der Sportpraxis gerecht zu werden. Beispielsweise muss das Vorwissen in implizit erworbenes und explizit zur Verfügung gestelltes Vorwissen unterschieden werden. Implizit erworbenes Vorwissen hat in der Regel einen positiven Einfluss auf die Gesamtleistung, während der Nutzen von explizit zur Verfügung gestelltem Vorwissen stark von der Qualität der Information sowie der Expertise der Sportler\*in abhängt (Magnaguagno & Hossner, 2020; Magnaguagno et al., 2022).

Drittens erfordert die Erhöhung der externen Validität häufig eine Übersetzung der

Problemstellung. Beispielsweise manipulierten Kording und Wolpert (2004) die visuelle Unsicherheit mit verschwommenen Pixeln, während beim Tennis die visuelle Unsicherheit von der Ballgeschwindigkeit sowie den entsprechend kürzeren Zeitintervallen abhängt, die zur Akkumulation der visuellen Information zur Verfügung stehen.

Auch in der Grundlagenwissenschaft wurde die Entwicklung der Erforschung menschlichen Verhaltens von einfachen, künstlichen Aufgaben hin zu komplexen, naturalistischen Anforderungen als eine der grössten aktuellen Herausforderungen in der Psychologie und der Neurowissenschaft erkannt und hervorgehoben (z. B., Cisek & Green, 2024; Maselli et al., 2023). Die virtuelle Welt bietet dafür eine probate Lösung im Kompromiss zwischen der internen Validität der experimentellen Forschung und der externen Validität für die Übertragung ins Feld (Cisek & Green, 2024; Tsay et al., 2024). Im Gegensatz zur Feldforschung, die an die Gesetze der Physik gebunden ist, können diese in der virtuellen Welt beliebig manipuliert werden. Beispielsweise muss die reale Tennisspieler\*in beim Aufschlag den Schläger so schwingen, dass der Ball dorthin fliegt, wo er tatsächlich hinfliegt. Dabei werden frühzeitig relevante kinematische Informationen zur Vorhersage der Ballflugbahn preisgegeben, deren Einfluss im realen Tennis nicht vom Einfluss des Vorwissens über Wahrscheinlichkeitsverteilungen unterschieden werden kann. Im virtuellen Tennis kann die Flugbahn des Balls gänzlich unabhängig von der Aufschlagbewegung manipuliert werden. Auf diese Weise lassen sich experimentelle Kausalzusammenhänge mit hoher externer Validität aufdecken.

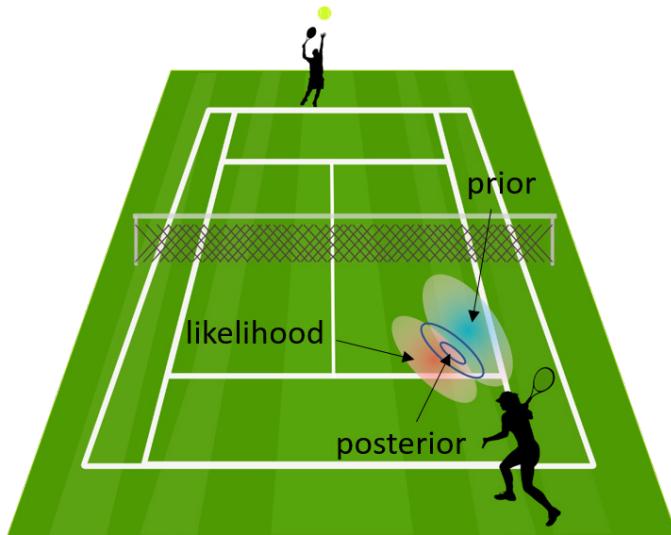
## 2 Serie empirischer Studien

Ziel der vorliegenden dreiteiligen empirischen Studienreihe dieser Dissertation ist es, den Mechanismus der Integration des Vorwissens zur Reduktion der sensomotorischen Unsicherheit anhand der motorisch komplexen Aufgabe des Tennisrückschlags zu untersuchen. Wie von Kording und Wolpert (2004) zur Veranschaulichung erläutert und in Abbildung 2 dargestellt, wird beim Tennisrückschlag die posteriore Wahrscheinlichkeitsverteilung für den Ballabsprungort durch die zuverlässigkeitsgewichtete Integration des Vorwissens (‘Wo wird der Ball aufgrund meiner bisherigen Erfahrungen mit der Gegner\*in wahrscheinlich landen?’) und einer Wahrscheinlichkeitsfunktion (‘Wie wahrscheinlich ist mein aktueller visueller Input angesichts verschiedener potenzieller Ballabsprungorte?’) gemäss der Bayes-Regel –  $Prior \sim Likelihood - Posterior$  kontinuierlich aktualisiert (siehe Unterkapitel 1.4 *Bayes-Integration des Vorwissens*).

Derselbe Prozess der kontinuierlichen posterioren Schätzung der Wahrscheinlichkeitsverteilung ist dabei auch für jeden anderen Ort, insbesondere für den Ballrückschlagort, anzunehmen. Daraus abgeleitet muss die Zuverlässigkeit des *Priors* und der *Likelihood* den *Posterior* (also die Wahrnehmung), die motorische Antwort und letztlich die Leistung beeinflussen. Dementsprechend wurde in Artikel II dieser Dissertation anhand von zwei Experimenten untersucht, ob die Wahrnehmung im Verlauf eines Tennisspiels zunehmend durch immer zuverlässigeres Vorwissen beeinflusst wird (Beck, Zahno, et al., 2024). Im Experiment unter Artikel III wurde der Einfluss des Vorwissens einer bimodalen Wahrscheinlichkeitsverteilung der Ballabsprungorte auf die Bewegungsausführung des Rückschlags bei verschiedenen Ballgeschwindigkeiten (unterschiedliche visuelle Unsicherheit) untersucht (Zahno, Beck, Hossner, et al., 2024). Schliesslich wurden im Experiment unter Artikel IV der Einfluss des Vorwissens auf die Leistung von Tennisspielern<sup>2</sup> und ihr kontinuierliches antizipative Entscheidungsverhalten während des Splitsteps in der Vorbereitungsphase des Rückschlags geprüft (Beck, Hossner, et al., 2024).

## Abbildung 2

*Bayes-Schätzung des erwarteten Ballabsprungorts beim Tennisrückschlag*



Anmerkung. Schematisch dargestellte Bayes-Integration des erwarteten Ballauftreffpunkts, nachgezeichnet aus Kording und Wolpert (2006, S. 320).

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<sup>2</sup> In diesem Experiment wurden ausschliesslich männliche Spieler untersucht.

## **2.1 Experiment 1 und 2 zur zunehmenden Gewichtung des Vorwissens im Blickverhalten**

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### **Artikel II**

**Beck, D.<sup>1</sup>, Zahno, S.<sup>1</sup>, Kredel, R. & Hossner, E.-J. (2024). From simple lab tasks to the virtual court: Bayesian integration in tennis. [Manuskript in Begutachtung im *Journal of Neurophysiology*].**

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Ziel dieser Studie war es, zentrale Vorhersagen, die aus der Bayes-Entscheidungstheorie (Körding & Wolpert, 2006) abgeleitet wurden, in der komplexen Aufgabe eines Tennisrückschlags zu testen.

Für die Schätzungen des Ballabsprungorts im Tennisrückschlag ergeben sich folgende Vorhersagen: Nachdem die Präferenzen (Wahrscheinlichkeitsverteilung) eines Gegenspielers<sup>3</sup> erfahren wurden, sind die Schätzungen des Ballabsprungorts in Richtung der zentralen Tendenz des *Priors* verzerrt, insbesondere wenn die sensorischen Informationen unzuverlässig sind. Des Weiteren sagt die Bayes-Entscheidungstheorie einen dynamischen Gewichtungsprozess auf zwei Zeitskalen voraus. Auf der Zeitskala eines Matches (einer experimentellen Tageseinheit) wird die gesammelte Erfahrung über die Aufschlagtendenzen des Gegners (der *Prior*) stets stärker gewichtet. Auf der Zeitskala eines einzelnen Aufschlags wird der *Prior* in frühen Phasen (wenn also die sensorischen Informationen über die Flugbahn des Balls noch nicht aussagekräftig sind) stark gewichtet; der *Prior* wird jedoch durch zuverlässigere visuelle Informationen, die in späteren Phasen des Ballflugs verfügbar werden, «überschrieben». Diese Vorhersagen konnten empirisch bestätigt werden, wie im Folgenden erläutert wird.

Zur empirischen Untersuchung dieser Vorhersagen wurde ein immersives virtuelles Tennis-Experiment entwickelt (siehe dazu das Video auf GitHub unter [https://github.com/ispw-unibe-ch/bayesian\\_integration\\_in\\_tennis](https://github.com/ispw-unibe-ch/bayesian_integration_in_tennis)). Die Aufgabe der je 32 Versuchspersonen (Noviz\*innen) pro Experiment bestand darin, Aufschläge eines Avatars im virtuellen Tennis zu retournieren. Nach einer Angewöhnungsphase mit gleichmäßig verteilten Ballabsprungorten (neutraler *Prior*) folgten 320 Aufschläge an Tag 1 entweder anhand der roten oder der blauen

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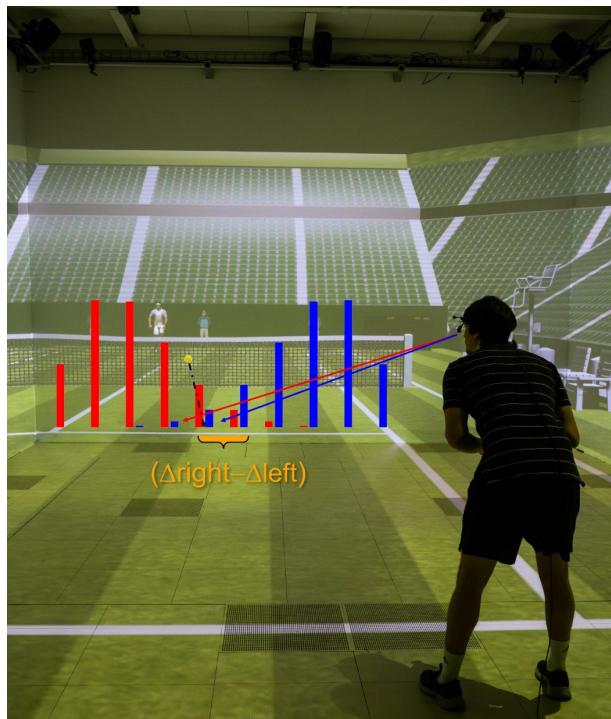
<sup>3</sup> In allen drei Experimenten wurde die Darstellung eines männlichen Avatars verwendet, da die Ballgeschwindigkeiten orientiert am professionellen Männertennis simuliert wurden.

Wahrscheinlichkeitsverteilung und vice versa an Tag 2 (Abbildung 3: rot vs. blau). Als Indikator für die frühe Schätzung des Ballabsprungorts durch die Versuchspersonen wurden die Blickfixationen nach der prädiktiven Sakkade in Richtung des erwarteten Ballabsprungorts analysiert. Zusätzlich gaben die Versuchspersonen eine explizite Schätzung des Ballabsprungorts mit einem Laserpointer nach dem Tennisrückschlag. Jeder 16. Versuch wurde auf einer der beiden zentralen Positionen gespielt (siehe Abbildung 3), da dies die anschliessende Berechnung von Unterschieden ( $\Delta\text{right}-\Delta\text{left}$ ) der Abweichungen der Fixationen und den expliziten Schätzungen zum tatsächlichen Ballabsprungort zwischen Tag 1 ( $\Delta\text{right}$  oder  $\Delta\text{left}$ ) und Tag 2 ( $\Delta\text{left}$  oder  $\Delta\text{right}$ ) bei kinematisch identischen Aufschlägen ermöglichte.

Mit diesem experimentellen Setup wurden zwei Studien durchgeführt. In Experiment 2 war die visuelle Unsicherheit erhöht, da der Ball schneller gespielt wurde (d. h., die verfügbare Zeit zur Verarbeitung visueller Informationen wurde verringert), während alle anderen Details identisch zu Experiment 1 blieben.

### **Abbildung 3**

*Blickverhalten und Wahrscheinlichkeitsverteilungen der Ballabsprungorte*



*Anmerkung.* Im Versuchsaufbau der virtuellen Realität wurden 320 Aufschläge am ersten Tag mit roter oder blauer Wahrscheinlichkeit verteilt und am zweiten Tag umgekehrt. Jeder 16. Versuch wurde auf einer der beiden zentralen Positionen gespielt, da dies die anschliessende Berechnung der Unterschiede im Blickverhalten und explizite Beurteilungen der

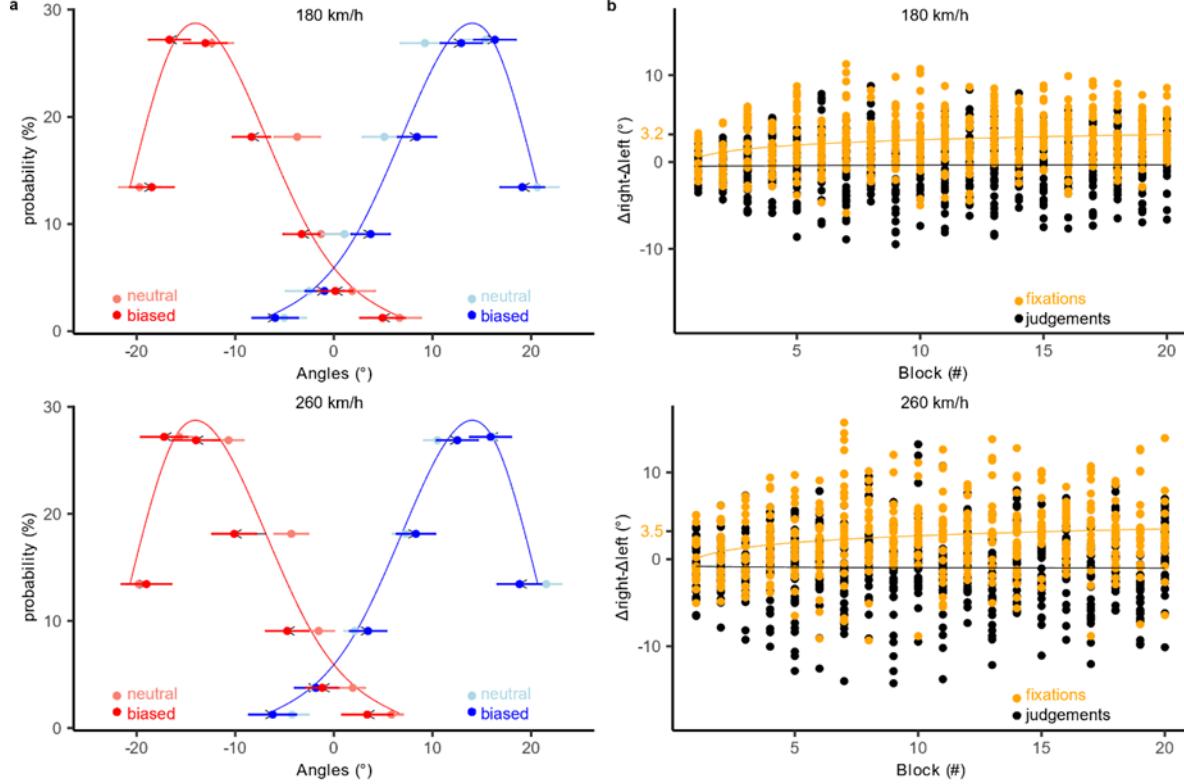
Ballabsprungstellen zwischen Tag 1 und Tag 2 für kinematisch identische Aufschläge ( $\Delta$ right– $\Delta$ left) ermöglichte.

Während in Abbildung 4 an allen Positionen (bis auf eine) die Fixationen nach der erfahrenen Poisson-Verteilung (dem tendenziell ausgerichteten *Prior*) zu dessen zentraler Tendenz hin verschoben sind, kann dieses Muster bei den Fixationen mit neutralem *Prior* nicht gefunden werden. Mit erhöhter Ballgeschwindigkeit in Experiment 2 sind die Verschiebungen nach erfahrenem, tendenziell ausgerichtetem *Prior* noch stärker, während wieder kein Muster bei den Fixationen mit neutralem *Prior* erkennbar ist. Dies veranschaulicht, dass akkumuliertes Vorwissen im prädiktiven Blickverhalten berücksichtigt wird, insbesondere bei höherer Aufschlaggeschwindigkeit.

Regressionsanalysen zur Entwicklung des Einflusses des tendenziell ausgerichteten *Priors* über ein ‹Match› (Einheit an einem Tag) ergaben einen signifikanten Anstieg der Unterschiede der Differenzwerte ( $\Delta$ right– $\Delta$ left) über die Zeit. Bei höherer Aufschlaggeschwindigkeit ist dieser stärker ausgeprägt, während für die expliziten Schätzungen keine Veränderungen über die Zeit feststellbar sind (siehe Abbildung 4). Dies bedeutet, dass angesammeltes Vorwissen das prädiktive Blickverhalten zunehmend beeinflusst, insbesondere unter der unsichereren Bedingung einer höheren Aufschlaggeschwindigkeit; das Vorwissen wird jedoch ‹überschrieben›, sobald zuverlässigere Wahrnehmungsinformationen über den tatsächlichen Absprungort des Balls verfügbar sind.

**Abbildung 4**

Blickverhalten und explizite Schätzungen des Ballabsprungorts bei unterschiedlichen Aufschlaggeschwindigkeiten



Anmerkung. a) Die horizontalen Achsen beziehen sich auf die Perspektive der Versuchspersonen in Richtung des Avatars, während auf den vertikalen Achsen die tatsächlichen Wahrscheinlichkeiten der jeweiligen Ballabsprungorte dargestellt sind. Die helleren Punkte stehen für die aggregierten Fixationen in der Bedingung mit gleichmässig verteilten Aufschlägen (neutrale *Prior*-Bedingung), während die dunkleren Punkte die aggregierten Fixationen in der Bedingung mit den in Abbildung 3 veranschaulichten Poisson-Verteilungen am Ende der Einheit (tendenziell ausgerichtete *Prior*-Bedingung) repräsentieren. Die Fehlerbalken spiegeln die 95 %-Konfidenzintervalle des arithmetischen Mittels über alle Versuchspersonen wider. b) Die orangefarbenen Punkte stellen die Unterschiede zwischen den Abweichungen des tatsächlichen Ballabsprungorts von der Fixationsposition für die rechte und die linke Verteilung dar ( $\Delta\text{right}-\Delta\text{left}$ ); diese wurden in jedem 16. Versuch für die beiden zentralen Positionen der überlappenden Verteilungen gemessen (siehe Abbildung 3). Die schwarzen Punkte zeigen die entsprechenden Differenzwerte für die expliziten Schätzungen der Versuchspersonen über die Ballabsprungpositionen für dieselben Versuche.

## 2.2 Integration des Vorwissens in die Bewegungsausführung des Rückschlags

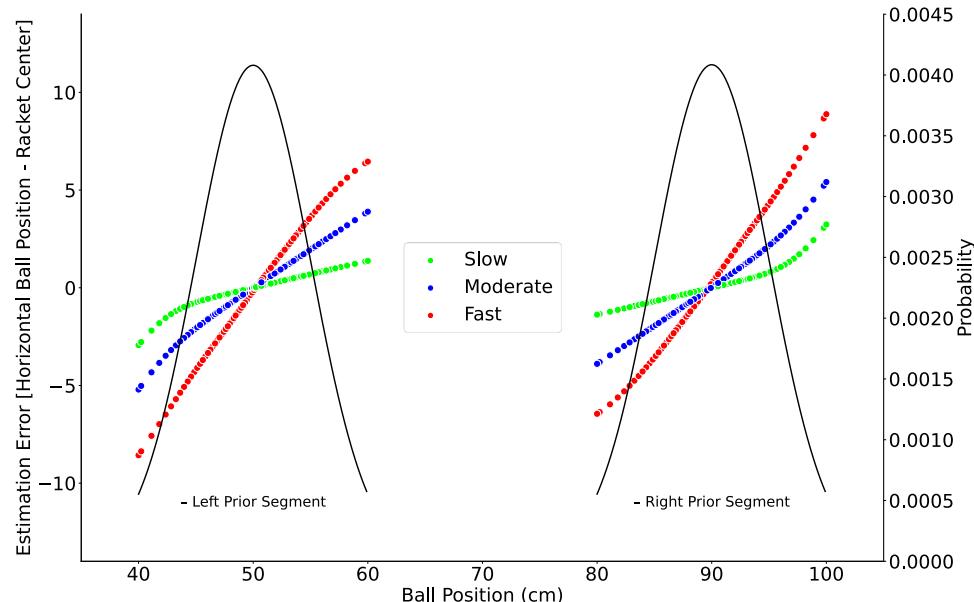
### Artikel III

Zahno, S.<sup>1</sup>, Beck, D.<sup>1</sup>, Hossner, E.-J. & Körding, K. (2024). Humans are able to learn bimodal priors in complex sensorimotor behaviour. [Unveröffentlichtes Manuskript].

Ziel dieser Studie war es, aufbauend auf Artikel II, weitere zentrale Vorhersagen aus der Bayes-Entscheidungstheorie (Körding & Wolpert, 2006) an der komplexen Aufgabe eines Tennisrückschlags zu testen. Aus der Bayes-Simulation in Abbildung 5 nach Ma (2023) ergeben sich für die Schätzung des Ballrückschlagorts folgende Vorhersagen: Nachdem Versuchspersonen die bimodale Aufschlagverteilung des Gegners erfahren und konsolidiert haben, sind (1) die Tennisrückschläge in Richtung der wahrscheinlichsten Orte verzerrt (bimodaler *Prior*-Effekt). (2) Das Ausmass des bimodalen *Prior*-Effekts hängt von der visuellen Unsicherheit ab, d. h., er ist bei schnellen Aufschlägen stärker ausgeprägt als bei moderaten und langsamen Aufschlägen. Diese Vorhersagen konnten empirisch bestätigt werden, was nachstehend noch erläutert wird.

**Abbildung 5**

*Bayes-Simulation für die Schätzfehler des Ballrückschlagorts mit bimodalem Prior*

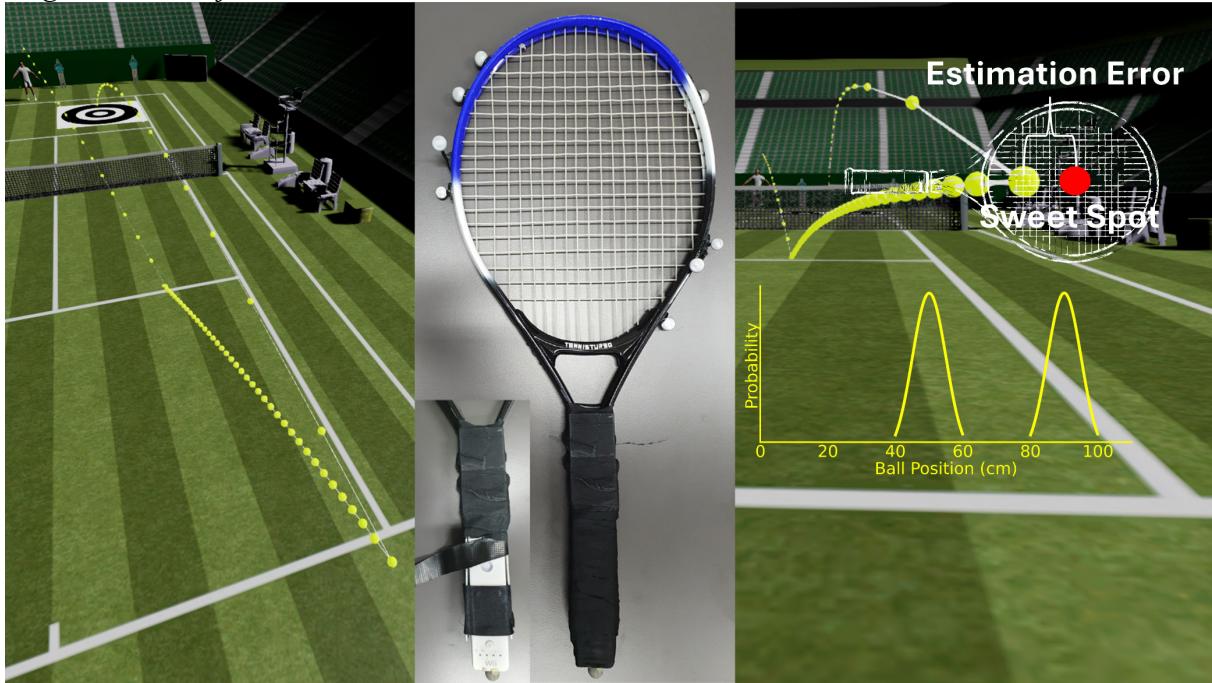


*Anmerkung.* Die Abbildung zeigt die simulierten Schätzfehler (horizontale Abweichung zwischen dem Ball und dem ‹Sweet Spot› des Schlägers) (y-Achse) im Verhältnis zu den tatsächlichen Ballpositionen (x-Achse). Das Simulationsskript ist auf GitHub verfügbar ([https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)).

Zur empirischen Untersuchung dieser Vorhersagen wurde das virtuelle Tennis-Experiment, das in den Experimenten des Artikel II verwendet wurde, weiterentwickelt (siehe Abbildung 6 sowie ein Video dazu auf Github: [https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)). Die Aufgabe der 24 rechtshändigen Versuchspersonen bestand darin, Tennisaufschläge in die Mitte eines Ziels auf dem gegnerischen Spielfeld zurückzuspielen. Die Aufschläge folgten einer vorgegebenen Trajektorie (siehe Abbildung 6, links) mit drei verschiedenen Anfangsgeschwindigkeiten des Balls: langsam ( $v = 108 \text{ km/h}$ ), moderat ( $v = 180 \text{ km/h}$ ), schnell ( $v = 252 \text{ km/h}$ ) und damit drei verschiedenen Stufen der visuellen Unsicherheit. Zur experimentellen Kontrolle wurden die zeitlichen Anforderungen jedoch in allen Bedingungen identisch gehalten. Technisch wurde dies realisiert, indem der tatsächlich zu treffende Ball ein unsichtbarer stationärer Ball war, der sich parallel zur Grundlinie der Ausgangsposition der Versuchspersonen auf der vorgegebenen Flugbahn befand und 200 ms vor bis 200 ms nach dem Passieren des sichtbaren Balls getroffen werden konnte. Die Abweichung des unsichtbaren Balls vom Schlägermittelpunkt (‘Sweet Spot’) auf der Achse parallel zur Grundlinie des Tennisplatzes bestimmte, wie nahe der Ball zum Zentrum des Ziels flog (siehe Abbildung 6, rechts). Nach jedem Rückschlag wurde auf einer Skala von 0 bis 100 als Rückmeldung angezeigt, wie gut die Versuchsperson den Ball getroffen hatte. Für die Versuchspersonen bestand ein finanzieller Anreiz in Form eines Wettbewerbs: Die drei leistungsstärksten Teilnehmenden erhielten Bücher-gutscheine.

**Abbildung 6**

Aufbau des virtuellen Tennis-Experiments: 3-D-Brille, Markercluster, Tennisschläger, mögliche Balltrajektorien



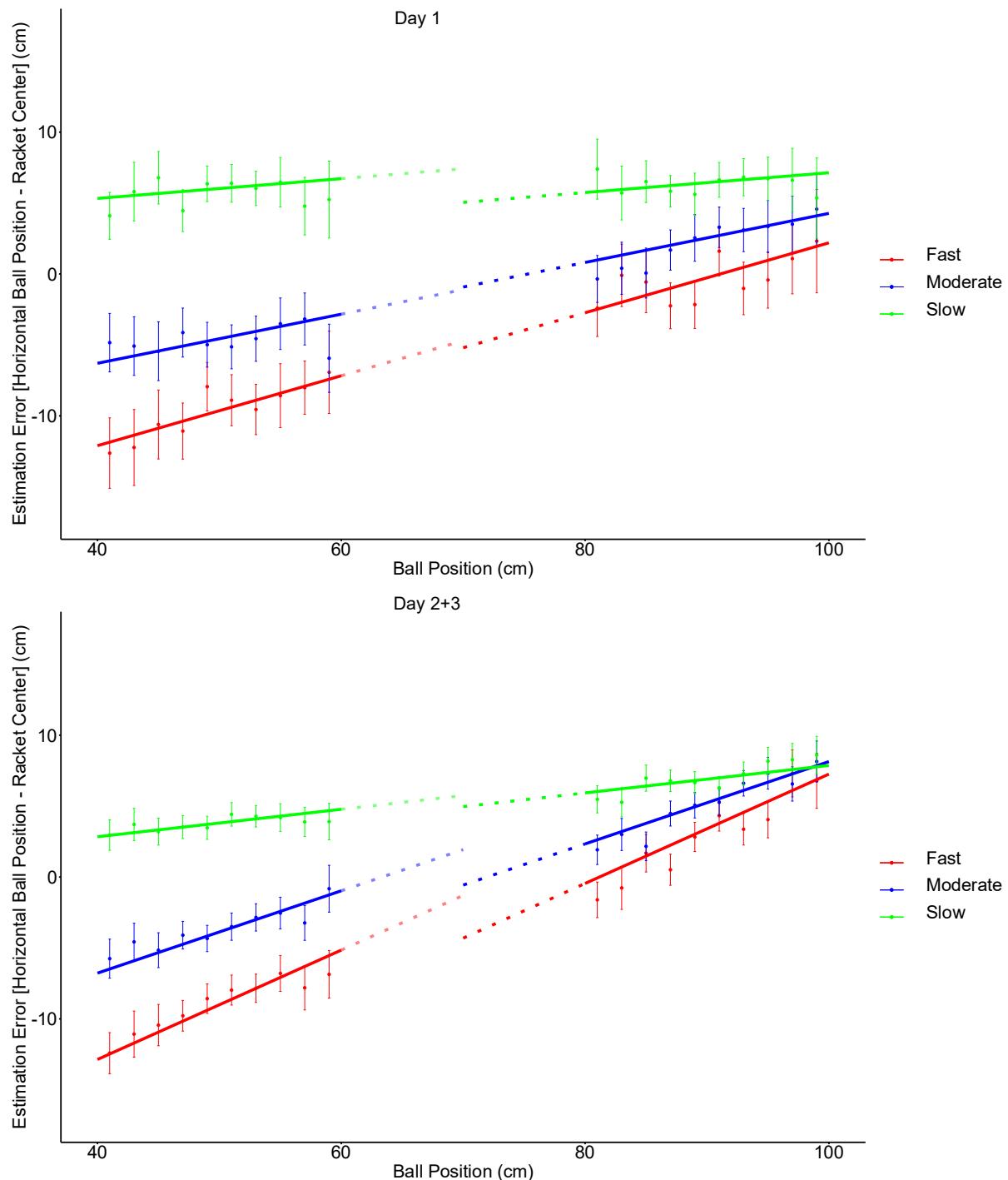
Anmerkung. Der Ball im Aufschlag folgte einer vorgegebenen Trajektorie (links). Der Rückschlag war ebenfalls durch eine Trajektorie festgelegt und wurde entsprechend dem Schätzfehler ausgerichtet (rechts in der Abbildung). Das Vorzeichen des Schätzfehlers war positiv, wenn der Schlägermittelpunkt (‘Sweet Spot’) zum Zeitpunkt des Rückschlags links vom Ball lag (im Beispiel rechts in der Abbildung ist der Schätzfehler also negativ). Die Aufgabe der Versuchspersonen bestand darin, den Ball in die Mitte des Ziels auf dem gegnerischen Platz zurückzuspielen (links in der Abbildung). Wurde der Ball perfekt mit dem Schlägermittelpunkt (‘Sweet Spot’) getroffen (null Schätzfehler), erfolgte der Rückschlag perfekt in Richtung Zielmitte und die maximale Punktzahl von 100 wurde angezeigt. Die Versuchspersonen hatten einen echten Schläger in der Hand mit einem integrierten Wii-Controller für haptisches Feedback. Am Schläger waren Marker platziert, um die Position aufzuzeichnen (Mitte der Abbildung).

Die Versuchspersonen spielten an drei unterschiedlichen Tagen innerhalb einer Woche jeweils 480 Rückschläge, aufgeteilt in zehn Blöcke von je 48 Versuchen. Die Aufschläge in jedem Block folgten der gleichen bimodalen Verteilung (siehe Abbildung 6, rechts). Ausgehend von der Annahme, dass die erworbenen Erfahrungen über den bimodalen *Prior* 24 Stunden benötigen, um sich während einer Nacht ausreichend zu konsolidieren (Körding & Wolpert, 2003), wurden alle Rückschläge am ersten Tag separat (siehe Abbildung 7, oben) sowie am

zweiten und dritten Tag zusammen ausgewertet (siehe Abbildung 7, unten). Sowohl am zweiten als auch am dritten Tag konnte eine Verzerrung des Schätzfehlers der Versuchspersonen beim Rückschlag durch den bimodalen *Prior* in Abhängigkeit von der Unsicherheitsbedingung anhand eines nichtlinearen ‹Sprungs› zwischen der linken und der rechten Seite der bimodalen Verteilung nachgewiesen werden (siehe Abbildung 7, unten). Dieser bimodale *Prior*-Effekt war in der Bedingung der schnellsten Bälle und somit höchster visueller Unsicherheit grösser als in der moderaten und langsamen Bedingung, was der Vorhersage aus der Bayes-Simulation entspricht (siehe Abbildung 5). Dieses Muster war am ersten Tag beim Erlernen des bimodalen *Priors* noch nicht vorhanden (siehe Abbildung 7, oben). Zusätzlich zum bimodalen *Prior*-Effekt wurde eine positive lineare Beziehung zwischen dem Schätzfehler und der Ballposition festgestellt. Dieser Effekt lässt sich gut durch biomechanische Randbedingungen und die damit verbundenen motorischen Kosten der möglichen Bewegungsabläufe erklären (z. B. Griessbach et al., 2022). Befand sich der Ball nahe am Körper der Versuchsperson (z. B. bei einer Ballposition von 40 cm), neigten die Versuchspersonen im Allgemeinen dazu, zu weit nach rechts zu schlagen, was zu einem negativen Fehler führte, insbesondere wenn die Bälle schnell waren. Die Daten von Tag 1 (ohne den bimodalen *Prior*-Effekt) deuten darauf hin, dass Bälle, die am rechten Ende der Skala gespielt wurden, mit einem fast gestreckten Arm getroffen wurden und so mit den geringsten motorischen Kosten erreicht werden konnten. Kam der Ball näher an den Körper, mussten die Versuchspersonen ihren Arm beugen oder einen kleinen Schritt nach links machen. Die Erkenntnis, dass Bewegungen in Richtung geringerer motorischer Kosten ausgerichtet sind, ist in der Literatur gut belegt (Gallivan et al., 2018; Wolpert & Landy, 2012). Damit überlagert sich der biomechanische Effekt mit dem bimodalen *Prior*-Effekt. Der verursachte nichtlineare ‹Sprung› des bimodalen *Prior*-Effekts kann aber ausschliesslich durch die Bayes-Integration erklärt werden.

**Abbildung 7**

*Bimodaler nichtlinearer Prior-Effekt in Abhangigkeit der visuellen Unsicherheit*



*Anmerkung.* Die Diagramme zeigen die Schatzfehler in Relation zum Abstand zwischen dem Schlägermittelpunkt (‘Sweet Spot’) und den Balltreffpunkten auf dem Schläger bei langsamer, moderater und schneller Ballgeschwindigkeit. Im oberen Teil sind die Daten von Tag 1 dargestellt, im unteren Teil die Daten von Tag 2 und 3 zusammen. Die Daten sind auf jeder Seite in zehn Abschnitte unterteilt; fur jeden Abschnitt werden das arithmetische Mittel und das 95 %-Konfidenzintervall wiedergegeben. Das Regressionsmodell wird mit den unabhangigen Faktoren der Ballposition und dem bimodalen Segmentfaktor (links 40–60 cm, rechts 80–100 cm) berechnet.

## ***2.3 Integration des Vorwissens in die kontinuierliche antizipative Entscheidungsfindung während des Splitsteps zur Leistungssteigerung***

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### **Artikel IV**

**Beck, D.**, Hossner, E.-J. & Zahno, S. (2024c). Tennis players exploit prior information to improve performance: Evidence for continuous anticipatory decision-making under uncertainty. [Unveröffentlichtes Manuskript].

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Mit der vorliegenden Studie wurden drei Ziele verfolgt. Erstens sollte untersucht werden, ob Tennisspieler Vorwissen in ihr antizipatives Verhalten während des Splitsteps integrieren und so die Leistung des Tennisrückschlags unter repräsentativen zeitlichen und räumlichen Anforderungen verbessern. Zweitens sollte das theoretische Verständnis von antizipativem Verhalten geklärt werden. Drittens sollte anhand des Tennisrückschlags ein Beitrag zum grundlegenden Verständnis der Bayes-Integration geleistet werden, wie Menschen Vorwissen und sensorische Informationen in der kontinuierlichen antizipativen Entscheidungsfindung bei komplexem ganzkörperlichem Verhalten nutzen.

Dazu wurden folgende Vorhersagen aufgestellt: Die Gewichtsverlagerung wird während des Splitsteps unter fortlaufendem Einbezug akkumulierten Wissens über situative Wahrscheinlichkeiten bezüglich der Aufschlagrichtung kontinuierlich angepasst. Vorwissen beeinflusst die Leistung zunehmend in kongruenten erwarteten vs. inkongruenten unerwarteten Versuchen. Das Einleiten einer Bewegung in die richtige Richtung und das Treffen des Balls können durch das Ausmass der Integration von Vorwissen anhand der Gewichtsverlagerung bereits in frühen Phasen des Splitsteps vorhergesagt werden. Diese Vorhersagen konnten empirisch bestätigt werden, wie im Folgenden erläutert wird.

Zur empirischen Untersuchung dieser Vorhersagen wurde das virtuelle Tennis-Experiment, das in den Experimenten des Artikel II verwendet wurde, weiterentwickelt (siehe ein Video dazu auf SwitchTube: <https://tube.switch.ch/videos/2otCdMkJpF>). Die Aufgabe der 14 erfahrenen Tennisspieler bestand darin, an zwei unterschiedlichen Tagen Aufschläge von einem Avatar im virtuellen Tennis zu retournieren. Dabei konnten sich die Versuchspersonen frei im Raum bewegen und hatten einen echten Schläger in der Hand (mit integrierter Vibrationsfunktion im Griff für die haptische Rückmeldung bei einem Treffer, siehe Abbildung 8 in der Mitte). Dabei wurden ihre Bewegungen mit fixierten Markerclustern (Reflektoren) im Raum gemessen (siehe Abbildung 8, links). Da der Avatar immer genau dieselben Bewegungen ausführte, konnten aus

dessen Bewegungskinematik keine Informationen über die folgende Ballflugbahn gewonnen werden. Es waren genau zwei verschiedene Ballflugbahnen möglich: entweder zur linken Seite bei Rückhandschlägen oder zur rechten Seite bei Vorhandschlägen (siehe Abbildung 8, rechts).

### Abbildung 8

*Aufbau des virtuellen Tennis-Experiments: 3-D-Brille, Markercluster, Tennisschläger, mögliche Balltrajektorien*



*Anmerkung.* Die Versuchspersonen wurden mit einer 3-D-Brille und sechs Markerclustern (links) sowie mit einem speziell angefertigten Tennisschläger mit integriertem Wii-Controller und weiteren Markern (Mitte) ausgestattet. Ihre Aufgabe bestand darin, virtuelle Aufschläge entweder mit der Vorhand oder der Rückhand zurückzuschlagen, wobei die Bälle einer von zwei möglichen Flugbahnen folgten, mit dem Ziel, die Mitte des Ziels auf der gegnerischen Seite des Platzes zu treffen (rechts).

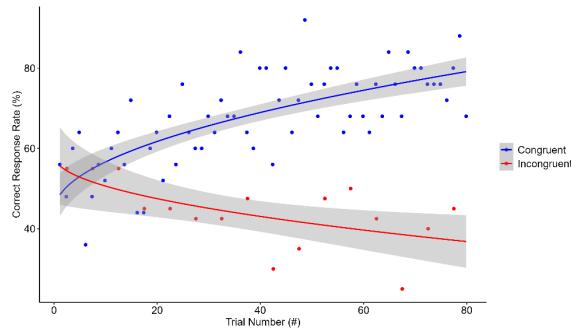
Nach den Aufwärmversuchen in einer Einheit wurden zwei Blöcke mit je 20 Aufschlägen mit einer Wahrscheinlichkeit von 50 % für jede Seite gespielt (neutrale Bedingung). Ohne weitere Instruktionen änderten sich die Wahrscheinlichkeiten (tendenziell ausgerichtete Bedingung) für die letzten vier Blöcke zu je 20 Versuchen auf 80 % für die eine Seite (kongruente Aufschläge) und 20 % für die andere Seite (inkongruente Aufschläge). Das Experiment war intraindividuell ausgeglichen durch ein exakt gespiegeltes Aufschlagmuster vom ersten zum zweiten Termin.

Die statistischen Analysen der mittleren Gewichtsverlagerung für die zweite Hälfte in der tendenziell ausgerichteten Bedingung ergaben, dass das Gewicht bereits 100 ms vor dem Aufschlag in Richtung der wahrscheinlicheren Seite verschoben ist und sich diese Tendenz im

Verlauf des entgegenkommenden Balls vergrössert. Je stärker die Gewichtsverlagerung in eine Richtung stattfindet, desto grösser wird auch die Wahrscheinlichkeit, dass bei der seitlichen Bewegungsinitiierung dieselbe Richtung eingeschlagen wird. Dies hat zur Konsequenz, dass mit zunehmender Erfahrung des tendenziell ausgerichteten *Priors* sowohl die Rate der korrekt eingeschlagenen Richtung (siehe Abbildung 9) als auch die Trefferrate (siehe Abbildung 10) im kongruenten Fall zunimmt und im inkongruenten Fall abnimmt. Folglich ist das erste Ziel erreicht, nämlich zu zeigen, dass die Integration des Vorwissens ins antizipative Verhalten während des Splitsteps zu einer Leistungssteigerung führt.

**Abbildung 9**

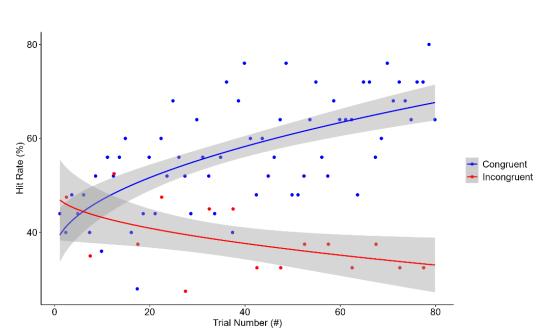
Entwicklung der Rate der korrekt eingeschlagenen Richtung



Anmerkung. Entwicklung der Rate korrekt eingeschlagener Richtung bei der seitlichen Bewegungsinitiierung im Tennisrückschlag bei kongruenten vs. inkongruenten Versuchen im Verhältnis 80:20 der Aufschlag-Richtungswahrscheinlichkeiten. Der Unschärfebereich stellt ein 95%-Konfidenzintervall der Regressionslinien dar.

**Abbildung 10**

Entwicklung der Trefferquote



Anmerkung. Entwicklung der Trefferquote beim Tennisrückschlag bei kongruenten vs. inkongruenten Versuchen im Verhältnis 80:20 der Aufschlag-Richtungswahrscheinlichkeiten. Der Unschärfebereich stellt ein 95%-Konfidenzintervall der Regressionslinien dar.

Das zweite Ziel bestand darin, das theoretische Verständnis in Bezug auf antizipatives Verhalten zu klären. Wie aus führenden motorischen Kontrolltheorien hervorgeht und in Unterkapitel 1.3 *optimale Feedback-Kontrolle* erläutert, sagt das interne Modell kontinuierlich zukünftige Zustände des sensomotorischen Systems vorher, um mit der Unsicherheit verzögter Signale umgehen zu können. Dementsprechend ist die Vorhersage des nächsten Zustands des Systems grundlegend für die Verhaltenskontrolle und kein spezifisches Merkmal von Handlungen, die aufgrund hoher zeitlicher Anforderungen eine ‹Antizipation› erfordern – wie im Fall des Tennisrückschlags. Der Unterschied zwischen Aufgaben mit geringem und hohem Zeitdruck besteht darin, dass im ersten Fall ausreichend Zeit zur Verfügung steht, um

auf die Bestätigung der eigenen Vorhersage durch eingehende reafferente Signale zu warten, während man sich im zweiten Fall der ‹Antizipation› auf die aktuell verwertbaren Vorhersagen verlassen muss, um die Handlung einzuleiten. In beiden Fällen stellt die Verhaltenskontrolle allerdings einen fortlaufenden Prozess antizipatorischer Online-Entscheidungen dar (Gallivan et al., 2018; Gordon et al., 2021).

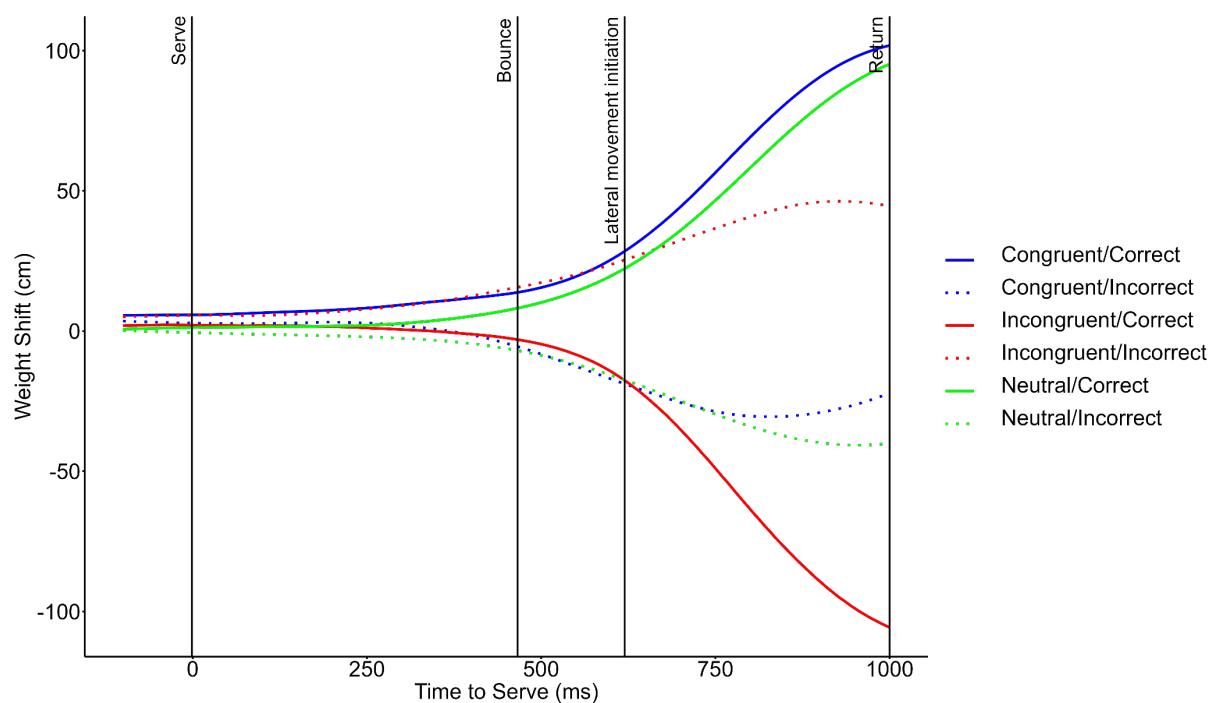
In Bezug auf das dritte Ziel finden sich in Abbildung 11 drei Hinweise für eine kontinuierliche antizipative Entscheidungsfindung entsprechend der Affordanz-Wettbewerbs-Hypothese (Cisek, 2007). Erstens sind die Gewichtsverlagerungen der kongruenten/korrekteten und inkongruenten/inkorrekteten Antworten bis zur Einleitung der seitlichen Bewegung nahezu deckungsgleich. Danach scheint es, dass die Spieler in den inkongruenten/inkorrekteten Fällen (aufgrund der eingehenden sensorischen Evidenz) zu erkennen beginnen, dass sie falsch liegen. Die gleiche (aber gespiegelte) Entwicklung der Gewichtsverlagerung ist bei den kongruenten/inkorrekteten und inkongruenten/korrekteten Rückschlägen zu beobachten. Dies deutet darauf hin, dass die Spieler ständig die Kosten der beiden Antwortmöglichkeiten abwägen und – wenn sie erkennen, dass sie sich auf der falschen Seite befinden – die Bewegung auslaufen lassen. Ein zweiter Aspekt betrifft die Beobachtung, dass bei inkongruent/korrekteten und kongruent/inkorrekteten Versuchen die Gewichtsverlagerung selbst in der sehr frühen Phase des Splitsteps nicht zur wahrscheinlicheren Seite tendiert, sondern nahe null bleibt (Abbildung 11). Dieses Muster könnte zwar auch auf eine vorgeplante Bewegungseinleitung zurückgeführt werden, etwa im Sinne des in der Kognitionspsychologie bekannten Phänomens der Gambler's Fallacy: Demnach erwarten Spieler\*innen nach mehreren aufeinanderfolgenden kongruenten Aufschlägen gelegentlich einen inkongruenten Aufschlag, da sie davon ausgehen, dass eine Variation wahrscheinlicher wird (z. B. beschrieben für Fußballtorhüter\*innen von Misirlisoy & Haggard, 2014).

Da auf dieser Basis jedoch eher negative als Nullwerte für die Gewichtsverlagerung zu erwarten wären, kann dieser Befund als weiterer Beleg für die Interpretation gewertet werden, dass die Spieler die beiden Antwortmöglichkeiten kontinuierlich evaluieren. Da die Gewichtsverlagerungen in frühen Phasen des Splitsteps um einen Mittelwert herum verteilt sind, lässt sich vorhersagen, dass Spieler gelegentlich mit einer weniger ausgeprägten Gewichtsverschiebung zur kongruenten Seite beginnen, was wiederum die Attraktivität der inkongruenten Seite erhöht. Diese zufällige Abweichung spiegelt sich dann in einer höheren Wahrscheinlichkeit wider, bei inkongruenten Versuchen eine Bewegung in die richtige Richtung einzuleiten, aber auch bei kongruenten Aufschlägen eine falsche Bewegung

auszuführen (vgl. Selen et al., 2012). Drittens – und ganz im Sinne dieser Erklärung – ist anzumerken, dass sich die Gewichtsverlagerungen bei kongruent/korrekteten und neutral/korrekteten Trials über den Splitstep nahezu parallel entwickeln (Abbildung 11). Dies bedeutet, dass – wenn bereits eine Präferenz zu einer Handlungsoption besteht – diese umso attraktiver wird, je schwieriger die alternative Option zu erreichen wird, da Letztere biomechanisch bedingte motorische Kosten verursacht (Griessbach et al., 2022). Der Vorteil der Integration von Vorwissen in einem frühen Stadium einer Handlung bleibt also während des gesamten Prozesses der kontinuierlichen antizipativen Entscheidungsfindung und sensomotorischen Steuerung erhalten.

**Abbildung 11**

*Verlauf der Gewichtsverlagerung während des Splitsteps beim Tennisrückschlag*



*Anmerkung.* Verlauf der Gewichtsverlagerung über den Splitstep bei kongruenten vs. inkongruenten Trials mit korrekten vs. inkorrekten Antworten, aggregiert über die letzten zwei Blöcke (2. Hälfte mit bereits erfahrenem, tendenziell ausgerichtetem *Prior*) mit Aufschlagrichtungswahrscheinlichkeiten von 80:20. Die Werte der Gewichtsverlagerung sind relativ zum tendenziell ausgerichteten *Prior* und somit positiv, wenn die Gewichtsverlagerung in Richtung der wahrscheinlichen Richtung (*Prior*) erfolgt. Im Vergleich dazu die Gewichtsverlagerungsdynamik für die neutrale Bedingung mit Aufschlagrichtungswahrscheinlichkeiten von 50:50, aufgetragen relativ zur korrekten Bewegungsrichtung.

### **3 Zusammenfassung, Diskussion und Ausblick**

Normative Theorien wie die Bayes-Entscheidungstheorie (Körding & Wolpert, 2006) bieten einen vereinheitlichenden Erklärungsrahmen im Umgang mit sensomotorischer Unsicherheit in Wahrnehmungs- und Handlungsprozessen. In der Übersichtsarbeit des Artikels I (Beck et al., 2023) wurde gezeigt, dass die meisten Studien zum Umgang mit Unsicherheit in komplexen sensomotorischen Bewegungsaufgaben, wie sie im Alltag oder – häufig in Extremform der Komplexität – im Sport auftreten, in den Rahmen normativer Theorien passen. Bis auf wenige Ausnahmen haben sich diese Studien allerdings nicht mit eindeutigen Vorhersagen befasst, die sich aus normativen Theorien ableiten lassen. Daher wurden in einem zweiten Schritt in dieser Dissertation in einer dreiteiligen empirischen Studienreihe Vorhersagen aus der Bayes-Entscheidungstheorie (Körding & Wolpert, 2006) abgeleitet und in den Sportkontext übersetzt sowie bestätigt. So konnte nachgewiesen werden, dass der Mechanismus der Bayes-Integration des Vorwissens zur Reduktion von Unsicherheit auch in einer komplexen Aufgabe wie dem Tennisrückschlag folgendermassen wirkt: Verschiedene Wahrscheinlichkeitsverteilungen (auch komplexe bimodale) können erlernt werden und beeinflussen mit zunehmender Verlässlichkeit das Blickverhalten und somit die Wahrnehmung, die Bewegungsausführung des Rückschlags sowie in dessen Vorbereitung die Gewichtsverlagerung im Splitstep und optimieren dadurch die daraus resultierende Leistung. Diese Ergebnisse untermauern somit zwei Jahrzehnte experimenteller Grundlagenforschung (Berniker et al., 2010; Chambers et al., 2018; Körding et al., 2004; Körding et al., 2007; Rubinstein et al., 2024; Tassinari et al., 2006).

Für die Sportpraxis ist es bedeutend, einen empirisch fundierten Erklärungsrahmen zu besitzen, wie Vorwissen die sportliche Leistung verbessert. Im Spitzensport wird der Nutzen von Vorwissen, etwa in Form aufbereiteter gegnerischer Spieler\*innen-Statistiken, bereits anerkannt und gezielt eingesetzt (Magnaguagno & Beck, 2024).

In der Studienreihe dieser Dissertation wurde indes nicht allein empirisch bestätigt, dass der Transfer der Bayes-Integration auf komplexe Aufgaben – trotz teils überlagernder biomechanischer Effekte (Artikel III, Zahno, Beck, Hossner, et al., 2024) – möglich ist. Vielmehr wurde auch ein Beitrag zum Verständnis geleistet, wie normative Theorien aus der Grundlagenforschung im Sport zu interpretieren sind. Dies lässt sich anhand von drei Aspekten näher ausführen. Erstens entsteht visuelle Unsicherheit im Sport selten durch visuelle Unschärfe wie im Grundlagenexperiment von Körding et al. (2004) – etwa bei aufkommendem Nebel beim Skifahren –, sondern in der Regel durch hohen Zeitdruck und und die daraus

resultierende begrenzte Akkumulation visueller Informationen, wie es beim Tennis-Rückschlag auf schnelle Bälle der Fall ist.

Dies hat zur Konsequenz, dass Vorwissen in der kontinuierlichen antizipativen Entscheidungsfindung unter hohem Zeitdruck frühe vorbereitende Bewegungen (Blickbewegungen und Gewichtsverlagerung im Splitstep) beeinflusst. Steht aber ausreichend Zeit zur Verfügung, können vorhergesagte Zustandsschätzungen durch eingehende sensorische Informationen überprüft und gegebenenfalls angepasst werden.

Diese Erkenntnis löst – als zweiter Aspekt – die scheinbar unvereinbaren Positionen in der klassischen Anticipationsforschung in der Sportwissenschaft auf, dass Anticipation einerseits der Schlüssel zum Tennisrückschlag ist (Williams & Jackson, 2019) und andererseits kein offenkundiges antizipatorisches Verhalten beobachtet würde, wenn Spieler\*innen tatsächlich reale Tennisaufschläge zurückspielen (Avilés et al., 2019). Tennisspieler\*innen sind nicht nur in der Lage, situative Wahrscheinlichkeiten zu extrahieren (Farrow & Reid, 2012; Loffing & Hagemann, 2014; Loffing et al., 2016; Murphy et al., 2016; Murphy et al., 2018), sondern nutzen tatsächlich aktiv Vorwissen, indem sie ihre Gewichtsverlagerung und ihr Blickverhalten in der Vorbereitung des Tennisrückschlags optimieren. In Anbetracht dieser empirischen Befunde – sowie im Kontext aktueller Sensomotorik-Theorie – ist für die Verhaltenskontrolle die Verwendung interner Vorhersagen zur Steuerung von Handlungen grundlegend und nicht nur ein spezifisches Merkmal von Handlungen, die aufgrund hoher zeitlicher Anforderungen ‹Anticipation› erfordern.

Drittens wurden insbesondere mit Artikel IV (Beck, Hossner, et al., 2024) frühere Studienergebnisse (Jackson et al., 2020; Mann et al., 2014) bestätigt, dass sich Spieler\*innen auf Vorwissen verlassen, was zu Leistungssteigerungen bei kongruenten Versuchen und umgekehrt zu Leistungsabnahmen bei inkongruenten Versuchen führt. Diese Ergebnisse wurden jedoch dahin gehend präzisiert, dass Leistungsabnahmen bei inkongruenten Versuchen nicht als ‹Fehler› des Systems betrachtet werden sollten. Vielmehr sollten die Kosten für Fehlentscheidungen in seltenen Fällen als funktionale Strategie zur Verbesserung der Gesamtleistung gelten, wie es die Bayes-Entscheidungstheorie vorhersagt. Diese Erkenntnisse tragen dementsprechend zur Präzisierung des Verständnisses der Anticipationsforschung der vergangenen 50 Jahre bei (Loffing & Canal-Bruland, 2017; Mann et al., 2014; Williams & Jackson, 2019).

In den drei empirischen Studien dieser Dissertation wurde veranschaulicht, wie der Einfluss verschiedener *Priors* mit zunehmender Verlässlichkeit steigt. Dabei waren die

Wahrscheinlichkeiten stabil und die Versuchspersonen waren daher grösstenteils mit erwarteter Unsicherheit konfrontiert. Im Sport, insbesondere im Tennisspiel, sind die Aufschlagtendenzen einer Spieler\*in nicht derart konstant. Psychischer Druck bei entscheidenden Punkten, Ermüdung, erster beziehungsweise zweiter Aufschlag oder Taktikanpassungen sind Kontexte, die eine Änderung der Aufschlagtendenzen mit sich bringen. Erklärungsansätze, wie mit solcher Volatilität und wechselnden Kontexten umgegangen werden kann, bietet der normative theoretische Ansatz probabilistischer Inferenz innerhalb der Bayes-Entscheidungstheorie im vereinheitlichenden Prinzip der «kontextuellen Inferenz» (Heald et al., 2021, S. 489). Diese erklärt, wie Vorwissen gebildet, welches Vorwissen adressiert und wie Vorwissen aktualisiert wird. Die Untersuchung kontextueller Inferenz anhand komplexer Aufgaben wie dem Tennisrückschlag wird entscheidend sein, um den Einfluss von Vorwissen zur Reduktion von Unsicherheit in dynamischen Situationen über längere Zeiträume, etwa während eines Tennisspiels, noch besser zu verstehen.

In dieser Dissertation lag der empirische Fokus auf der Untersuchung des Mechanismus (2) *Integration des Vorwissens*. Sowohl aus der Sportwissenschaft (Beck et al., 2023; Gredin et al., 2020; Harris, Arthur, Broadbent, et al., 2022) als auch aus den Grundlagenwissenschaften Psychologie und Neurowissenschaft (Cisek & Green, 2024; Maselli et al., 2023; Tsay et al., 2024) wird generell ein Transfer von einfachen Laboraufgaben zu komplexem Bewegungsverhalten gefordert. Wie insbesondere aus Artikel I (Beck et al., 2023) hervorgeht, existiert in Bezug auf diesen Transfer in den anderen Mechanismen (1) *Multisensorische Integration*, (3) *Risiko-Optimierung*, (4) *Redundanz-Ausnutzung* und (5) *Impedanzkontrolle* noch Forschungsbedarf. Die Studienreihe dieser Dissertation sowie vereinzelte weitere Studien (z. B., Arthur & Harris, 2021; Zahno, Beck, Kredel, et al., 2024) zeigen, wie durch den Einsatz virtueller Welten dieser Transfer von einfachen Laboraufgaben zu komplexem Bewegungsverhalten unter strengen experimentellen Bedingungen und gleichzeitig hoher externer Validität konkret gelingen kann.

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## **Appendix: Zeitschriftenbeiträge der kumulativen Dissertation**

### **Artikel I**

**Beck, D.**, Hossner, E.-J. & Zahno, S. (2023). Mechanisms for handling uncertainty in sensorimotor control in sports: A scoping review. *International Review of Sport and Exercise Psychology*, 1–35. <https://doi.org/10.1080/1750984X.2023.2280899>

### **Artikel II**

**Beck, D.<sup>4</sup>**, Zahno, S.<sup>1</sup>, Kredel, R. & Hossner, E.-J. (2024). From simple lab tasks to the virtual court: Bayesian integration in tennis. [Manuskript in Begutachtung im *Journal of Neurophysiology*].

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### **Artikel III**

Zahno, S.<sup>1</sup>, **Beck, D.<sup>1</sup>**, Hossner, E.-J. & Körding, K. (2024). Humans are able to learn bimodal priors in complex sensorimotor behaviour. [Unveröffentlichtes Manuskript].

Später veröffentlicht unter: <https://doi.org/10.1101/2025.02.12.637788>

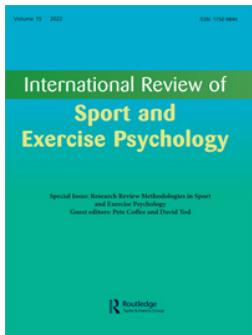
### **Artikel IV**

**Beck, D.**, Hossner, E.-J. & Zahno, S. (2024). Tennis players exploit prior information to improve performance: Evidence for continuous anticipatory decision-making under uncertainty. [Unveröffentlichtes Manuskript].

Später veröffentlicht unter: <https://doi.org/10.21203/rs.3.rs-7154501/v1>

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<sup>4</sup> Diese Autoren haben gleich viel zum Forschungsprojekt beigetragen und teilen sich die Erstautorenschaft der Beiträge.



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Damian Beck, Ernst-Joachim Hossner & Stephan Zahno

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# Mechanisms for handling uncertainty in sensorimotor control in sports: a scoping review

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## ABSTRACT

In complex naturalistic sensorimotor behaviour, uncertainty arises from ambiguities and delays in sensory inputs as well as noise in sensory detection and motor execution. In sports, where human capacity reaches its limits, handling uncertainty is crucial. In fundamental motor-control research, five mechanisms for handling uncertainty – multisensory integration, prior-knowledge integration, risk optimisation, redundancy exploitation, and impedance control – have been proposed based on a rich body of evidence, mostly investigating simple arm and hand movement tasks. Here we review the literature investigating more complex tasks and examine to what extent these mechanisms explain handling uncertainty in sensorimotor control in sports. A systematic search following the PRISMA guidelines resulted in the consideration of 82 studies. These studies provide robust empirical evidence for the mechanisms of multisensory integration, prior-knowledge integration, and redundancy exploitation in complex naturalistic behaviour, whilst only a few publications focused on the other two mechanisms. Furthermore, only a few studies test model-based predictions that can be derived from the theoretical frameworks to a satisfactory extent. Finally, beyond discussing these explanatory mechanisms in isolation, we propose a unifying model that builds upon the theory of optimal feedback control, in which the mechanisms can be related to each other coherently.

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## 1. Introduction

Our world is riddled with uncertainty. In sports, for instance, when a climber jumps to a hold she has never touched before, a number of – maybe vital – questions arise. How far is the jump and how big is the swing that has to be absorbed? How good is the hold in terms of shape and friction? Where exactly is the sweet spot of the hold? What is the optimal sequencing of subsequent actions and what is the optimal timing for this sequence? What are the consequences of a fall? In such cases of natural sensorimotor behaviour, uncertainties like these arise from different sources; particularly from ambiguities in the sensed environment (e.g. Kersten et al., 2004; Witt & Riley, 2014) as well as from

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noise in sensory and motor systems (e.g. Faisal et al., 2008; Kording & Wolpert, 2006). Moreover, we have to handle sensory-input delays and typically, the multiple possible solutions to solve a motor task (e.g. Franklin & Wolpert, 2011).

When relating these considerations for behavioural control to probabilities, uncertainty can be defined as ‘possible states or outcomes measured by assigning probabilities to each possible state or outcome’ (Sternad, 2018, p. 184). This definition can be further specified by the differentiation between expected and unexpected uncertainty and volatility (Bland & Schaefer, 2012). Expected uncertainty regards cases when the outcome probabilities are known and stable, like the outcome uncertainty of rolling a six from a dice. Unexpected uncertainty would occur if the dice was suddenly changed to a cheat dice with unusual probabilities, whose probabilities can no longer be predicted by past experience. Finally, volatility means a frequent change in probabilities, for example, due to a frequent change over several cheat dice.

In sports, where human capacities are characteristically brought to their limits, successfully handling different types of uncertainty is crucial. Thus, the question arises of how humans are able to master this challenge. In fundamental sensorimotor-control research, a rich body of evidence has been provided for five mechanisms contributing to the scientific explanation of how humans handle uncertainty in behavioural control (for reviews, e.g. Franklin & Wolpert, 2011; Gallivan et al., 2018; Kording & Wolpert, 2006; Todorov, 2004):

#### (1) *Multisensory integration*

In order to reduce sensory ambiguity and to obtain a more robust state estimate, information from different sensory modalities can be combined and weighted according to their relative reliability; as commonly approached by the principles of Bayesian statistics (Ernst & Banks, 2002).

#### (2) *Prior-knowledge integration*

Similar to integrating different sensory inputs, uncertainties about the current state can be reduced by integrating current sensory information and existing prior knowledge according to Bayesian principles (Kording & Wolpert, 2004).

#### (3) *Risk optimisation*

As real-world tasks typically exhibit motor equivalence, meaning that many possible movement variants exist to solve a given task, it is valuable to estimate the uncertainty connected to these movement variants to consider the associated risks. To obtain an optimal trade-off between outcome-related costs and rewards, inherent motor noise should be taken into account in motor planning and control (Trommershäuser et al., 2003).

#### (4) *Redundancy exploitation*

Behavioural control can be conceptualized as searching for an optimal variant in a redundant task-solution space. This implies that uncertainty due to motor noise only needs to be minimized if goal-relevant variables vary beyond the range of optimal solutions – an

idea that can be traced back to Bernstein (1987) and has been formulated thereafter in the uncontrolled-manifold hypothesis (Scholz & Schöner, 1999) or the principle of minimal intervention (Todorov & Jordan, 2002).

### (5) *Impedance control*

As an alternative to actively handling noise-related uncertainty, robust motor-task solutions can also be achieved by adapting one's resistance to expected uncertainty. Specifically, by co-contracting muscles and thereby increasing muscle stiffness and impedance to respond to an expected range of perturbations, unexpected perturbations within the expected intensity range are immediately damped (Burdet et al., 2001; Hogan, 1984).

Since the five reported mechanisms are drawn from foundational motor-control research, most of which examines simple pointing or reaching movements, the question arises whether or to what extent the same mechanisms hold for the handling of sensorimotor uncertainty in more complex real-world situations, as are common in sports. The main goal of this review is therefore to investigate the external validity of these mechanisms. On the one hand, there is no reason to necessarily doubt this, but on the other hand, the external validity of basic research results cannot be taken for granted (see, e.g. Wolpert et al. (2011, p. 748) in their review on computational mechanisms of human motor learning: 'It is not clear whether the learning models that are developed will generalize to tasks such as tying shoelaces or learning to skateboard.'). Hence, it seems extremely valuable for both sports scientists and practitioners to take a closer look at exactly this question in order to gain a well-grounded knowledge base for handling uncertainty in complex, in particular sports-related tasks. Furthermore, the present review can claim relevance for contexts beyond sports, such as questions of complex sensorimotor control in professional fields or traffic.

In a recent narrative review, Gredin et al. (2020b) propose a Bayesian framework to explain anticipatory behaviour in sports. They summarize multiple studies with overall good evidence in favour of the integration of contextual information into perception. The authors conclude that athletes reduce perceptual uncertainty by weighting different contextual and kinematic information sources according to their reliability and, by this means, enhance anticipatory behaviour. However, this conclusion on multi-sensory integration was drawn from foundational research on pointing and reaching-and-grasping tasks. Furthermore, by focusing on Bayesian inference in anticipation, Gredin et al. (2020b) do not address additional mechanisms for handling uncertainty in complex motor behaviour; namely, risk optimisation, redundancy exploitation, and impedance control.

Therefore, in the present scoping review, we systematically list and discuss all original articles on handling uncertainty in natural sensorimotor, in particular sports-related tasks. This approach not only builds from a narrative to a scoping review, but also extends investigations on anticipatory behaviour to consider control mechanisms beyond Bayesian inference. Furthermore, we substantially broaden the current view by relating our findings to theoretical approaches rooted in either the ecological or the cognitive branch of motor coordination and control theory.

## 2. Method

This review followed the guidelines of Tricco et al. (2018) for the Preferred Reporting Items for Systematic Reviews and Meta-Analyses extension for scoping reviews (PRISMA-ScR). The respective checklist can be found in Appendix A.

### 2.1. Inclusion and exclusion criteria

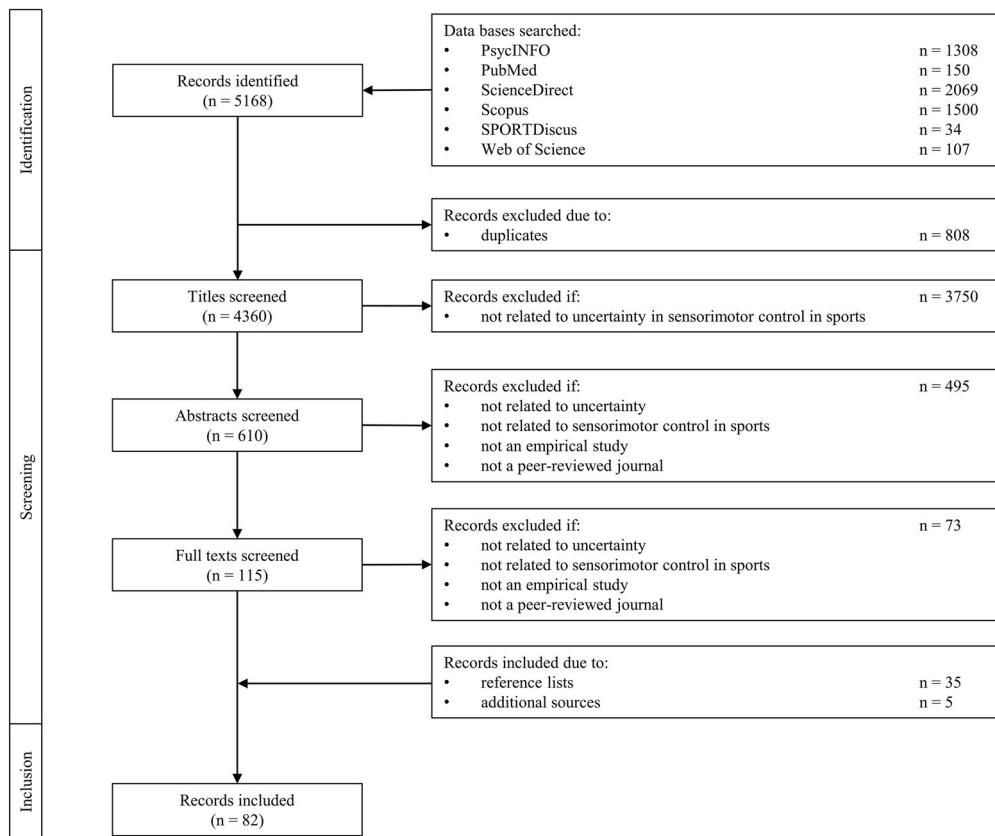
To be included in the review, the studies had to examine uncertainty aspects related to sensorimotor control in sports. No studies on sensorimotor learning or optimisation were included (e.g. focussing on the optimal degree of fluctuations in practice; Hossner et al., 2016). Moreover, studies on scattering in motion were excluded from the current review if there was no examination of task-relevant or -irrelevant variables (e.g. Den Hartigh et al., 2015). Studies on Fitts' or Hick's law were excluded as they do not address uncertainty at the core (e.g. Sanderson, 1983). Furthermore, no clinical or paediatric studies were considered as the focus was not on impairments or the development of the reviewed mechanisms.

The exclusion criterion for studies 'not related to sensorimotor control in sports' pertained to those which investigated decision-making behaviour with uncertainty, however, did not deploy a sensorimotor task (e.g. Adie et al., 2020). To be considered sports-related and included in the present review, the studies had to meet at least one of the following two conditions: Studies were included that used naturalistic sports-related stimuli (e.g. Gredin et al., 2018; Helm et al., 2020) or required a motor response beyond pointing or reaching-and-grasping movements, i.e. tasks involving whole-body movements such as throwing or catching (e.g. Stevenson et al., 2009). To clarify, if only a simple motor action was requested, but a natural sports-related stimulus was used, the study was still considered, because the complexity of reacting to, for instance, videos of moving persons with a high degree of dynamics in it (even with a button press) seems to be sufficiently close to real-world tasks like pulling the brake at the right moment in downhill biking. However, studies in which no motor response (i.e. exclusively perceptual tasks) was required at all were not included in the review.

Further, only original articles with empirical data published in peer-reviewed journals in English language were included. Finally, it should be noted that the paper of Scott et al. (1997) summarizes the data of several other studies (Berg et al., 1994; Hay, 1988; Hay & Koh, 1988; Lee et al., 1982), which will not be considered separately in the results section.

### 2.2. Identification and screening

The following six academic databases were searched: PsycINFO, PubMed, ScienceDirect, Scopus, SPORTDiscus and Web of Science. The last search was conducted on July 15, 2023, using all searching fields with the following terms: (uncertainty OR noise) AND (sensor\* OR motor) AND control AND sport AND movement. Moreover, the search was filtered (if possible) to English and original articles that have undergone a peer-review process. In the Scopus database, the subject area was further limited to social science or psychology due to many hits from other scientific disciplines (e.g. engineering or



**Figure 1.** PRISMA flow diagram for the literature search.

computer science). The exact search strategy applied to each database is documented in Appendix B.

As illustrated in Figure 1, a total of 5,168 hits were exported to EndNote. Two raters independently screened all titles and abstracts after removing duplicates. The abstracts were then merged, meaning that the articles remained in the pool for full-text screening if at least one of the two raters judged the abstract as fulfilling the inclusion criteria. Furthermore, in an iterative process, the reference lists of all included studies were systematically screened such that 35 additional articles were included for review. Appendix C contains a table indicating which articles were found in the initial search and which were included from the reference lists. An additional five studies were found by forward citation searches and screening of the reference lists of theoretical articles. In the end, 82 articles were included in the review.

### 3. Results

The final 82 studies are listed in Table 1. The studies are subdivided into the five core mechanisms addressed: multisensory integration, prior-knowledge integration, risk optimisation, redundancy exploitation, and impedance control (including a sixth residual category of further studies). For each subdivision, the studies are sorted alphabetically

**Table 1.** Studies on mechanisms for handling uncertainties in sensorimotor control in sports, sorted by mechanism and ordered alphabetically.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
Multisensory integration	1	Ankarali et al. (2014)	Juggling	Juggling a virtual ball on a screen with a paddle	N = 18 novices, experimental lab study, within-subject design	Additional haptic feedback enhanced juggling performance.
	2	Cañal-Brunland et al. (2018)	Tennis	Predicting the ball's location in occluded videos of rallies	N = 23 experienced players, experimental lab study, within-subject design	Louder tennis stroke sounds were associated with predictions of farther ball flight distances.
	3	Gray (2009)	Baseball	Batting virtual baseballs in video-based situations	N <sub>1</sub> = 10, N <sub>2</sub> = 16 experts, experimental lab study, within-subject design	Visual feedback was given more weight when incongruent with auditory or tactile feedback.
	4	Heinen et al. (2014)	Trampoline	Vertical jumping in synchronisation with a partner	N = 20 experts, quasi-experimental field study, within-subject design	Jump synchronisation was achieved faster when only visual peripheral information was available than when only auditory information was given. Synchronisation was achieved the fastest when both visual and auditory information was available.
	5	Kennel et al. (2015)	Hurdling	Running as fast as possible with manipulated auditory feedback	N = 20 novices, quasi-experimental field study, within-subject design	Performance degraded with delayed auditory feedback, though it could be compensated in later trials.
	6	Krabben et al. (2018)	Judo	Fighting with and without a blindfold	N = 24 experts, quasi-experimental field study, within-subject design	Impaired vision decreased judo performance.
	7	O'Brien et al. (2020)	Golf	Hitting occluded golf balls with the sonification of the club movement	N = 20 novices, quasi-experimental field study, within-subject design	Sonification of the golf club's speed significantly reduced the variability in the distance from the target and ball location estimation.
	8	O'Brien et al. (2021)	Golf	Hitting golf balls with the sonification of the club movement	N = 40 novices, quasi-experimental field study, between + within-subject design	Online error-based sonification feedback with personalised mean velocity profiles reduced variability in the execution and timing of the swing movement more than auditory guidance.
	9	Petri et al. (2020)	Table tennis	Playing strokes under normal or impaired hearing conditions	N <sub>1</sub> = 15 novices, N <sub>2</sub> = 13 advanced players, quasi-experimental field study, within-subject design	Impaired auditory information did not influence hit quality and subjective effort, neither for novices nor for advanced players.
	10	Santello et al. (2001)	Drop jumps	Conducting jumps from different heights with or without vision	N = 8 novices, experimental lab study, within-subject design	The same force patterns were revealed to absorb the jump with or without vision. However, the landing was less smooth, and there was higher intra-individual variability in the force patterns without vision.
	11	Schaffert et al. (2020)	Rowing	Rowing with a target frequency with normal or masked hearing	N = 20 experts, quasi-experimental field study, within-subject design	The masked auditory information led to an increased deviation of the target stroke frequency.

(Continued)

**Table 1.** Continued.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
Prior-knowledge integration	12	Sinnett and Kingstone (2010)	Tennis	Anticipating the stroke direction from video and sound	N = 33 novices, experimental lab study, within-subject design	Additional sound of white noise affected accuracy and slowed down the response time.
	13	Sors et al. (2018)	Volleyball	Predicting a serve's length as fast and as accurately as possible	N <sub>1</sub> = 21, N <sub>2</sub> = 21, N <sub>3</sub> = 17 advanced players, experimental lab study, within-subject design	With incongruent auditory and visual stimuli, players' predictions followed the auditory information. Only with auditory information the prediction accuracy was higher than chance.
	14	Sors et al. (2017)	Soccer and Volleyball	Anticipating the speed of occluded penalties and smashes	N <sub>1</sub> = 18, N <sub>2</sub> = 17 advanced players, experimental lab study, within-subject design	When only auditory information was provided, the response time was shorter than for videos without audio. In videos without audio, participants were better than chance at guessing the ball speed. Visual, in addition to auditory information, did not improve the accuracy of speed estimation.
	15	Takeuchi (1993)	Tennis	Playing tennis under normal or impaired hearing conditions	N = 3 advanced players, explorative field study, within-subject design	The players lost more games with earplugs and were less successful in performing returns.
	16	Zelic et al. (2012)	Juggling	Juggling with vibrotactile or auditory feedback	N = 7 novices, experimental lab study, within-subject design	Jugglers' performance improved with the addition of well-scaled auditory and tactile cues.
	17	Abernethy et al. (2001)	Squash	Returning serves with occluded vision	N = 12 (6 experts, 6 less-skilled players), quasi-experimental field study (no inferential statistics)	Only the experts could exploit context information about situational probabilities in cases of early occlusion of kinematic information to initiate movements in the appropriate direction better than chance.
	18	Arthur and Harris (2021)	Racket sport	Returning bouncing virtual balls	N = 54 novices, experimental lab study, within-subject design	The recent context was more important in the unexpected uncertainty situation than in the expected volatile environment. The gaze behaviour was in line with the simulated predictions of an optimal Bayes integrator.
	19	Berg and Hughes (2017)	Ball catching	Catching vertically dropped balls of different weights	N = 28 novices, experimental lab study, within-subject design	When the ball's weight was unknown, participants showed relatively constant muscle activations for different weights at a level equivalent to the muscle activation for an intermediate weight in the known weight condition.
	20	Berg and Hughes (2020)	Ball catching	Catching vertically dropped balls of different weights	N = 29 novices, experimental lab study, between + within-subject design	When the ball's weight was unknown, participants showed relatively constant muscle activation with different weights at a level equivalent to the muscle activation for the heaviest weight in the known weight condition.

(Continued)

**Table 1.** Continued.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
	21	Cognier and Féry (2005)	Tennis	Conducting volleys with occluded vision	N = 17 experts, quasi-experimental field study, within-subject design	The higher the player's tactical initiative, the higher the accuracy of the opponent's anticipated stroke. Controlling rallies reduced the number of options the opponent had, which increased the likelihood of accurate anticipation.
	22	Eckerle et al. (2012)	Ball catching	Catching vertically dropped balls of different weights	N = 29 novices, experimental lab study, within-subject design	When the ball's weight was unknown, participants showed relatively constant muscle activation with different weights at a level equivalent to the muscle activation for an intermediate weight in the known weight condition.
	23	Farrow and Reid (2012)	Tennis	Predicting the ball's location from videos	N = 29 experts (15 late teens, 14 early teens), experimental lab study, between-subject design	Experts benefitted from situational probability information based on the current game score to decrease their response time. This effect was only found in the older athletes.
	24	Gray (2002)	Baseball	Batting virtual baseballs in video-based situations	N = 6 experienced players, experimental lab study, within-subject design	Prior expectations affected the timing of the baseball swing. A two-state Markov model, which considers the preceding state to predict the current state with fixed transition probabilities, worked well for modelling participants' error prediction.
	25	Gray and Cañal-Brunland (2018)	Baseball	Batting virtual baseballs in video-based situations	N <sub>1</sub> = 20, N <sub>2</sub> = 20 experts, experimental lab study, within-subject design	The contextual information about the probability of a fast/curved ball had a greater impact on the number of successful hits under earlier rather than later occlusion conditions. The number of successful hits was higher when the probabilities of the different throws were not equally distributed.
	26	Gredin et al. (2018)	Soccer	Predicting the outcome of virtual 2:2 counterattacks	N = 31 (16 experts, 15 novices), experimental lab study, between + within-subject design	Experts profited from explicit knowledge about the action tendencies in congruent trials but not from knowledge that had to be acquired implicitly. In incongruent trials, explicit knowledge had a higher negative impact on anticipatory judgments in novices than in experts.
	27	Gredin, Bishop, et al. (2020)	Soccer	Predicting the outcome of virtual 2:2 counterattacks	N = 15 experts, experimental lab study, within-subject design	Explicit contextual prior information improved performance. This effect decreased when the reliability of the kinematic information increased. Only explicit prior knowledge with high reliability enhanced performance when the reliability of the kinematic information was also high.

(Continued)

**Table 1.** Continued.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
	28	Gredin, Broadbent, et al. (2020)	Soccer	Predicting the outcome of virtual 2:2 counterattacks	N = 15 experts, experimental lab study, within-subject design	Explicit contextual prior information improved performance. This effect decreased with increased cognitive task load.
	29	Gredin et al. (2019)	Soccer	Predicting the outcome of virtual 2:2 counterattacks	N = 18 experts, experimental lab study, within-subject design	Explicit contextual prior information improved performance. Judgment utility reduced this effect and let the focus switch to the highest reward and the most minor loss.
	30	Gülden-penning et al. (2023)	Basketball	Predicting the direction of virtual passes with or without head-fake	N <sub>1</sub> = 31, N <sub>2</sub> = 32 novices, experimental lab study, within-subject design	Implicit and explicit information about action-outcome probabilities increased the head-fake effect with increasing outcome probability. The tendency to respond in accordance with the player's head direction increased linearly with its outcome probability.
	31	Güldenpenning et al. (2018)	Basketball	Slapping a ball of regular or disguised virtual passes	N = 68 novices, experimental lab study, between-subject design	With a low frequency of disguised passes, the reaction time was shorter, and the deception effect in terms of more errors was higher than when the frequency of disguised passes was high.
	32	Harris et al. (2022)	Racket sport	Returning bouncing virtual balls	N = 44 novices, experimental lab study, within-subject design	A hierarchical Bayesian inference model explained anticipatory eye movements better than a simple associative learning model. Pupillary signalling of surprise was associated with estimates of precision-weighted prediction error and learning rates, however, not with beliefs about the volatility of the bouncing ball.
	33	Helm et al. (2020)	Handball	Deciding whether morphed penalty throws are genuine or disguised	N = 23 novices, experimental lab study, within-subject design	Explicit information about the action preferences affected the classification of genuine and disguised throws. This effect was commensurate with the different degrees of ambiguity. When there was low kinematic uncertainty, the explicit information about action tendencies had no influence.
	34	Jackson et al. (2020)	Soccer	Intercepting an approaching virtual opponent	N = 30 (15 experts, 15 novices), experimental lab study, within-subject design	Explicit probability information regarding prior expectations affected performance, especially when aligned with a faked direction. Deceptive actions got 'super-deceptive' as a confirmation bias. For experts, the negative effects outweighed the positive effects.
	35	Leukel et al. (2012)	Fitness	Conducting drop jumps or landings	N = 10 novices, experimental lab study, within-subject design	The muscle activity differed for the conditions with and without uncertainty in task execution. The possibility for a landing reduced muscle activity because less

(Continued)

**Table 1.** Continued.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
36	Loffing and Hagemann (2014)	Tennis		Anticipating the directions of occluded baseline shots	N = 52 (26 experts, 26 novices), Experimental lab study, between-subject design	muscle activity is required for a landing than for a drop jump. Experts outperformed novices, and both groups improved under later occlusion conditions. Experts relied more on the opponents' court position in early occlusion time. Novices showed by tendency the same behaviour but less distinctively.
37	Loffing et al. (2016)	Tennis		Anticipating the directions of occluded baseline shots	N = 40 (20 experts, 20 novices) experimental lab study, between-subject design	Experts outperformed novices, and both groups improved under later occlusion conditions. The opponent's court position was only relevant in the early stage of the movement but not anymore at the moment of racket-ball contact.
38	Loffing et al. (2015)	Volleyball		Predicting the type of attack in different contexts	N = 51 (20 experts, 31 novices), experimental lab study, between-subject design	Both groups expected a continuation of the currently played pattern. The prediction accuracy was higher in congruent trials, and the response time was shorter than in incongruent trials. The congruence effect was slightly higher for experts than for novices.
39	Magnaguagno and Hossner (2020)	Handball		Acting as a central defender in virtual video-based situations	N = 24 (12 experts, 12 near experts), experimental lab study, between/within-subject design	All players improved in terms of explicit reports of their teammates' defensive quality and the correctness of their movements. Experts outperformed near experts in all aspects and benefited from a superior self-generated, implicit knowledge base.
40	Magnaguagno et al. (2022)	Handball		Acting as a central defender in virtual video-based situations	N = 57 (30 youth elite, 27 youth near-elite players), experimental lab study, between-subject design	Providing explicit information improved performance in congruent but impaired performance in incongruent trials. This effect of providing explicit knowledge diminished over time due to the accumulation of implicit knowledge.
41	Mann et al. (2014)	Handball		Predicting the direction of virtual handball throws	N = 20 experts, experimental lab study, between-subject design	Implicitly learned priors helped to improve the goalkeeper's chance to save the ball in congruent trials but decreased performance in incongruent trials.
42	McIntyre et al. (2001)	Ball catching		Catching balls on Earth or in space	N = 4 novices, explorative field study, within-subject design	The peak muscle activation was earlier in space than on Earth according to the time of contact with the ball, meaning that the lack of gravity could not be fully adjusted.

(Continued)

**Table 1.** Continued.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
	43	Milazzo et al. (2016)	Karate	Reacting to fighting attacks	N = 28 (14 experts, 14 novices), quasi-experimental field study, between-subject design	Only experts enhanced their performance in terms of faster and more accurate responses from the implicitly acquired context regarding repeated attacks every four actions.
	44	Misirlisoy and Haggard (2014)	Soccer	Saving penalties	N = 361 penalties (FIFA World Cups, UEFA Euro Cups), explorative field study	Goalkeepers showed a pattern of a gambler's fallacy by choosing the left or right side, which is not optimal because the kickers showed a pattern close to randomness.
	45	Murphy et al. (2016)	Tennis	Predicting the ball's location in normal and animated videos	N = 36 (16 experts, 20 novices), experimental lab study, between-subject design	When provided only with contextual information and no postural information about the opponent, experts and novices were able to anticipate shots better than by chance. Both groups performed better with the addition of the opponent's postural information.
	46	Murphy et al. (2018)	Tennis	Predicting the ball's location in animated videos	N <sub>1</sub> = 24, N <sub>2</sub> = 24 (12 experts, 12 novices), experimental lab study, between-subject design	Contextual information related to the opponent was weighted more than contextual information related to the ball. However, players integrated all available information sources when making decisions.
	47	Navia et al. (2013)	Soccer	Saving penalties	N = 9 novices, quasi-experimental field study, within-subject design	Explicit situational information about a player's action preference improved the chance for goalkeepers to choose the right corner.
	48	Nakamoto et al. (2022)	Baseball	Batting virtual baseballs in video-based situations	N = 13 experts, experimental lab study, within-subject design	Explicit estimations of ball speed were affected by the speed of the pitcher's movement, especially in conditions with high ball speed and thus less reliable ball flight information. In tendency, this effect was more pronounced for higher-skilled batters.
	49	Runswick et al. (2018)	Cricket	Predicting the ball's location in occluded videos	N = 36 (18 experts, 18 novices), experimental lab study, between-subject design	Both pre-release/contextual information and post-release/kinematic information were considered for anticipation. While the importance of post-release/kinematic information increased over time, the importance of pre-release/contextual information decreased.
	50	Sinn et al. (2023)	Ball catching	Catching vertically dropped balls of different weights	N = 37 novices, experimental lab study, within-subject design	Due to a relatively constant intermediate muscle activation for variable unknown ball weights, catching errors with the lightest ball were characterised by higher and with the heaviest ball by lower reflexive compensatory muscle activation.

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**Table 1.** Continued.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
	51	Stevenson et al. (2009)	Surfing simulation	Balancing on a board and steering a cursor as close as possible to a target	N = 10 novices, experimental lab study, within-subject design	Subjects steered the movements slower and with less amplitude under increased feedback uncertainty conditions, implying that under greater uncertainty, the human control system integrates information over a longer period.
	52	Triolet et al. (2013)	Tennis	Initiating strokes in ATP tennis matches	N = 3000 strokes by N = 10 experts, explorative field study	Under unfavourable conditions, players initiated their movements earlier and with less response accuracy. When the movement was initiated later than 140 ms after ball contact, the movement almost always went in the right direction.
	53	Wang et al. (2019)	Soccer	Predicting the direction of penalties	N = 50 (25 experts, 25 novices), experimental lab study, between + within-subject design	Prior cues affected the response accuracy of experts and novices in congruent situations positively and in incongruent situations negatively.
	54	Whittier et al. (2022)	Step	Moving the centre of mass to a virtual target	N = 57 novices, experimental lab study, within-subject design	As incoming visual information became less reliable, more weight was given to previously learned body positions as prior knowledge. The position of the centre of mass was estimated consistent with Bayesian inference approaches.
	55	Yamamoto et al. (2019)	Tennis	Estimating the variance of one's own serves	N = 31 (experts and novices), experimental lab study, between + within-subject design	A large isotropic bias was found regardless of experience level, so the estimated eccentricity was lower than observed. No effects of the intervention were revealed.
	56	Zago et al. (2004)	Ball punching	Punching real or virtual falling balls	N = 20 novices, experimental lab study, within-subject design	An integrated prior was found that gravity accelerates the falling ball, even when the virtual ball was not accelerated. This effect decreased with training.
Risk optimisation	57	Bertucco et al. (2020)	Snowboard	Balancing on a rocker board and controlling a virtual snowboard	N = 15 novices, experimental lab study, within-subject design	When the sensitivity of the rocker board was higher, participants chose a safer path by accepting smaller accelerations to reduce the risk of additional penalty points, meaning that participants considered different cost functions according to execution noise.
Redundancy exploitation	58	Bardy and Laurent (1998)	Gymnastics	Conducting somersaults	N = 5 (3 experts, 2 advanced), quasi-experimental field study, within-subject design	Without vision, experts showed a stable, gradually increasing variance of body orientation. Whilst under normal vision conditions, there was a variance increase in the first part of the somersault; experts showed a

(Continued)

**Table 1.** Continued.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
	59	Betzler et al. (2014)	Golf	Conducting strokes at a target	N = 285 (all expertise levels), explorative field study, between + within-subject design	decrease in the second part, i.e. the crucial movement phase for approaching the floor. Expertise corresponded to a reduction of variance in several (e.g., club head speed, path angle) but not all variables.
	60	Bootsma and van Wieringen (1990)	Table tennis	Conducting forehand drives as fast and accurately as possible	N = 5 experts, explorative field study, within-subject design	The variance of the timing and direction of the initial movement of the bat was higher than for the moment of ball-bat contact.
	61	Burgess-Limerick et al. (1991)	Field hockey	Conducting hockey drives	N = 7 (4 experts, 3 novices), explorative field study, between-subject design	Novices showed less backswing variance than experts but more downswing variance.
	62	Davids et al. (1999)	Volleyball	Serving volleyballs as hard and accurately as possible	N = 6 experts, explorative field study, between-subject design	Experts stabilised the vertical position of the ball at the zenith and contact with the ball but allowed variability in the x-y plane, which they could compensate for.
	63	Dupuy et al. (2000)	Ball throwing	Throwing balls at a target on the floor	N = 8 novices, experimental lab study, within-subject design	The observed angle-speed combinations were close to the mechanical optimum to reduce variance in the throwing distance.
	64	Franks et al. (1985)	Hockey	Conducting hockey drives	N = 1 expert, explorative field study, within-subject design	High variance in the initiation of the stroke was found (i.e. preparation and backswing), but a consistent and accurate downswing.
	65	Hiley et al. (2013)	Gymnastics	Performing giant circles on the high bar	N = 4 (2 elites, 2 near elite athletes), explorative lab study, between + within-subject design	Elite athletes only showed less variance in the mechanically important aspects of the performed technique compared to near-elite athletes.
	66	Horan et al. (2011)	Golf	Conducting strokes at a target	N = 38 experts, explorative lab study, within-subject design	The variance of the club head and hand trajectory decreased from the top of the backswing to the ball contact.
	67	Iino et al. (2017)	Table tennis	Conducting strokes at a target as fast and accurately as possible	N = 17 (9 experts, 8 near experts), explorative lab study, between + within-subject design	The vertical racket face angle variance tended to decrease towards ball impact and increased immediately afterwards.
	68	Morrison et al. (2014)	Golf	Conducting strokes at a target	N = 4 experts, explorative lab study, within-subject design	The variance of the club head position trajectory increased from take-off to the top of the backswing and then decreased again until impact.
	69	Morrison et al. (2016)	Golf	Conducting strokes at a target	N = 22 (11 experts, 11 advanced players), explorative field study, between + within-subject design	The variance of the club head position decreased at impact, while the variance of its orientation was lower over the early downswing. The higher-skilled players showed less variance in the club head location than the advanced players.

(Continued)

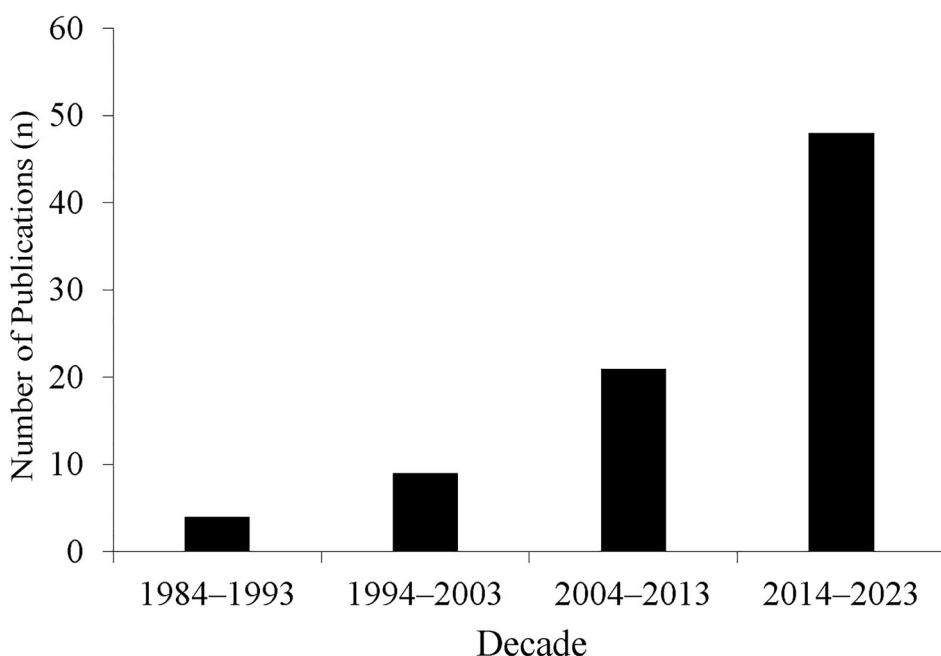
**Table 1.** Continued.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
Impedance control	70	Nakano et al. (2020)	Basketball	Conducting free throws	N = 8 experts, explorative lab study, within-subject design	The players minimised the speed release to minimise the effect of release parameter errors rather than optimally handling parameter errors. This implies that they pursued a robust strategy according to release errors.
	71	Scholz et al. (2000)	Shooting	Shooting at a target after turns as fast and accurately as possible	N = 9 novices, experimental lab study, within-subject design	The arm configuration variables that do not change the orientation of the gun vector relative to the target did not affect performance and were less controlled than the arm configuration variables with an impact on the orientation of the gun.
	72	Scott et al. (1997)	Athletics	Conducting long jumps	N = 101 (71 elite athletes, 9 advanced athletes, 11 novices), explorative field study and reanalysis of data	Regardless of expertise level, long jumpers generally showed a high variance in the footsteps over the beginning and a low variance over the end of the run-up. The novices showed far more variance over the beginning but almost equal variance over the end.
	73	Sheppard and Li (2007)	Table tennis	Returning services as fast and accurately as possible	N = 24 (12 advanced players, 12 novices), explorative field study, between +within-subject design	In the approach to contact, batters reduced the variability of bat direction and orientation. However, this was not observed for the bat's position, speed and acceleration. Advanced players tended to reduce the variability of the crucial variables when batting at higher speeds.
	74	Tucker et al. (2013)	Golf	Conducting strokes at a target	N = 16 experts, explorative lab study, within-subject design	The variance of the hand trajectory decreased from the top of the backswing to the ball contact. Movement variance was not related to ball speed variance.
	75	van Soest et al. (2010)	Table tennis	Smashing at a target with occluded vision	N = 7 experts, quasi-experimental field study, within-subject design	The variance of the timing and direction of the initial movement of the bat was higher than for the moment of ball-bat contact, both under normal and occluded vision, as well as in an additionally conducted simulation.
	76	Blenkinsop et al. (2016)	Gymnastics	Performing handstands under different perturbation levels	N = 12 experts, experimental lab study, within-subject design	Performance under perturbation led to increased muscle stiffness and, ultimately, greater wrist joint torque.
	77	Reeves et al. (2013)	Stick balancing	Balancing a stick with an additional mass at its end	N = 9 novices, experimental lab study, within-subject design	When the task became more difficult (the mass was lower down) and the angular velocity of the stick increased, agonist and antagonist muscle activation increased, meaning that the increased joint stiffness allowed for control of the stick at a higher frequency.

(Continued)

**Table 1.** Continued.

Mechanism	#	Author(s)	Sport	Task	Type	Main Findings
others	78	Reeves et al. (2016)	Stick balancing	Balancing a stick with an additional mass at its end	N = 9 novices, experimental lab study, within-subject design	Participants' agonist and antagonist muscle activation increased when tasked to balance a stick with limited visual focus on the lower end of the stick. The increased joint stiffness resulted in better stick control at higher oscillation frequencies.
	79	Bar-Eli et al. (2007)	Soccer	Saving penalties	N = 286 penalties from top leagues, explorative field study	Whilst the norm is to jump right or left, goalkeepers had the highest chance to save the penalty if they stayed in the goal's centre.
	80	Goodman et al. (2009)	Rifle shooting	Shooting at a target	N = 28 (14 experts, 14 novices), explorative field study, between + within-subject design	In the final phase of shooting, the fluctuations in aiming remained at a constant level. Participants waited until the target was as close as possible to pull the trigger. This effect was found for experts as well as for novices.
	81	Mather (2008)	Tennis	Deciding 'in' or 'out' on tennis strokes under real game conditions	N = 1473 challenges by N = 246 professional athletes, explorative field study	94% of the challenges were within a zone of 100 mm next to the line, and line judges were slightly more accurate than players. A simple perceptual model with intrinsic positional uncertainty could well explain challenges.
	82	Mazyn et al. (2007)	Ball catching	Catching balls under visually occluded conditions	N = 20 novices, experimental lab study, within-subject design	Under occlusion conditions, movements were initiated later, and movement times were shorter than without occlusion. This effect increased after training.



**Figure 2.** Number of publications on mechanisms for handling uncertainty in sensorimotor control in sports as a function of year of publication.

and characterized by the researched sport, the deployed task, the study type, and the main findings.

Overall, when considering the year of publication, it is clear that the popularity of the topic of uncertainty in sensorimotor control in sports has been growing. As illustrated in Figure 2, the number of publications has rapidly increased over the last ten years.

However, there are extensive differences in research interest when it comes to the five mechanisms (1)–(5) specified in the present paper. While a number of studies focus on the question of how multiple sensory inputs are integrated (16 studies), the largest portion of studies examine integrating prior knowledge (40 studies), either to reduce uncertainty in perception, action or to enhance performance. Aspects of risk optimisation have not been addressed to a notable degree thus far (1 study). Alternately, more attention has been attracted to redundancy exploitation (18 studies), relating to the question of which variables have to be controlled for superior performance and which variables are either not task-relevant or can be compensated. To date, the mechanism of impedance control appears to be under researched in sports science (3 studies). Finally, four studies remained with a focus on handling uncertainty in sensorimotor control in sports that cannot be related to the five mechanisms outlined above.

In regard to the type of the study, considerably more laboratory studies (54 studies) were included in the review than field studies (28 studies). However, the ratio of laboratory to field studies seems to depend on the investigated mechanism. While multisensory integration is rather equally studied in both laboratory (8 studies) and field (8 studies), more laboratory (33 studies) than field (7 studies) studies have been conducted on

prior-knowledge integration, whereas there are even slightly more field studies (10 studies) investigating the redundancy exploitation than laboratory studies (8 studies). In general, the findings obtained in laboratory and field studies are in line with each other, so this distinction will not be considered further.

The researched sport, deployed tasks and main findings of the included studies are reported in more detail in the following paragraphs, subdivided by the mechanism assumed to be responsible for handling uncertainty in sensorimotor control in sport.

### **3.1. Studies on multisensory integration**

Of the 16 studies focusing on multisensory integration (see [Table 1](#)), almost the entirety reaches the conclusion that multiple sources of sensory information are taken into account in order to control complex sports behaviour. As a rare exception, distorted auditory information was found to have no effect on the performance of a table-tennis counter-hit ([Petri et al., 2020](#)). In the other two exceptions, the addition of visual information alongside auditory information did not improve the accuracy of ball-velocity estimations in soccer penalty shots and volleyball smashes ([Sors et al., 2017](#); [Sors et al., 2018](#)). In contrast, there is considerable evidence that performance decreases when sensory information that is normally available is disturbed ([Heinen et al., 2014](#); [Kennel et al., 2015](#); [Krabben et al., 2018](#); [Santello et al., 2001](#); [Schaffert et al., 2020](#); [Sinnett & Kingstone, 2010](#); [Sors et al., 2017](#); [Takeuchi, 1993](#)) and that performance can be improved by the provision of additional sensory information ([Ankarali et al., 2014](#); [Gray, 2009](#); [O'Brien et al., 2020](#); [O'Brien et al., 2021](#); [Zelic et al., 2012](#)). In line with these findings, it had been shown that providing misleading additional sensory information in a hurdling task ([Kennel et al., 2015](#)) or experimentally manipulating sound intensity when estimating stroke distances ([Cañal-Bruland et al., 2018](#)) decreases performance. However, athletes seem to be capable of compensating for misleading auditory signals over time ([Kennel et al., 2015](#)).

Five of the studies on multisensory integration explicitly reference Bayesian inference. However, apart from the fact that any evidence in favour of the integration of different input sources can be counted as generally fitting the Bayesian framework, according to Bayesian inference, multisensory integration should be based on a weighting procedure according to the inputs' estimated reliabilities. In this more specific regard, different levels of reliability are considered in three studies. [Petri et al. \(2020\)](#) reported no effects of auditory information in a table-tennis counter-hit regardless of information's reliability. [Kennel et al. \(2015\)](#) found that delayed – and thus misleading – additional auditory information initially impairs performance in a hurdling task, though this source is increasingly ignored with adaptation over time. In terms of weighting sensory inputs, the most compelling study was conducted by [Gray \(2009\)](#). When only one source of information is available in a baseball-batting simulation, [Gray \(2009\)](#) found that accuracy is best enhanced by visual information. Therefore, this input should be expected to deliver the most reliable information. As consequently predicted, visual information was found to be weighted most heavily when different sources of information are combined in a contradictory manner.

### **3.2. Studies on prior-knowledge integration**

From the total of 82 studies, almost half of the studies (40) are conducted with an either explicit or at least implicit focus on the effects of prior knowledge on perception, action,

or performance. There is considerable evidence that prior knowledge influences perception (Arthur & Harris, 2021; Gredin et al., 2018; Harris, Arthur, Vine, et al., 2022b; Nakamoto et al., 2022; Yamamoto et al., 2019) as well as action (Berg & Hughes, 2017, 2020; Eckerle et al., 2012; Gray, 2002; Gredin et al., 2018; Güldenpenning et al., 2023; Güldenpenning et al., 2018; Helm et al., 2020; Leukel et al., 2012; Loffing et al., 2015; Loffing et al., 2016; Magnaguagno et al., 2022; Magnaguagno & Hossner, 2020; McIntyre et al., 2001; Milazzo et al., 2016; Misirlisoy & Haggard, 2014; Sinn et al., 2023; Stevenson et al., 2009; Triolet et al., 2013; Whittier et al., 2022; Zago et al., 2004), and generally improves performance (Abernethy et al., 2001; Cognier & Féry, 2005; Farrow & Reid, 2012; Gray & Cañal-Bruland, 2018; Gredin et al., 2018; Gredin et al., 2019; Gredin et al., 2020c; Gredin et al., 2020a; Helm et al., 2020; Loffing et al., 2015; Loffing & Hagemann, 2014; Magnaguagno et al., 2022; Magnaguagno & Hossner, 2020; Mann et al., 2014; Milazzo et al., 2016; Murphy et al., 2016; Murphy et al., 2018; Navia et al., 2013; Runswick et al., 2018; Wang et al., 2019). Only a few incongruences can be reported; namely, considering the role of participants' expertise levels and the either explicit or implicit provision of contextual information. While Gredin et al. (2018) reported that experts only benefited from explicit (but not from implicit) prior knowledge other studies have shown that experts (but not novices) were able to use implicit prior knowledge (Abernethy et al., 2001; Loffing et al., 2016). Further specifying the findings that prior knowledge generally improves performance, it has been reported that the explicit provision of uncertain prior knowledge can also have an overall negative effect on performance, especially for expert athletes (Jackson et al., 2020; Magnaguagno et al., 2022), a finding that we will discuss in more depth below.

Half of the studies on prior-knowledge integration (20/40 studies) refer to principles of Bayesian inference, which provides a tool for identifying statistically optimal solutions and deriving predictions of human behaviour that can be put to empirical test (Griffiths et al., 2012). However, most of the studies included in the present review just refer to Bayesian inference as a theoretical framework; meaning that the examined behaviours are not compared to statistically optimal solutions and that the reported results are limited to the general conclusion that prior knowledge influences perception, action, or performance per se. Nevertheless, there is clear evidence of a simplified Bayesian model of reliability-weighted integration of prior knowledge and sensory information into perception, supported by 12 studies. However, only sparse evidence (4 studies) favours quantitative optimality derived from the Bayesian framework; particularly demonstrated by Arthur and Harris (2021) and Harris, Arthur, Vine, et al. (2022b) examining gaze strategies in returning bouncing balls. Notably, when it comes to the interactions of prior-knowledge integration with both the level of expertise and the distinction of explicitly instructed vs. implicitly self-generated knowledge as reported above, such calculations on information-gain estimates can also be found in the handball studies published by Magnaguagno et al. (2022). In these studies, the gain estimates were calculated as a function of certainty of explicitly provided contextual knowledge. These calculations are based on the consideration that if explicit prior knowledge is weighted too heavily, the negative consequences in incongruent trials will outweigh the positive effect in congruent trials. Therefore, the congruence between prior knowledge and actual situational probabilities should also be considered as a crucial factor. Regarding the factor of expertise, it seems plausible that experts are better at estimating the reliability of implicit prior knowledge

since they know from experience which information is important and trustworthy – as argued by Williams et al. (2011). Taken together, the summarized findings support the call of Gredin et al. (2020b) for a ‘Bayesian integration framework’ examining the combination of contextual priors and kinematic information in anticipation in sport. However, Bayesian predictions should not only be tested in a more quantitative manner but also be extended from the context of anticipation to the issue of handling noise and uncertainty in complex, naturalistic sensorimotor behaviour in general.

### **3.3. Studies on risk optimisation**

The only included study that focused on risk optimisation was the one published by Bertucco et al. (2020), which showed that inherent noise is taken into account in motor planning in order to optimize potential costs and rewards of the movement outcome. In this study, participants steered a virtual snowboard in a computer game by balancing on a rocker board. As participants passed through different acceleration zones on the slope, they received more financial rewards for reaching faster speeds. When the sensitivity of the rocker board was increased to induce higher inherent noise, the participants chose a larger safety distance to the off-piste penalty zone with the consequence of less acceleration in the middle of the slope. This implies that participants weighed the risk of a penalty with the amount of acceleration – according to different levels of noise – to maximize the financial outcome.

Bertucco et al. (2020) discuss their findings with respect to the theoretical framework of risk optimisation as introduced by Trommershäuser et al. (2008), but also in regards to optimal-control theory (Körding & Wolpert, 2006; Todorov, 2004), which posits that, motor control ultimately comes down to decision making with a focus on maximizing the utility of the movement outcome in the face of sensory, motor and task uncertainty (Wolpert & Landy, 2012).

### **3.4. Studies on redundancy exploitation**

The redundancy exploitation has been introduced above as an alternative – or perhaps supplementary – strategy of weighting available information. Particularly, it provides an alternate approach to handling uncertainty such that sensorimotor noise is only minimized when the noise significantly concerns goal-relevant variables. All 18 studies within this category (Table 1) confirmed that athletes do not try to reduce movement variance in its entirety, but only in certain task dimensions. This is observed in experts behaviour (Bardy & Laurent, 1998; Betzler et al., 2014; Bootsma & van Wieringen, 1990; Burgess-Limerick et al., 1991; Davids et al., 1999; Franks et al., 1985; Hiley et al., 2013; Horan et al., 2011; Iino et al., 2017; Morrison et al., 2014; Morrison et al., 2016; Nakano et al., 2020; Scott et al., 1997; Sheppard & Li, 2007; Tucker et al., 2013; van Soest et al., 2010) as well as in novices behaviour (Burgess-Limerick et al., 1991; Dupuy et al., 2000; Scholz et al., 2000; Scott et al., 1997; Sheppard & Li, 2007). This prioritisation particularly pertains to task-relevant variables in which superior athletes exhibit less movement variance (Bardy & Laurent, 1998; Betzler et al., 2014; Hiley et al., 2013).

In the more recent articles (Iino et al., 2017; Morrison et al., 2016; Nakano et al., 2020), the distinction between goal-relevant and goal-irrelevant variables is theoretically

anchored in the uncontrolled-manifold hypothesis (Scholz et al., 2000; Scholz & Schöner, 1999). Accordingly, the variance in the control variables is split into a part that affects the task variables and a part that does not. The ratio of these variances then serves as a measure for the degree of redundancy exploitation, and thus also as a measurement of expertise (Iino et al., 2017; Morrison et al., 2016). To make the distinction between relevant and irrelevant variables for goal achievement, the majority of the reviewed studies draw from the behaviour of experts. In contrast to this purely empirically driven approach, five studies distinguish relevant from irrelevant variables based on functional arguments and compare optimal with actual human behaviour (Betzler et al., 2014; Dupuy et al., 2000; Hiley et al., 2013; Nakano et al., 2020; Scholz et al., 2000). In this regard, the study on underarm precision throwing by Dupuy et al. (2000) demonstrated that people exploit the laws of physics and minimize the variability of the throwing distance adapting both the release angle and speed close to the predicted mechanical optimum.

### **3.5. Studies on impedance control**

Three studies included in the present review focused on handling uncertainty and noise by adapting one's impedance with optimal muscular co-contractions. Empirical findings supporting this strategy include performing a handstand with vs. without vibrations of the floor, where vibrations lead to higher muscle co-contractions and wrist torque stiffness (Blenkinsop et al., 2016). Furthermore, when the task of balancing a more or less inert stick on the hand became more difficult due to visual-focus instructions or mass distribution and the angular velocity of the stick increased, agonist and antagonist muscle activation increased. The increased joint stiffness due to increased activation of agonist and antagonist allowed the stick to be controlled at a higher frequency (Reeves et al., 2013; Reeves et al., 2016).

Although not precisely termed as such, motor control in these studies is interpreted as the optimisation of muscular activities as well as joint stiffness through co-activation (Blenkinsop et al., 2016; Reeves et al., 2013; Reeves et al., 2016). These studies can thus be taken as general empirical support for the notion of impedance control as a means for handling noise-related uncertainty by adapting one's resistance against expected uncertainty. However, more specific predictions regarding the degree to which impedance should be exploited to optimize performance have not been tested so far; though would be a highly desirable exploration for the future.

### **3.6. Further studies**

Due to distinctly different foci, the three remaining studies cannot be assigned to the defined categories. Bar-Eli et al. (2007) show that in penalty situations, soccer goalkeepers tend to jump more often than optimal to the side rather than staying in the middle of the goal. This implies cost functions of the highest relevance are not so obvious, since in the present example, the spectator-related social costs of not acting at all may play a co-decisive role. Goodman et al. (2009) found that rifle shooters wait in a certain range of random movement until the aiming sight happens to point perfectly at the target. The authors explain this strategy by the higher accuracy of the visual than the motor system as a potential further strategy to deal with uncertainty in complex sensorimotor tasks. On

the basis of a simple perceptual model with intrinsic positional uncertainty in order to explain challenges in tennis, Mather (2008) recommends, due to perceptual uncertainties, that tennis players should generally take advantage of all the challenges available to them. Finally, Mazyn et al. (2007) tested participants in a trade-off situation where they had to catch a ball and the light was switched off immediately after movement initiation. In this situation participants accepted increased signal-dependent noise of a faster catching movement to gather more ball-flight information.

Although not explicitly relating to one of the mechanisms (1)–(5) identified, these studies should be considered as valuable additions to further our understanding of how humans handle uncertainty in complex motor behaviour.

## 4. Discussion

This scoping review aimed to examine how humans handle uncertainty in sensorimotor control in naturalistic tasks such as sports and to determine to what extent the well-investigated underlying mechanisms (1)–(5) can be transferred from more fundamental to more complex tasks. The importance of testing the external validity of these mechanisms from fundamental research can be seen in the rapidly growing research interest in uncertainty in sensorimotor control in sports over the last ten years (illustrated in Figure 2). However, there are pronounced differences in research interest when it comes to the five mechanisms (1)–(5).

### (1) *Multisensory integration*

Regarding multisensory integration (Ernst & Banks, 2002), the reported empirical findings are generally in line with a Bayesian framework. There is some evidence (Gray, 2009; Kennel et al., 2015) that the weighting of sensory information sources is based on reliability in complex sensorimotor tasks. However, so far, there is no study that compares the empirically observed with the optimal weighting.

### (2) *Prior-knowledge integration*

When it comes to prior-knowledge integration (Körding & Wolpert, 2004) based on Bayesian principles, there is clear evidence (12 studies) that the reliability-weighted integration of prior knowledge both improves performance and reduces noise and ambiguity in perception and action in complex sensorimotor tasks. This conclusion perfectly aligns with the review by Gredin et al. (2020b). Moreover, some evidence has been provided that this integration process is close to optimal (Arthur & Harris, 2021; Harris, Arthur, Vine, et al., 2022b; Helm et al., 2020; Whittier et al., 2022).

### (3) *Risk optimisation*

Regarding risk optimisation (Trommershäuser et al., 2003), the only study on this mechanism in a complex sensorimotor setting (Bertucco et al., 2020) provides evidence that the utility of movement outcome is maximized in the face of motor noise.

#### (4) *Redundancy exploitation*

Concerning the redundancy exploitation, theoretically substantiated by the uncontrolled-manifold hypothesis (Scholz & Schöner, 1999) or the principle of minimal intervention (Todorov & Jordan, 2002), 13 studies showed that experts as well as novices distinguish between task-relevant and task-irrelevant variables. Five further studies demonstrated that variability is only reduced in functional goal-relevant variables to an optimal degree (Dupuy et al., 2000).

#### (5) *Impedance control*

Three studies that considered impedance control (Burdet et al., 2001; Hogan, 1984) in complex sensorimotor tasks provide evidence that perturbations can be absorbed using higher muscle stiffness resulting from muscular co-contraction.

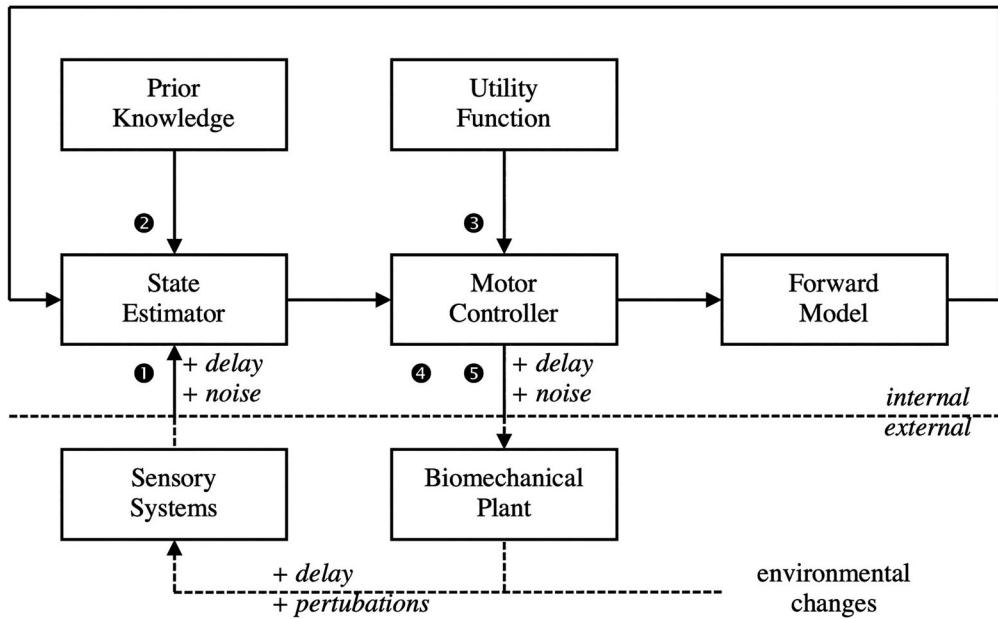
Taken together, these findings – from a broad range of study types and investigated tasks – show that the mechanisms (1), (2), and (4) have been convincingly empirically proven in naturalistic complex sensorimotor tasks. The mechanisms (3) and (5) remain under-researched with some empirical evidence for their external validity in a naturalistic environment. Moreover, regarding the (frequently) self-imposed theoretical framework, the empirical tests of the mechanisms did not always match to a satisfactory extent. Future research should thus more specifically focus on how these mechanisms are utilized by testing clear predictions derived from theoretical models rather than just scratching the surface to show that, for instance, prior knowledge is considered *per se*. In this respect, the study of Arthur and Harris (2021) could be regarded as a landmark for future research. In this study, not only empirically quantitative predictions of an optimal Bayesian observer were made and compared with actual behaviour, but also eye movements as the first movements in anticipatory behaviour were investigated. Examining eye movements may, therefore, provide conclusive insights into the process of prior-knowledge integration. Further, Magnaguagno et al. (2022) presented quantitative predictions about expected anticipatory behaviour, broadening the empirical focus by considering the effects of further variables, such as the level of expertise or implicit prior-knowledge accumulation versus explicit prior-knowledge provision can be expected to provide additional depth to understand the mechanisms in even more detail. Finally, while considerable evidence for mechanisms (1), (2), and (4) has been provided, the mechanisms of (3) risk optimisation and (5) impedance control are still poorly researched in sports science so far. Therefore, further research is urgently required to determine these mechanisms' additional or interacting contributions to handling uncertainty in sensorimotor control in naturalistic complex, in particular sports-related tasks. Furthermore, it becomes clear that for future research, different emphases should be set for each mechanism.

Having discussed five explanatory mechanisms largely in isolation, the question arises as to whether and, if so, how these mechanisms might be placed in a single theoretical framework. In seeking such a framework, it should first be noted that not all of the studies included in this scoping review are based on a cognitive approach. In contrast to the Bayesian idea of an accentuated cognitive weighting of probabilities, Gray (2002) applies an alternative model with high predictive power; namely a non-Bayesian

two-state Markov model with a fairly simple win-stay, loose-switch heuristic. Moreover, dynamical-systems theory and the ecological approach to movement coordination can undoubtedly contribute to the examination of handling uncertainty. As illustrated in this review by juxtaposing the cognitive principle of minimal intervention (Todorov & Jordan, 2002) and the uncontrolled-manifold hypothesis (Scholz & Schöner, 1999) rooted in dynamical-systems theory – cognitive and ecological explanations of handling uncertainty in human behaviour may arrive at similar conclusions (e.g. in comparison, Davids et al., 1999, p. 439; Franklin & Wolpert, 2011, p. 429). On this basis, a unifying framework considering the empirical evidence from fundamental research (for reviews, e.g. Franklin & Wolpert, 2011; Gallivan et al., 2018; Körding & Wolpert, 2006; Todorov, 2004) as well as the empirical evidence in more complex, in particular sports-related tasks seems even more highly desirable. To this end, the assumption that coordinated behaviour requires sufficiently reliable online predictions of changes in the world might provide a guiding direction. This idea is presented in more detail in [Figure 3](#), where the framework of optimal feedback control (according to Körding & Wolpert, 2006; and Todorov, 2004) is used to integrate the highlighted mechanisms (1)–(5).

This proposed model is based on the assumption of a close interaction between an internal and an external control loop. The motor controller generates efferent signals dependent on both the estimation of the current state and the specifics of the motor goal according to the utility function. In the internal loop, a forward model predicts how the current state would change based on an internal copy of emitted efferences. In the external loop, the actual changes produced by the biomechanical plant under altering conditions in the external world are observed by the sensory systems. This observation is carried out with a considerable time delay and is corrupted by noise and ambiguities. To reduce uncertainty about the current state, the mechanisms of (1) multi-sensory integration and (2) prior-knowledge integration come into play. These mechanisms form a continuous integration of all available information sources – perhaps either by Bayesian or alternative procedures – including internal state predictions derived from the forward model. Risk optimisation as mechanism (3) becomes relevant when, on the basis of the estimated state, details of the current motor goal are specified. This regards the intended effect as well as a utility function, where the costs of all possible movement outcomes are considered – especially due to noise and delays in movement execution. Based on internal predictions of the resulting effects, the motor controller determines which manipulations of control variables are required to achieve the desired effect whilst preferably staying within or entering the subspace of optimal task-solutions – thereby instantiating mechanism (4) on redundancy exploitation. Finally, as an alternative to actively handling noise and delays, the motor controller may also adapt the impedance of parts of the biomechanical plant as an optimal solution to the given motor task in terms of mechanism (5) of impedance control such that external perturbations are immediately damped.

In [Figure 3](#), we chose optimal feedback control as our theoretical framework because it has become a highly influential theory within the engineering approach to understanding sensorimotor behaviour over the past few decades and, moreover, has been widely confirmed empirically (for reviews, e.g. Franklin & Wolpert, 2011; Gallivan et al., 2018; Körding & Wolpert, 2006; Todorov, 2004). In the present context, however, the model serves only as a framework to systematically place and illustrate basic mechanisms for



**Figure 3.** Optimal feedback-control loops (Körding & Wolpert, 2006, p. 323; Todorov, 2004, p. 910; combined and modified by the authors) with indication of mechanisms (1)–(5) for handling uncertainty in sensorimotor control: (1) multisensory integration, (2) prior-knowledge integration, (3) risk optimisation, (4) redundancy exploitation, and (5) impedance control.

dealing with uncertainty in complex sensorimotor behaviour. This being said it is obvious that alternative models could have been chosen as a framework as well. In our view, this is particularly true for the idea of active inference (Friston, 2010; in regards to prior-knowledge integration, see Harris, Arthur, Broadbent, et al., 2022a), which operates more at a neuro-implementational rather than an engineering level of explanation. While certain differences in specific theory elements are discussed in the scientific community (for details, see Friston, 2011), the two approaches share the theoretical core of viewing perception and action as fundamentally probabilistic based on online predictions and the integration of information according to Bayesian principles. More specifically, and referring to Figure 3, the approaches share key theoretical concepts by asserting the need for an internal forward/generative model, Bayesian integration of sensory information and prior knowledge/beliefs, and behavioural control optimisation according to costs/surprise. This convergence at the level of key concepts is, in our view, good news for joint and coherent progress in this area.

In precisely this sense, the present review and proposed integrative framework should primarily be understood as a heuristic for stimulating future research on handling uncertainty in complex sensorimotor behaviour, including interactions between multiple mechanisms; for example, how prior knowledge affects impedance control. It is expected that such empirical work will advance our understanding at a theoretical level, hopefully moving us from a general framework to a concise theory enabling the derivation of novel and testable predictions. We would be grateful if readers felt invited to participate in this scientific endeavour.



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## Data availability statement

Data available within the article or its supplementary materials.

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## Appendices

### Appendix A. PRISMA-ScR checklist

**Table A1.** Preferred reporting items for systematic reviews and meta-analyses extension for scoping reviews (PRISMA-ScR) checklist.

SECTION	ITEM	PRISMA-ScR CHECKLIST ITEM	REPORTED ON PAGE #
TITLE			
Title	1	Identify the report as a scoping review.	0
ABSTRACT			
Structured summary	2	Provide a structured summary that includes (as applicable): background, objectives, eligibility criteria, sources of evidence, charting methods, results, and conclusions that relate to the review questions and objectives.	1
INTRODUCTION			
Rationale	3	Describe the rationale for the review in the context of what is already known. Explain why the review questions/objectives lend themselves to a scoping review approach.	2–4
Objectives	4	Provide an explicit statement of the questions and objectives being addressed with reference to their key elements (e.g. population or participants, concepts, and context) or other relevant key elements used to conceptualize the review questions and/or objectives.	2–4
METHODS			
Protocol and registration	5	Indicate whether a review protocol exists; state if and where it can be accessed (e.g. a Web address); and if available,	*

(Continued)

**Table A1.** Continued.

SECTION	ITEM	PRISMA-ScR CHECKLIST ITEM	REPORTED ON PAGE #
		provide registration information, including the registration number.	
Eligibility criteria	6	Specify characteristics of the sources of evidence used as eligibility criteria (e.g. years considered, language, and publication status), and provide a rationale.	4–6
Information sources*	7	Describe all information sources in the search (e.g. databases with dates of coverage and contact with authors to identify additional sources), as well as the date the most recent search was executed.	5
Search	8	Present the full electronic search strategy for at least 1 database, including any limits used, such that it could be repeated.	Appendix B
Selection of sources of evidence†	9	State the process for selecting sources of evidence (i.e. screening and eligibility) included in the scoping review.	4–6**
Data charting process‡	10	Describe the methods of charting data from the included sources of evidence (e.g. calibrated forms or forms that have been tested by the team before their use, and whether data charting was done independently or in duplicate) and any processes for obtaining and confirming data from investigators.	4–6
Data items	11	List and define all variables for which data were sought and any assumptions and simplifications made.	4–5
Critical appraisal of individual sources of evidence§	12	If done, provide a rationale for conducting a critical appraisal of included sources of evidence; describe the methods used and how this information was used in any data synthesis (if appropriate).	***
Synthesis of results	13	Describe the methods of handling and summarizing the data that were charted.	****
RESULTS			
Selection of sources of evidence	14	Give numbers of sources of evidence screened, assessed for eligibility, and included in the review, with reasons for exclusions at each stage, ideally using a flow diagram.	5–6
Characteristics of sources of evidence	15	For each source of evidence, present characteristics for which data were charted and provide the citations.	Table 1
Critical appraisal within sources of evidence	16	If done, present data on critical appraisal of included sources of evidence (see item 12).	***
Results of individual sources of evidence	17	For each included source of evidence, present the relevant data that were charted that relate to the review questions and objectives.	Table 1
Synthesis of results	18	Summarize and/or present the charting results as they relate to the review questions and objectives.	6–12
DISCUSSION			
Summary of evidence	19	Summarize the main results (including an overview of concepts, themes, and types of evidence available), link to the review questions and objectives, and consider the relevance to key groups.	12–16
Limitations	20	Discuss the limitations of the scoping review process.	12–16
Conclusions	21	Provide a general interpretation of the results with respect to the review questions and objectives, as well as potential implications and/or next steps.	12–16
FUNDING			
Funding	22	Describe sources of funding for the included sources of evidence, as well as sources of funding for the scoping review. Describe the role of the funders of the scoping review.-	



## Comments

**\*Item 5, protocol and registration:** No protocol was preregistered. However, specific objectives of the review and methods were defined a priori:

- (1) Objectives: To provide a complete overview of peer-reviewed research on the topic of handling uncertainty in sensorimotor control in sports, focusing on collating all empirical evidence and contrasting different theoretical approaches.
- (2) Methods: Based on the review's objective, (a) eligibility criteria (pp. 4–6), (b) information sources (pp. 5–6), and (c) search strategy (pp. 5–6) were specified before conducting the review.

**\*\*Item 9, study selection:** Two raters independently screened all titles and abstracts. The abstracts were then merged, meaning that the record remained in the pool for full-text screening if at least one of the two raters judged the abstract as fulfilling the inclusion criteria. Furthermore, in an iterative process, the reference lists of all included studies were systematically screened, and in appendix C is documented which article is referred to by the other articles. The full-text screening was conducted by the first author. Potentially ambiguous cases were discussed with the other authors and resolved by consensus after referring to the inclusion and exclusion criteria.

**\*\*\*Item 12 / 16, critical appraisal:** Only studies published in peer-reviewed journals were considered. Based on the current review's objective, no quality assessment of individual studies was sought. However, regarding a critical appraisal, theoretical assumptions and their empirical foundation were critically discussed.

**\*\*\*\*Item 13 synthesis of results:** Based on the current review's objective and the inherent diversity in methodologies and different mechanisms to handle uncertainty, the synthesis of the evidence was made by comparing the number of studies supporting a mechanism and how powerful the theoretical prediction was made (e.g. normative models).

## Appendix B. Electronic search strategy

Last search:

15 July, 2023, via Campus Network ...

### PsycINFO (via OvidSP)

((uncertainty or noise) and (sensor\* or motor) and control and movement and sport).af.  
limit 1 to (peer reviewed journal and english language and '0110 peer-reviewed journal' and english)

### PubMed pubmed.gov

((((uncertainty OR noise)) AND (sensor\* OR motor)) AND control) AND sport) AND movement

### ScienceDirect

(uncertainty OR noise) and (sensory OR motor) and control and sport and movement

### Scopus

(uncertainty OR noise) AND (sensory OR motor) AND control AND sport AND movement AND  
(LIMIT-TO (PUBSTAGE, 'final')) AND (LIMIT-TO (DOCTYPE, 'ar')) AND (LIMIT-TO (LANGUAGE, 'English')) AND (LIMIT-TO (SUBJAREA, 'PSYC') OR LIMIT-TO (SUBJAREA, 'SOCI'))

### SportDiscus (via EBSCOhost)

(uncertainty OR noise) AND (sensor\* OR motor) AND control AND sport AND movement

### Web of Science

uncertainty OR noise (All Fields) and sensor\* OR motor\* (All Fields) and control (All Fields) and sport (All Fields) and movement (All Fields) and Articles (Document Types) and English (Languages)

## Appendix C

**Table C1.** Identification of the studies.

	Author(s)	cited in	found by
1	(Abernethy et al., 2001)	3,14,18,28,32,36,40,42,41,43,45,53,54,57,75,78,71,72	initial search
2	(Ankarali et al., 2014)		initial search
3	(Arthur & Harris, 2021)	30	initial search
4	(Bar-Eli et al., 2007)	71	reference list
5	(Bardy & Laurent, 1998)	16,35,64	initial search
6	(Berg & Hughes, 2017)	7	initial search
7	(Berg & Hughes, 2020)		initial search
8	(Bertucco et al., 2020)		additional
9	(Betzler et al., 2014)	52	reference list
10	(Blenkinsop et al., 2016)		initial search
11	(Bootsma & van Wieringen, 1990)	5,12,15,35,51,52,53,63,68,77	initial search
12	(Burgess-Limerick et al., 1991)		initial search
13	(Cañal-Bruland et al., 2018)	25,65,72	reference list
14	(Cognier & Féry, 2005)	40,41,43,49,53,54,57,75	reference list
15	(Davids et al., 1999)		initial search
16	(Dupuy et al., 2000)	56	reference list
17	(Eckerle et al., 2012)	7,69	initial search
18	(Farrow & Reid, 2012)	21,24,28,29,32,36,40,41,43,44,45,49,53,54,61,63,78,	initial search
19	(Franks et al., 1985)	5,11,12,15	initial search
20	(Goodman et al., 2009)		initial search
21	(Gray & Cañal-Bruland, 2018)	3,25,26,27,29,30,32,36,53,78	initial search
22	(Gray, 2002)	23,36,41,44,45,53,54,75	reference list
23	(Gray, 2009)	21,25,26,27,38	reference list
24	(Gredin et al., 2018)	2,11,12,13,16,21,22,29,34	initial search
25	(Gredin et al., 2019)	26,27,44	reference list
26	(Gredin, Bishop, et al., 2020a)		additional
27	(Gredin, Broadbent, et al., 2020c)	26	initial search
28	(Güldenpenning et al., 2018)	29,36	reference list
29	(Güldenpenning et al., 2023)		reference list
30	(Harris, Arthur, Vine, et al., 2022b)		reference list
31	(Heinen et al., 2014)	38	reference list
32	(Helm et al., 2020)	26,29,36,43,44,53	initial search
33	(Hiley et al., 2013)		initial search
34	(Horan et al., 2011)	51,52,76	initial search
35	(Iino et al., 2017)		initial search
36	(Jackson et al., 2020)	29,44	reference list
37	(Kenneil et al., 2015)		additional
38	(Krabben et al., 2018)		initial search
39	(Leukel et al., 2012)		initial search
40	(Loffing & Hagemann, 2014)	24,28,32,41,42,43,44,45,53,54,63,78	reference list
41	(Loffing et al., 2015)	24,27,28,29,32,36,42,43,44,53,54,63,78,	initial search
42	(Loffing et al., 2016)	32,54,60,78	initial search
43	(Magnaguagno & Hossner, 2020)	44	reference list
44	(Magnaguagno et al., 2022)		initial search
45	(Mann et al., 2014)	21,24,27,28,29,32,36,41,43,44,49,53	initial search
46	(Mather, 2008)		additional
47	(Mazyn et al., 2007)		initial search
48	(McIntyre et al., 2001)	81	reference list
49	(Milazzo et al., 2016)	29,36,54,60	reference list
50	(Misirlisoy & Haggard, 2014)	41	reference list
51	(Morrison et al., 2014)	52	reference list
52	(Morrison et al., 2016)	35	reference list
53	(Murphy et al., 2016)	24,25,36,43,44,54,63,72,78	reference list
54	(Murphy et al., 2018)	43,44,78,60	reference list
55	(Nakamoto et al., 2022)		reference list
56	(Nakano et al., 2020)		initial search
57	(Navia et al., 2013)	24,25,27,29,32,36,41,43,44,45,49,53,54,78	reference list
58	(O'Brien et al., 2020)		initial search

(Continued)

**Table C1.** Continued.

	Author(s)	cited in	found by
59	(O'Brien et al., 2021)		initial search
60	(Petri et al., 2020)		initial search
61	(Reeves et al., 2013)	62	reference list
62	(Reeves et al., 2016)		initial search
63	(Runswick et al., 2018)	25,26,27,29,64,78	reference list
64	(Santello et al., 2001)	6	reference list
65	(Schaffert et al., 2020)		additional
66	(Scholz et al., 2000)	52	reference list
67	(Scott et al., 1997)	35,51,52,68	reference list
68	(Sheppard & Li, 2007)	35	reference list
69	(Sinn et al., 2023)		reference list
70	(Sinnett & Kingstone, 2010)	13,82	reference list
71	(Sors et al., 2017)	13,60,65,72	initial search
72	(Sors et al., 2018)	65	reference list
73	(Stevenson et al., 2009)	3,44	reference list
74	(Takeuchi, 1993)	13,38,65,71,72	reference list
75	(Triplet et al., 2013)	24,26,53,54,63	initial search
76	(Tucker et al., 2013)	51,52	reference list
77	(van Soest et al., 2010)	35	reference list
78	(Wang et al., 2019)	60	reference list
79	(Whittier et al., 2022)		reference list
80	(Yamamoto et al., 2019)		initial search
81	(Zago et al., 2004)		reference list
82	(Zelic et al., 2012)	3	initial search

1 RESEARCH ARTICLE

2 RUNNING HEAD: Bayesian integration in virtual tennis

3 **From simple lab tasks to the virtual court: Bayesian  
4 integration in tennis**

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10 **ABSTRACT**

11 Two decades of research suggest that humans integrate sensory information and prior expectations in a  
12 Bayesian way to guide behavior. However, while Bayesian integration provides a powerful framework for  
13 perception, cognition, and motor control, evidence is largely limited to simple lab tasks. In two  
14 experiments with 32 participants each, we provide evidence for core Bayesian predictions in a complex  
15 sensorimotor task: returning tennis serves. Participants returned serves in a virtual reality setup with  
16 unconstrained movements and task demands matching real tennis. They faced two opponents with  
17 distinct distributions of serve locations. We measured predictive gaze behavior and explicit judgments to  
18 assess participants' estimations of the ball-bounce location. In the second experiment, we increased visual  
19 uncertainty with higher ball speeds. Confirming Bayesian predictions, participants' gaze was biased  
20 towards the opponent's preferred serve locations, particularly when visual uncertainty was increased by  
21 higher ball speeds. Furthermore, we found a dynamic reliability-weighted integration on two timescales:  
22 (1) The prior effect grew over the 'match' (i.e., with increasing reliability of prior information). (2) The  
23 prior affected early estimates of ball-bounce location (i.e., gaze behavior); however, these estimates were  
24 'overwritten' by incoming sensory inputs during ball flight. Our results demonstrate that Bayesian theory  
25 provides a principled explanation of how our sensorimotor system solves complex challenges at the limit  
26 of human performance, such as returning 260 km/h tennis serves.

27 **NEW & NOTEWORTHY**

28 This study tests Bayesian integration in a complex sensorimotor task: returning tennis serves. We found  
29 reliability-based prior-likelihood integration on two timescales: (1) over a 'match' (increasing reliability of  
30 prior information) and (2) over a single serve (increasing reliability of sensory information). Furthermore,  
31 this study shows how leveraging virtual reality technology provides a means to reduce the internal vs.  
32 external trade-off and study motor control under real-world task demands while ensuring rigorous  
33 experimental control.

34 **Keywords:** Bayesian inference, sensorimotor control, complex task, predictive gaze, virtual reality

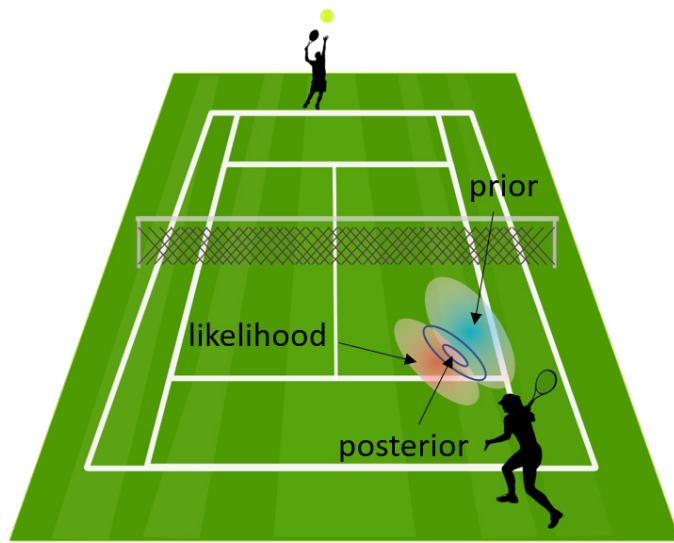
35

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## 36 INTRODUCTION

37 Over the past twenty years, Bayesian theory has become highly influential as a unifying framework for  
38 perception (1-4), higher-level cognition (5-8) and motor control (9-12). As a fundamental challenge in  
39 human behavior, we continuously perceive the world and act upon it under uncertainty due to incomplete  
40 information (13), noise and delays in our nervous system (14, 15), as well as ambiguities in the sensed  
41 environment (1). Bayesian theory provides a principled framework on how to deal with those  
42 uncertainties (16, 17).

43 The Bayesian framework is often illustrated by a tennis example originally introduced by Kording and  
44 Wolpert (10). To return a tennis serve, estimating where the ball will bounce is crucial. However, as  
45 sensory inputs are noisy and delayed, they provide no more than an uncertain estimate of the actual  
46 bounce location. To reduce uncertainty, the Bayesian strategy suggests combining sensory observations  
47 – the ‘likelihood’ (red area in Fig. 1) – with prior expectations based on the opponent’s preferred serve  
48 locations – the ‘prior’ (blue area in Fig. 1) – and integrating both information sources based on their  
49 respective reliabilities to obtain an optimized estimate – the ‘posterior’ (narrower ellipses between the  
50 red and blue areas in Fig. 1). Accordingly, Bayesian integration predicts that, after experiencing the  
51 preferences of an opponent, (1) estimates of the bounce location are biased towards the prior, (2)  
52 particularly when sensory observations are unreliable (e.g., when ball speeds are very high). Furthermore,  
53 Bayesian integration predicts a dynamical weighting process on two timescales. On the time scale of a  
54 match, (3) prior expectations should be increasingly weighted with accumulated experience about the  
55 opponent’s serve tendencies. On the timescale of a single serve, (4) the prior should be weighted heavily  
56 in early phases (i.e., when sensory information of the ball trajectory is yet uninformative); however, it  
57 should be ‘overwritten’ by more reliable sensory information becoming available during the later phases  
58 of the ball flight.



59  
60  
61 **Fig. 1 | Bayesian estimation in tennis returns.** As explained by Kording and Wolpert (11) for illustrative  
62 purposes, the posterior probability distribution for the ball-bounce location is continuously updated by  
63 the reliability-weighted integration of prior knowledge (Where is the ball likely to land based on my  
64 accumulated experience with the opponent?) and a likelihood function (How probable is my current visual

65 input given different potential ball bounce locations?) according to Bayes rule: posterior ~ prior \*  
66 likelihood.

67

68 Extensive empirical research shows that humans use a Bayesian strategy in simple lab tasks that require  
69 reaching (10), pointing (18), recognizing objects (19), pursuing random dot kinematograms (20) and  
70 localizing visual and auditory stimuli (21), as well as estimating speeds (22), forces (23) and timings (24).  
71 This research impressively demonstrates the explanatory power of Bayesian theory in well-controlled  
72 experiments. However, the demands in these tasks, in which participants remain seated and are asked to  
73 react to abstract stimuli with simple arm movements or button presses, differ substantially from the task  
74 demands encountered in typical real-world situations. Recently, advancing human behavior research from  
75 simple, reductionist tasks to complex, naturalistic tasks has been increasingly emphasized as a major  
76 challenge in psychology and neuroscience (25-30), especially when aiming to transfer findings to applied  
77 settings, such as rehabilitation or sports. Recent efforts to extend Bayesian principles to complex full-body  
78 movements (31, 32) and naturalistic stimuli (33-35) are promising, and an increasing number of findings  
79 in complex motor behavior are interpreted and discussed within the Bayesian framework (36-38).  
80 However, empirical evidence for core Bayesian predictions in complex sensorimotor behavior remains  
81 sparse (39) and is completely lacking regarding the dynamical features of prior-likelihood weighting on  
82 different timescales; specifically, the prediction that humans increasingly rely on the prior with  
83 accumulated experience over repeated situations and on the likelihood with accumulated sensory  
84 evidence within an evolving situation.

85 Here – 20 years after the seminal Kording and Wolpert (10) paper – we test whether Bayesian integration  
86 explains human behavior in a pronouncedly complex task popularly used for illustrative purposes, namely  
87 the task of actually returning a tennis ball. We developed an immersive virtual reality (VR) setup that  
88 enables the study of realistic and unconstrained movement behavior with spatial and temporal  
89 constraints that match real tennis while simultaneously ensuring full experimental control. In our  
90 experiments, participants faced two opponents with distinct distributions of serve locations. On day 1,  
91 participants returned serves of the first opponent, which followed a Poisson distribution with a central  
92 tendency either closer to the left or to the right side of the service box. On day 2, they faced a new  
93 opponent with opposite serving tendencies; that is, the serves exactly mirrored the distribution of the  
94 first day but with a central tendency closer to the right or the left. This design allows for comparing serves  
95 that provide identical visual information and differ only in terms of the participants' prior knowledge of  
96 the opponent's action tendencies accumulated before the current trial. In all trials, we measured  
97 participants' gaze behavior since there is strong evidence from vision research that humans typically  
98 perform a predictive saccade to the location where they expect the ball to bounce in fast interception  
99 tasks (33, 40-45). As an indicator of participants' estimate of the bounce location *in action*, we thus  
100 analyzed the fixation location following a predictive saccade. Additionally, we asked the participants to  
101 indicate where they perceived the ball bounce *after the action*. With this experimental setup, we  
102 conducted two studies. In Experiment 2, we increased visual uncertainty by increasing ball speeds (i.e.,  
103 decreasing time available to process sensory information), while all other specifics remained identical to  
104 Experiment 1.

105 Our results show that prior knowledge acquired through playing tennis affected participants' predictive  
106 gaze behavior in a Bayesian manner: (1) After experiencing the opponent's serve location probabilities,

107 participants' gaze behavior shifted towards the central tendency of the prior, (2) particularly when ball  
108 speeds were high (i.e., with greater uncertainty of sensory information). (3) Importantly, the effect of  
109 prior knowledge grew with increasing experience over the 'match' (i.e., with increasing reliability of prior  
110 information). Finally, (4) prior knowledge affected gaze behavior (i.e., early estimates in action); however,  
111 it did not affect participants' explicit judgments after the action (i.e., after reliable information on the ball-  
112 bounce location became available).

## 113 MATERIALS AND METHODS

### 114 Participants

115 Thirty-two healthy subjects (22 females and 10 males;  $M_{age} = 21.0$  years,  $SD = 2.5$ ) with no tennis  
116 experience participated in Experiment 1. For comparability with Experiment 1, 32 subjects (7 females and  
117 25 males) in the same age group ( $M_{age} = 20.6$  years,  $SD = 1.6$ ) participated in Experiment 2. The  
118 experiments were approved by the ethics committee of the Faculty of Human Science at the University of  
119 Bern (Approval Number: 2017-12-00003) and were conducted in accordance with the Declaration of  
120 Helsinki. All participants provided written informed consent.

### 121 Virtual reality setup

122 Participants performed tennis returns in a custom life-sized virtual-reality CAVE environment (Fig. 2 and  
123 video on [https://github.com/ispw-unibe-ch/bayesian\\_integration\\_in\\_tennis](https://github.com/ispw-unibe-ch/bayesian_integration_in_tennis)). The virtual tennis  
124 environment was developed in Unreal Engine 4.27 and displayed monoscopically in high resolution (pixel  
125 size 2.35 mm) using 11 projectors (Barco F50, 2560 × 1600 pixels, 60 Hz) driven by 11 cluster workstations  
126 on a 6.00 m × 3.75 m front wall, two 11.00 m × 3.75 m sidewalls, and a floor measuring 6.00 m × 11.00 m  
127 (Fig. 2). To ensure the accurate rendering of perspective from the participants' point of view, the  
128 participants' head positions were tracked with an Optitrack 3D-Motion-Capture system at a rate of 200  
129 Hz and processed in real-time.

130 To track their tennis strokes, the participants held a Wii controller with a marker cluster in their hands. In  
131 the experimental task, the perceptual demands in tracking the ball were high because of speeds like those  
132 delivered in professional tennis matches. A racquet was visually displayed in standard size. However, the  
133 effective (but invisible) collision surface that interacts with virtual balls was substantially larger, thereby  
134 enabling the participants to reach the balls played at a speed comparable to that of professional male  
135 tennis players (Experiment 1: 180 km/h; Experiment 2: 260 km/h). The flight distance, time in the air, and  
136 ball velocity remained constant throughout the experiment.

137 During the task, eye movements were recorded with a lightweight binocular eye-tracking system from  
138 Pupil-Labs synchronous to head movements (Optitrack) to allow automated gaze analyses. The eye  
139 tracker was calibrated prior to starting the experimental session. We checked the accuracy of gaze  
140 measurements before each trial by displaying a target and simultaneously having the Wii controller  
141 vibrate to capture attention. Participants were then required to gaze at the center of the target and  
142 confirm that they were looking as instructed by pressing a button. A short break was given after every  
143 32<sup>nd</sup> trial with a gaze accuracy check. To ensure high accuracy of eye-tracking measurements and avoid  
144 movement artefacts, the participants were instructed to stay in the same place when returning (behind  
145 the baseline, 12.69 m away from the net, and 3.95 m away from the mid-line). To allow participants to  
146 reach balls at the edges of the service box, the racquet position was scaled along the baseline so that the  
147 entire field could be reached at arm's length. Positional data acquired from the Optitrack system were

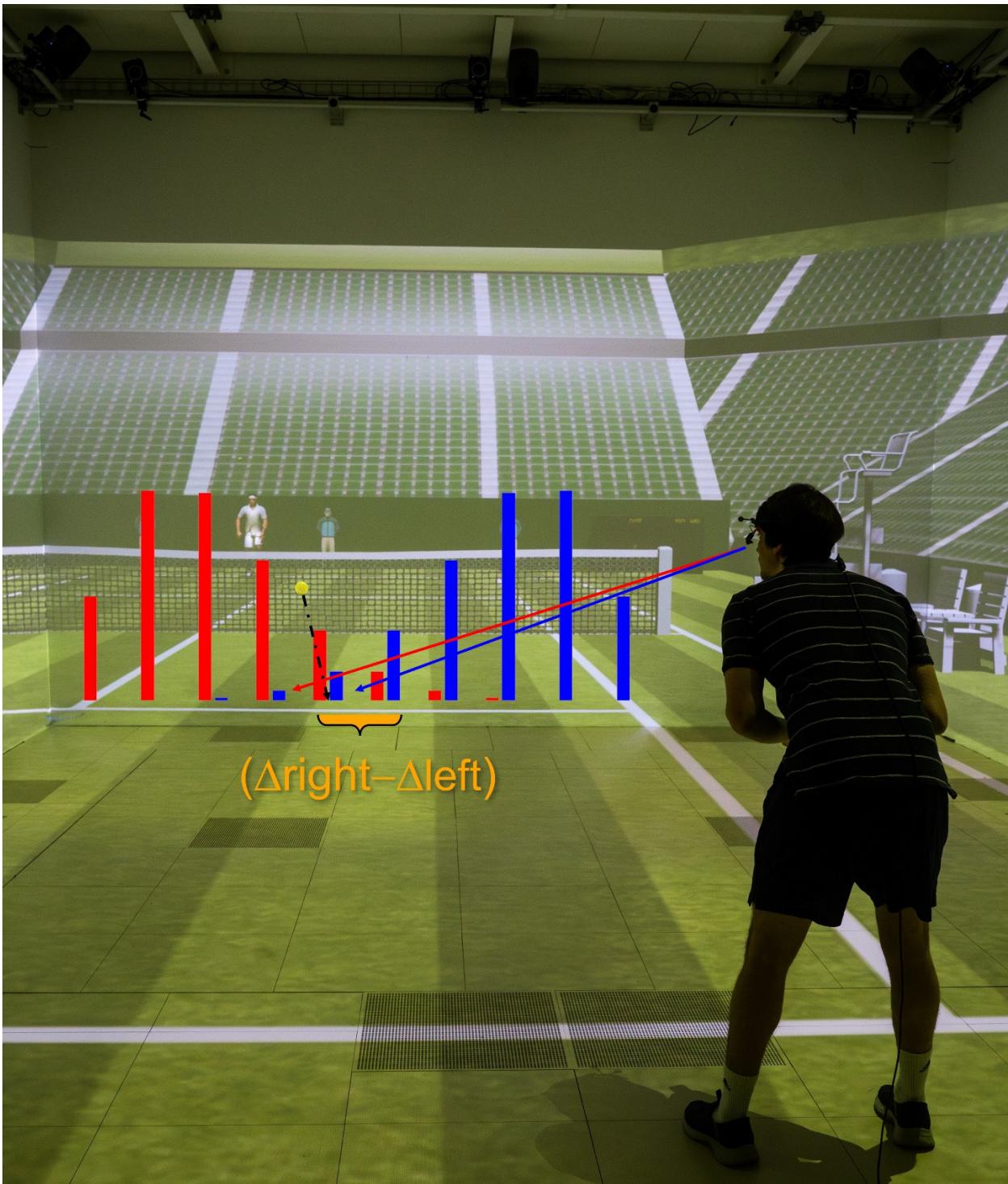
148 streamed in real-time to the tennis game (Unreal Engine 4.27), wherein the interactive elements were  
149 dynamically computed. All the systems used for the experiment were coordinated simultaneously using  
150 Streamix, an in-house development (<https://tpf.philhum.unibe.ch/portfolio/streamix>) based on the  
151 theoretical work by Maurer (46).

152 **Experimental design**

153 The participants' task was to return tennis serves. On two days, with a one-week break in between, the  
154 participants played against two different opponents with distinct serving distributions. Both distributions  
155 had the same ten potential bounce locations (Fig. 2). We chose the bounce locations in a way that  
156 maintained a consistent angle difference from the participant's perspective. The bounce locations were  
157 sufficiently close together to create the subjective impression of a continuous distribution. The body  
158 movements of the serving avatar were identical for all serves; therefore, the kinematic information  
159 extracted from the serving motion was uninformative regarding the ball's trajectory. Thus, the  
160 participants could only rely on two sources of information: current sensory information regarding the ball  
161 trajectory and prior information derived from previous trials.

162 Both days started with 60 warm-up serves equally distributed over the entire service box (neutral  
163 distribution), meaning that the ball was played to each bounce location six times in random order. In these  
164 first 60 trials, the warm-up opponent wore a blue shirt. Participants were then informed that they were  
165 now playing against another opponent, and the avatar was given either a white or yellow shirt  
166 (counterbalanced). Subsequently, the participants returned 320 serves, which followed a Poisson  
167 distribution with a central tendency either closer to the left or the right side of the service box on day 1  
168 and vice versa on day 2 (Fig. 2: red vs. blue). To measure the formation of the prior on both days at regular  
169 intervals, every 16<sup>th</sup> serve was played over one of these central positions. When the participants returned  
170 to the lab one week later, they faced a new opponent with opposite serving tendencies; that is, the serves  
171 exactly mirrored the distribution of the first day but with a central tendency closer to the right (blue in  
172 Fig. 2) or the left (red in Fig. 2) of the service box. Importantly, this design allows for the comparison of  
173 serves that provide identical visual information – due to the same service motions and ball trajectories –  
174 and only differ in terms of the participants' prior knowledge of the opponent's action tendencies  
175 accumulated before the current trial.

176 The experimental session was organized in 20 blocks of 16 trials. The trials were displayed in a quasi-  
177 random order with two boundary conditions. First, each block of 16 trials had the same central tendency.  
178 Second, in each block, the eighth trial landed in the middle of the field, specifically alternating between  
179 central positions 5 and 6 (Fig. 2). Each participant stayed on the same side of the playing field; however,  
180 the side was counterbalanced between the participants. Consequently, a total of four experimental  
181 protocols were used to counterbalance the side of the playing field and the central tendency closer to the  
182 mid- or side-line.



183

184 **Fig. 2 | Experimental serve distributions.** In the experimental virtual-reality setup, 320 serves were  
185 distributed with either the red or the blue probability on day 1 and vice versa on day 2. Every 16<sup>th</sup> trial  
186 was played on one of the two central positions, as this allowed the subsequent calculation of differences  
187 in gaze behavior and explicit judgments of ball bounce locations between day 1 and day 2 for kinematically  
188 identical serves ( $\Delta\text{right} - \Delta\text{left}$ ).

189 With this experimental setup, we conducted two studies, each involving 32 participants. In Experiment 2,  
190 we increased visual uncertainty, while all other specifics remained identical to Experiment 1. As a natural  
191 way to raise uncertainty, in contrast to visual blurring (which is regularly used in classic (10) as well as  
192 more recent studies (31, 32) on Bayesian integration), we increased the ball speeds and thus decreased  
193 the time available to process sensory information on the ball trajectory. Specifically, we raised the serve  
194 velocities from 180 km/h in Experiment 1 (about the average speed in male professional tennis) to 260  
195 km/h in Experiment 2 (in the range of the fastest serves measured in male professional tennis).

## 196 Measures

### 197 Fixation location after predictive saccade

198 As an indicator of participants' expectations of the ball-bounce location *in action*, we identified the first  
199 gaze fixation following a predictive saccade before the actual bounce. We then used the lateral shift of  
200 gaze away from the true location of the bounce as a measure of participants' prior expectation bias. The  
201 gaze shift was calculated in degrees from the participant's perspective. Eye movements were recorded  
202 with a lightweight binocular eye-tracking system from Pupil-Labs at a frequency of 120 Hz. The procedure  
203 to obtain our measure consisted of six steps.

204 1. *Confidence-based data filtering*: The Pupil-Labs software provides a confidence value ranging from 0 to  
205 1 for each frame, indicating the reliability of the eye model calculation. We excluded frames with  
206 confidence below a threshold of 0.9, and missing data were interpolated using cubic interpolation for  
207 sequences with fewer than 10 consecutive frames. Sequences over 10 frames were assumed to involve  
208 blinking and were treated as missing values.

209 2. *Savitzky-Golay filtering and resampling*: The data in each dimension underwent Savitzky-Golay filtering  
210 with a window length of 11. Subsequently, we resampled the data using cubic interpolation to achieve  
211 equidistance with a frequency of 120 Hz.

212 3. *Fixation identification using the Dispersion-Threshold (IDT) algorithm*: We implemented the IDT  
213 algorithm, which is optimized to identify fixations on planar surfaces (47). To allow fixation detection in  
214 3D space, we applied a coordinate transformation to each frame to account for the changing orientation  
215 of the plane perpendicular to the eye-bounce location vector. We identified a fixation when the gaze  
216 stayed within a 1.5° window for at least 6 frames (50 ms) (48). After completion of the fixation calculations,  
217 the two following fixations were checked to confirm a gap of less than 10 ms with a deviation of less than  
218 1.5°. If so, we merged the fixations.

219 4. *Correction quaternions calculation*: Participants had to look at a target before each trial – with a  
220 vibrating Wii controller to gain their attention – and confirm with a button press that they had fixed the  
221 target's center. We calculated the fixations in the period from -0.3 to 0.3 seconds around the button press,  
222 and we used the fixation starting closest to the button press to calculate the difference quaternion to the  
223 middle of the target. The uncorrected fixations and correction quaternions were saved.

224 5. *Correction quaternion averaging*: We filled the missing correction quaternions with the linearly  
225 weighted mean of the neighbor quaternions. Because the validation point (looking at the middle of the  
226 target) itself is a value with an error (participants could have looked somewhere else, even if they pressed  
227 the button), we averaged the correction quaternions over 15 trials using a moving average. We identified  
228 outliers and removed them based on the Mahalanobis distance of the norm of the components'  
229 differences between two consecutive correction quaternions.

230 6. *Fixations after predictive saccades:* We calculated and corrected the fixations following predictive  
231 saccades using the previously applied correction quaternions. Fixations were identified based on spatial  
232 and temporal criteria, as specified by the IDT algorithm. The duration of the ball flight from the hit of the  
233 server's racquet until the bounce was 0.54 seconds in Experiment 1 and 0.39 seconds in Experiment 2.  
234 We calculated the fixations in the time interval of 0.1 seconds after the server's racquet hit and 0.15  
235 seconds after the ball bounce. This choice of interval assumes that a complete reaction cycle lasts at least  
236 0.1 seconds and the restriction that a fixation must last at least 0.05 seconds. In these time intervals, we  
237 took the fixation after the largest saccade in the vertical direction as the indicator of the expected bounce  
238 location, which was the dependent variable of the experiment. We excluded fixations when participants  
239 were clearly not yet looking close to the bounce location (higher than 9° in vertical direction above the  
240 bounce location, which is approximately the top height of the tennis net).

#### 241 Explicit judgment of ball-bounce location

242 As an indicator of the participants' estimates *after the action*, we asked participants on selected trials to  
243 explicitly judge where they had perceived the ball bounce. Specifically, we asked them after every 16<sup>th</sup>  
244 trial (trials played through the center) and, to reduce predictably, after two randomly selected additional  
245 trials per block. After completion of such returns, the Wii controller vibrated, and the displayed racquet  
246 transformed into a virtual laser pointer, allowing participants to indicate their perceived ball-bounce  
247 location by pointing and pressing a button on the Wii controller. As for the gaze fixation, the horizontal  
248 difference between the judgment and the true location of the bounce was used as a measure.

#### 249 Statistical analyses

##### 250 1. Comparison of gaze fixations before vs. after experiencing opponents' distributions

251 For all ten bounce locations (Fig. 2), we compared participants' fixation locations at the beginning of the  
252 experiment with equally distributed serves (neutral condition) vs. in the last four blocks of the  
253 experimental session, that is, after extensive exposure to the Poisson distributed serve locations (biased  
254 condition). Mean values for all bounce positions were calculated based on all participants and trial data.  
255 As every participant had multiple data points for each bounce position, the error values were not  
256 independent; consequently, we considered the hierarchical structure of the data to calculate the  
257 arithmetic means (49). We compared the aggregated mean fixation locations descriptively and plotted  
258 them in Fig. 3 left. Outliers were detected according to the Mahalanobis distance and removed based on  
259 an alpha level of 5%. Furthermore, we calculated the 95% confidence intervals of the arithmetic means.  
260 We applied the R-package 'nlme' (50).

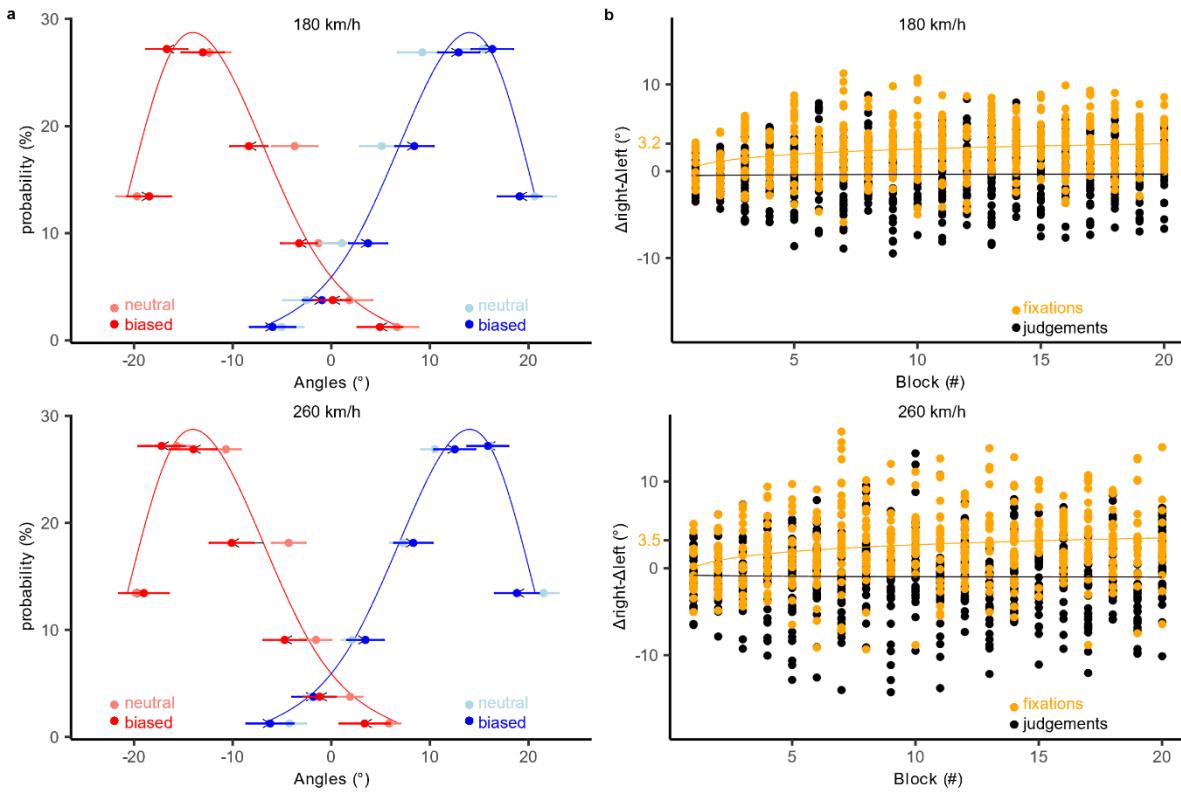
##### 261 2. Development of prior knowledge effect over time

262 To analyze how the prior knowledge effect develops over time, we calculated multilevel logarithmic  
263 regression analyses of the shift differences in both the gaze fixations and the explicit judgments.  
264 Specifically, we analyzed the serves played to the central positions (positions 5 and 6) and calculated how  
265 the differences between participants' fixation locations or explicit judgments and the actual bounce  
266 location when experiencing the right vs. left distribution ( $\Delta$ right– $\Delta$ left) developed over the session. The  
267 sign of the shift differences was defined in such a way that a positive shift difference corresponded to a  
268 sum of both shift differences towards the central tendencies of the two distributions. We didn't include  
269 any other dependent variables. As 20 measurements (time series) of each participant (every 16<sup>th</sup> trial)  
270 were taken, the error values were not independent; consequently, the hierarchical structure of the data  
271 had to be considered (49). We calculated the fixed effects in a hierarchical regression analysis (lowest

272 level). Furthermore, according to the exponential law of practice (51) (or logarithmic with a base of the  
273 natural value 'e' as the reverse function), we considered the logarithmic values of the time (block  
274 numbers) as the independent variables. Under the assumption that missing values occur randomly,  
275 hierarchical regression analysis can handle missing values (49). We detected outliers with the Cook's  
276 distance and removed them if values affected the regression more than three times as much as the  
277 average value. Homoscedasticity and normality of the residuals were checked graphically. We built  
278 regression models in several steps, as recommended in the literature (49), by adding model complexity  
279 step by step: grand mean, log(block), log(block) with random intercepts, log(block) with random intercept,  
280 and random slopes. Descriptively, we compared models considering the Akaike Information Criterion  
281 (AIC), Bayesian Information Criterion (BIC), and log-likelihood (Table 1, Table 2, Table 3, and Table 4 in  
282 extended data). Inferential statistically, we used the log-likelihood ratio  $\chi^2$  test for the model comparison.  
283 We report the values of the random intercept models as the models with random intercepts and slopes  
284 have reduced AIC and BIC values, no significantly changed log-likelihood ratio values, and for the explicit  
285 judgments, no converging solutions. As the time points were equally spaced, we used a first-order  
286 autoregressive covariance structure (49). Further, we used the maximum likelihood for model estimations  
287 and tested regression coefficients with the Wald test for significance. For all inferential tests, we choose  
288 an alpha level of 5%. We applied the R-package 'nlme' (50).

## 289 **RESULTS**

290 In both experiments, the participants' fixations systematically shifted away from the actual ball bounce  
291 location and towards the central tendency of the distribution they had been exposed to (Fig. 3 left). While  
292 there is no recognizable pattern in fixation locations during the warm-up trials (neutral prior; lighter dots  
293 in Fig. 3 left), all fixations (with one exception) at the end of each session shifted towards the central  
294 tendency of the experienced serves (biased prior; darker dots in Fig. 3 left), suggesting that the  
295 participants implicitly learned probability distributions and used this information to generate predictive  
296 saccades. Consistent with Bayesian theory, the shifts towards the prior were more pronounced in  
297 Experiment 2 (higher uncertainty due to 260 km/h serves; Fig. 3 bottom left) than in Experiment 1 (lower  
298 uncertainty due to 180 km/h serves; Fig. 3 top left). Interestingly, the fixations were drawn more towards  
299 the mode rather than towards the arithmetic mean of the probability distributions.



300 **Fig. 3 | Gaze behavior and explicit judgments at different serve speeds.** **A,** The horizontal axes relate to  
 301 the participant's view in the direction of the avatar, and the vertical axes show the actual probability of  
 302 each bounce location. The lighter dots depict aggregated fixation locations for equally distributed serves  
 303 (neutral prior), and the darker dots correspond to aggregated fixation locations for the distributions  
 304 shown in Fig. 2 at the end of the session (biased prior). Error bars represent the 95% confidence intervals  
 305 of the arithmetic mean across participants. While all biased fixations (except for one) are shifted towards  
 306 the central tendency, no such pattern was found for the fixations with the neutral prior. This shows that  
 307 accumulated prior knowledge is taken into account in predictive gaze behavior, especially for the higher  
 308 serve speed. **B,** The orange dots represent differences between the deviations of the actual ball bounce  
 309 location from the fixation location for the right and for the left distribution, respectively ( $\Delta_{right} - \Delta_{left}$ );  
 310 these were measured on every 16<sup>th</sup> trial for the two central positions of the overlapping distributions (Fig.  
 311 2). The black dots show the corresponding difference values for the participants' explicit judgments of the  
 312 ball-bounce locations for the same trials. For gaze behavior, hierarchical logarithmic regression analyses  
 313 revealed a significant increase in difference values over time that was more pronounced for the higher  
 314 serve speed, whereas no change was found for the explicit judgments. This suggests that accumulated  
 315 prior knowledge increasingly affects predictive gaze behavior, especially under the more uncertain  
 316 condition of a higher serve speed; however, the prior is 'overwritten' as soon as more reliable perceptual  
 317 information about the actual ball-bounce location becomes available.

318

319 To test whether the gaze shifts towards the prior distribution increased over time (i.e., with growing  
320 experience), we analyzed the serves played to the central positions (positions 5 and 6 in Fig. 2) and  
321 calculated how the differences between participants' fixation locations and the actual bounce location  
322 when experiencing the right vs. left distribution ( $\Delta$ right– $\Delta$ left) developed over the session (Fig. 3 right). In  
323 Experiment 1, a hierarchical logarithmic regression analysis showed that these differences ( $\Delta$ right– $\Delta$ left)  
324 increased over the session (orange dots in Fig. 3 top right). A medium significant fixed effect for increasing  
325 differences over time was revealed ( $N_{\text{subjects}} = 32$ ,  $N_{\text{measurements}} = 533$ ,  $\text{intercept} = 0.54 [-0.27 - 1.35]$ ,  $b = 0.88$   
326 [0.58 – 1.18],  $t(500) = 5.80$ , one-sided  $p < .001$ ,  $R^2_{\text{marginal}} = .050$ ) (see Methods and Extended Data for  
327 information on the hierarchical regression and model selection). In Experiment 2, with higher ball speeds,  
328 we replicated the effect with an increased slope, as predicted by Bayesian theory (orange dots in Fig. 3,  
329 bottom right). The hierarchical logarithmic regression shows a significant medium fixed effect over time  
330 of the shift differences towards the central tendency of the prior distribution ( $N_{\text{subjects}} = 32$ ,  $N_{\text{measurements}} =$   
331 477,  $\text{intercept} = 0.09 [-1.09 - 1.26]$ ,  $b = 1.14 [0.70 - 1.57]$ ,  $t(444) = 5.07$ , one-sided  $p < .001$ ,  $R^2_{\text{marginal}} =$   
332 .053). These results confirm that participants increasingly rely on the prior with continuously growing  
333 experience of the opponents' action tendencies and use this information in a Bayesian manner to  
334 generate predictive saccades.

355 To test whether initial estimations in action (as reflected in the participants' gaze) are 'overwritten' by  
356 more reliable visual information becoming available in the course of a single serve, we assessed the  
357 development of explicit judgments after the action. We did not observe any shifts in the explicit judgments  
358 of the bounce location as a function of experience (black dots in Fig. 3 right dots), either in Experiment 1  
359 ( $N_{\text{subjects}} = 32$ ,  $N_{\text{measurements}} = 595$ ,  $\text{intercept} = -0.50 [-1.34 - 0.35]$ ,  $b = 0.06 [-0.28 - 0.40]$ ,  $t(562) = 0.35$ , one-  
360 sided  $p = .364$ ,  $R^2_{\text{marginal}} < .001$ ) or in Experiment 2 ( $N_{\text{subjects}} = 32$ ,  $N_{\text{measurements}} = 619$ ,  $\text{intercept} = -0.81 [-1.85$   
361 – 0.23],  $b = -0.07 [-0.48 - 0.33]$ ,  $t(586) = -0.349$ , one-sided  $p = .364$ ,  $R^2_{\text{marginal}} < .001$ ). This result confirms  
362 the Bayesian prediction that prior expectations are weighted heavily in early phases of the ball flight,  
363 when visual information is yet unreliable, but are weighted less as more reliable sensory information  
364 becomes available.

## 345 DISCUSSION

346 Our results are consistent with the hypothesis that humans integrate sensory and prior information in a  
347 Bayesian way when returning tennis serves, as Körding and Wolpert (10) classically proposed for  
348 illustrative purposes. Extending recent studies in which findings on complex motor behavior are discussed  
349 within a Bayesian framework (31-38, 43, 52), our results confirm core Bayesian predictions. In particular,  
350 we show that participants' behavior follows a dynamic reliability-based weighting process of sensory and  
351 prior information on two timescales: (1) Over the course of a 'match' (i.e., an experimental session), the  
352 effect of prior information grew with accumulating experience of the opponent's preferred serve locations  
353 (the prior becoming increasingly more reliable), particularly in the condition with higher ball speeds  
354 (sensory information becoming less reliable). (2) In the course of a single serve, the prior was weighted  
355 heavily for early estimates but was 'overwritten' by incoming sensory information during ball flight.

356 These results strengthen two decades of experimental lab-based work (10, 18-24, 53-55) by  
357 demonstrating that Bayesian principles extend to complex naturalistic behavior. We show that Bayesian  
358 theory provides a principled functional-level explanation of how our sensorimotor system solves  
359 impressive challenges at the limits of human performance, such as returning a 260 km/h tennis serve. This  
360 extension is particularly valuable for applied fields, such as rehabilitation or sports performance,

361 suggesting that Bayesian theory provides a well-founded, unifying framework for addressing and  
362 structuring real-world problems to – ultimately – advance practice.

363 Beyond Bayesian theory, our work embodies current calls to advance hypothesis-driven research on  
364 human behavior from simple lab tasks to complex naturalistic demands in general. Human motor control  
365 research has traditionally prioritized internal over external validity. Recently, however, investigating  
366 naturalistic tasks (28) and understanding behavior, as well as the underlying processes on the level of  
367 neural implementation in situations they have evolved to function in (53), has been increasingly  
368 emphasized as a major challenge of psychology and neuroscience. In this context, we show that leveraging  
369 advances in VR technology provides a means to reduce the trade-off between internal and external  
370 validity (56) by designing experiments that capture real-world task demands (e.g., returning a tennis  
371 serve) while maintaining rigorous experimental control (e.g., ball trajectories, distributions, or velocities).  
372 We are convinced that this novel avenue of experimental studies under real-world conditions – teamed  
373 up with complementary, large-scale exploratory analyses (57) – will contribute valuable new insights to  
374 the field of human motor control research.

375 **APPENDIX**

376 **Table 1.** Model comparison for the gaze shift differences in Experiment 1

Model	df	AIC	BIC	logLik	Test	L.Ratio	p
1 Intercept	2	2666.820	2675.377	-1331.410			
2 Log(block)	4	2623.076	2640.190	-1307.538	1 vs 2	47.74388	<.0001
3 Log(block)RI	5	2581.483	2602.876	-1285.742	2 vs 3	43.59296	<.0001
4 Log(block)RS	7	2583.710	2613.659	-1284.855	3 vs 4	1.77356	0.412

377 Note df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion,  
 378 LogLik = log-likelihood, L.Ratio = log-likelihood ratio, RI = random intercepts, RS = random intercept and  
 379 slopes

380 **Table 2.** Model comparison for the explicit point estimation differences in Experiment 1

Model	df	AIC	BIC	logLik	Test	L.Ratio	p
1 Intercept	2	3125.508	3134.285	-1560.754			
2 Log(block)	4	3123.857	3141.411	-1557.928	1 vs 2	5.65080	0.0593
3 Log(block)RI	5	3105.439	3127.381	-1547.719	2 vs 3	20.41829	<.0001
4 Log(block)RS	7	nan	nan	nan	3 vs 4	nan	nan

381 Note df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion,  
 382 LogLik = log-likelihood, L.Ratio = log-likelihood ratio, RI = random intercepts, RS = random intercept and  
 383 slopes

384 **Table 3.** Model comparison for the gaze shift differences in Experiment 2

Model	df	AIC	BIC	logLik	Test	L.Ratio	p
1 Intercept	2	2698.432	2706.767	-1347.216			
2 Log(block)	4	2670.878	2687.548	-1331.439	1 vs 2	31.55394	<.0001
3 Log(block)RI	5	2643.441	2664.278	-1316.720	2 vs 3	29.43691	<.0001
4 Log(block)RS	7	2644.868	2674.041	-1315.434	3 vs 4	2.57233	0.2763

385 Note df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion,  
 386 LogLik = log-likelihood, L.Ratio = log-likelihood ratio, RI = random intercepts, RS = random intercept and  
 387 slopes

388 **Table 4.** Model comparison for the explicit point estimation differences in Experiment 2

Model	df	AIC	BIC	logLik	Test	L.Ratio	p
1 Intercept	2	3537.743	3546.599	-1766.871			
2 Log(block)	4	3533.562	3551.274	-1762.781	1 vs 2	8.180925	0.0167
3 Log(block)RI	5	3511.146	3533.287	-1750.573	2 vs 3	24.415808	<.0001
4 Log(block)RS	7	nan	nan	nan	3 vs 4	nan	nan

389 Note df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion,  
 390 LogLik = log-likelihood, L.Ratio = log-likelihood ratio, RI = random intercepts, RS = random intercept and  
 391 slopes

## 392 DATA AVAILABILITY

393 All data used for statistical analysis and figure generation with the corresponding R-scripts, as well as a  
394 video of the experimental task, are available at GitHub ([https://github.com/ispw-unibe-ch/bayesian\\_integration\\_in\\_tennis](https://github.com/ispw-unibe-ch/bayesian_integration_in_tennis)). Raw eye-tracking and motion-capture data (> 1 TB) are available  
395 on reasonable request. Correspondence and requests for materials should be addressed to Damian Beck  
396 (damian.beck@unibe.ch).

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401 Lab, and Jürg Schmid for statistical advice.

## 402 DISCLOSURES

403 There is no conflict of interest.

## 404 AUTHOR CONTRIBUTIONS

405 As co-first authors, D.B. and S.Z. contributed equally to the work. E.-J.H. came up with the experimental  
406 idea. D.B., S.Z., and E.-J.H. collaborated on further conceptualization and writing. R.K., D.B., and S.Z.  
407 developed the experimental setup. D.B. and S.Z led the experiment. R.K. provided technical supervision.  
408 D.B. analyzed the data under the supervision of R.K.

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531

1 **Humans are able to learn bimodal priors in complex sensorimotor behaviour**

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8

9 **Abstract**

10 Extensive experimental work suggests that humans integrate prior and sensory information  
11 according to Bayesian principles to reduce uncertainty in perception and action. However,  
12 while Bayesian integration provides a unifying theory, the question remains to what extent it  
13 explains human behaviour in more naturalistic situations including more complex movements  
14 and distributions. In this study, we examine whether humans are able to learn and use bimodal  
15 priors in a complex sensorimotor task: returning tennis serves. Participants returned serves in  
16 an immersive virtual reality setup with realistic movements and spatiotemporal task demands  
17 matching real tennis. The location of the opponent's serves followed a bimodal distribution.  
18 We manipulated visual uncertainty by introducing three levels of ball speeds: slow, moderate,  
19 and fast. After extensive exposure to the opponent's serves, participants' movements were  
20 biased towards the prior. As predicted by Bayesian theory, the bias was stronger with higher  
21 levels of uncertainty. Further, our data indicate that in this complex task, participants'  
22 movements were not only biased by prior expectations but also by biomechanical constraints  
23 and associated motor costs. Interestingly, an explicit knowledge test after completion of the  
24 experiment revealed that, despite incorporating the prior knowledge of the opponent's serve  
25 distribution into their behaviour, participants were not explicitly aware of the pattern. Our  
26 results show that humans can implicitly learn bimodal priors and utilize them in complex  
27 sensorimotor behaviour.

28

29 **Keywords:** Bayesian integration, probabilistic inference, complex tasks, naturalistic  
30 behaviour, sensorimotor control

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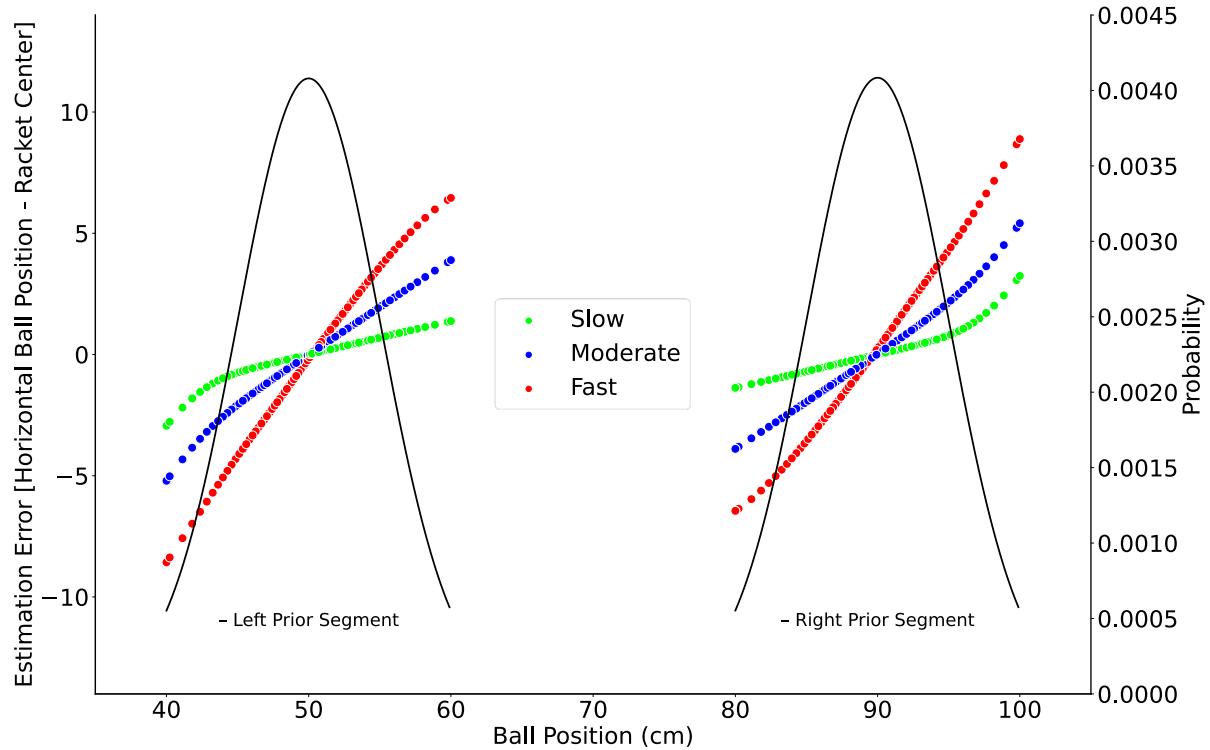
32 **Introduction**

33 Due to inherent noise and delays in the nervous system, humans are required to perceive the  
34 world and act upon it under a considerable amount of uncertainty (Faisal et al., 2008; Franklin  
35 & Wolpert, 2011; van Beers et al., 2002). A functional strategy to reduce uncertainty,  
36 formalised by Bayesian integration, is to combine current sensory information and prior  
37 expectations and integrate both sources of information based on their respective reliability  
38 (Körding, 2007; Körding & Wolpert, 2006; Maloney & Mamassian, 2009). A rich body of  
39 research in the field of motor control and perception (for an overview: Berniker & Körding,  
40 2011) shows that human behaviour is consistent with Bayesian integration in well-controlled  
41 experiments that require reaching (e.g., Körding & Wolpert, 2004) or pointing (e.g., Tassinari  
42 et al., 2006). However, the question remains to what extent it explains behaviour in complex  
43 situations that we face in our daily lives (Beck et al., 2023).

44 In recent years, testing major theories of human behaviour in complex, naturalistic tasks has  
45 been increasingly highlighted as a key challenge in the field (Cisek & Green, 2024; Haar et al.,  
46 2020; Ibanez, 2022; Maselli et al., 2023; Tsay et al., 2024). On closer examination, the demands  
47 in classical laboratory tasks differ from many real-world tasks in two regards. First, in most  
48 experiments, striving for high experimental control, subjects remain seated and are asked to  
49 react to well-defined stimuli with simple arm movements or button presses in a highly  
50 constrained manner. Many real-world tasks – think of returning a tennis serve – entail dynamic  
51 situational changes and require the coordination of complex movements. Only recently, an  
52 increasing number of studies have started to take on the challenge of testing Bayesian  
53 predictions in more complex movement tasks (Arthur & Harris, 2021; Beck et al., 2024;  
54 Stevenson et al., 2009; Whittier et al., 2022). Second, in most experiments on Bayesian  
55 integration, participants learned regularities in the task that follow a simple Gaussian  
56 distribution whereas many real-world tasks contain more complex patterns of regularities.  
57 Again, tennis provides a natural example: Typically, the serves of your opponent will not be  
58 normally distributed around one location but rather contain two peaks of highly probable ball  
59 locations – a wide vs. T serve (Tea & Swartz, 2023) – following a bimodal distribution. Despite  
60 the fact that Bayesian theory makes clear predictions on how bimodal priors should be  
61 integrated, thereby providing a particularly hard test for Bayesian integration (Körding &  
62 Wolpert, 2004), the extent to which humans can learn and exploit bimodal priors has been  
63 addressed only in a few studies so far and remains a subject of current debate (Acerbi et al.,  
64 2014; Acerbi et al., 2012; Körding & Wolpert, 2004).

65 In this study, we investigate whether humans can learn and use bimodal priors in a complex,  
66 naturalistic sensorimotor task, namely the task of actually returning a tennis serve. We use and  
67 extend an immersive virtual reality (VR) setup developed in a previous study (Beck et al.,  
68 2024) that enables the examination of natural movement behaviour with spatial and temporal  
69 constraints that match real tennis while simultaneously ensuring full experimental control. In  
70 three experimental sessions, participants had the task of returning tennis serves. The locations  
71 of the opponent's serve followed a bimodal distribution with peaks at 50 cm and 90 cm to the  
72 right of the participants' starting position (see Figure 1). We did not inform the participants  
73 about the pattern of the opponent's serves. We manipulated the uncertainty of visual  
74 information by varying between three levels of ball speeds: slow (i.e., ball trajectories being  
75 easily observable), moderate and fast (i.e., ball trajectories being very hard to perceive). As a  
76 measure of the subjects' estimation error, we compute the horizontal deviation between the ball  
77 and the racket's sweet spot at the time of contact.

78 To test whether participants learned the bimodal prior and integrate it with sensory information  
79 according to Bayesian principles, we analyse the relationship between the estimation error (y-  
80 axis in Figure 1) and the true ball location (x-axis in Figure 1) analogous to the analyses in  
81 classical Bayesian experiments (Körding & Wolpert, 2004). Figure 1 illustrates the predictions  
82 based on the Bayesian model with a bimodal prior for the three uncertainty conditions: slow  
83 (green), moderate (blue), fast (red) serves. In general, the Bayesian model predicts that  
84 participants' movements are biased toward the prior, with the bias increasing as uncertainty  
85 rises. Specifically, the Bayesian model with a bimodal prior predicts a nonlinear relationship  
86 between the estimation error and the true ball location, which can be quantified with a "jump"  
87 between the left and right segments of the distribution. Throughout the paper, we refer to this  
88 jump as "bimodal prior effect". Based on Bayesian integration, we predict that, after extensive  
89 exposure to the opponent's serve distribution, (1) a bimodal prior effect can be detected and  
90 (2) the magnitude of the bimodal prior effect increases as a function of uncertainty, namely,  
91 more pronounced under conditions of fast serves compared to moderate and slow serves.

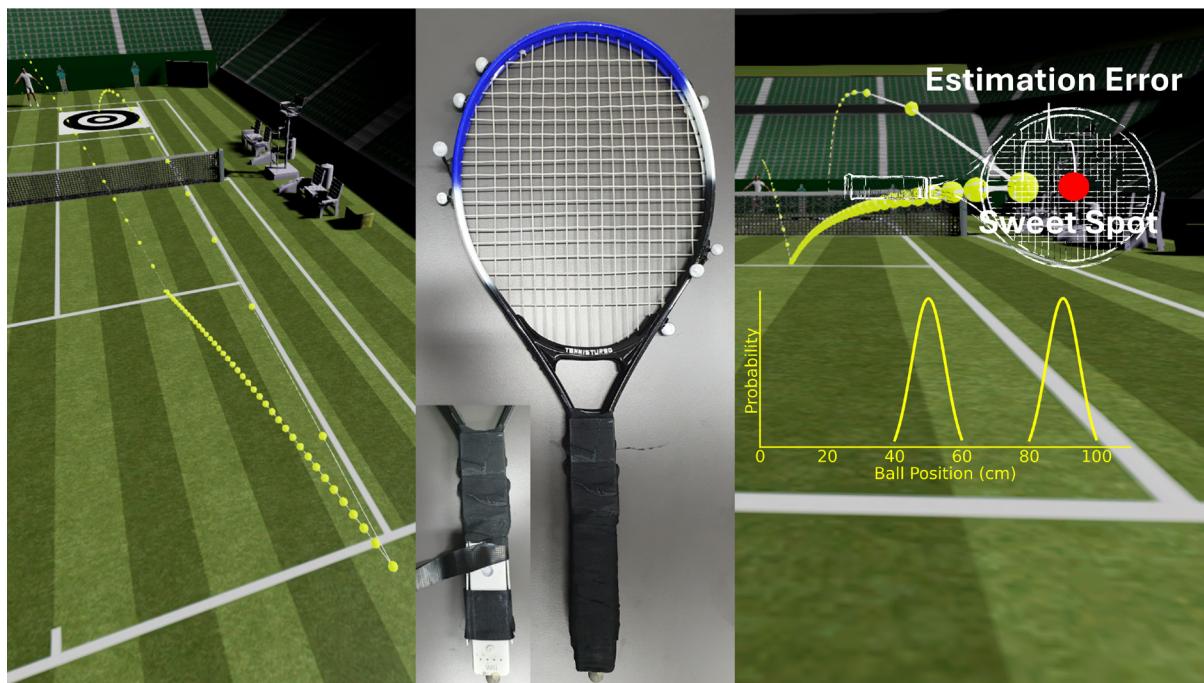


92  
93 **Fig. 1 | Expectations from the Bayesian simulation.** For model prediction, we ran a Bayesian  
94 simulation according to Ma et al. (2023) with three different levels of visual uncertainty (slow,  
95 moderate, fast ball speed) and a bimodal prior. The figure shows the simulated estimation errors  
96 (horizontal deviation between the ball and the racket's sweet spot) (y-axis) in relation to the  
97 actual ball positions (x-axis). The simulation script is available on GitHub  
98 ([https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)).  
99

## 100 Results

101 In a within-subjects design, the task of the 24 right-handed participants was to return tennis  
102 serves toward the centre of a target on the opponent's field in a customized life-sized VR CAVE  
103 environment. The serves followed a prespecified serve spline trajectory (see Figure 2, left) with  
104 three different initial ball speed conditions: slow ( $v = 108 \text{ km/h}$ ), moderate ( $v = 180 \text{ km/h}$ ), fast  
105 ( $v = 252 \text{ km/h}$ ), and thus three different levels of visual uncertainty. However, we controlled  
106 that the temporal timing demands were the same in all conditions. Unknown to the participants,  
107 the ball actually to be struck was an invisible stationary ball located parallel to the ground line  
108 from participants' fixed starting position on the prespecified trajectory that could be hit 200 ms  
109 before until 200 ms after the visibly displayed ball passed the position of the invisible stationary  
110 ball. The deviation of the invisible ball from the sweet spot at impact on the axes parallel to the  
111 tennis ground line determined how close the ball flew toward the centre of the target (see Figure

112 2, right). After each return, points were displayed on how well the participant hit the ball on a  
113 scale of 0 to 100, and a monetary reward was given to the top three participants.  
114 The avatar always performed exactly the same serving motion, so that no information could be  
115 obtained from the movement kinematics. Despite the constant serving motion, the ball  
116 trajectories were manipulated according to a bimodal probability distribution such that  
117 participants could hit the ball on their right forehand side in the range between 40 cm to 60 cm  
118 and 80 cm to 100 cm, respectively (see Figure 2, right). In each of the three sessions,  
119 participants played 480 returns divided into 10 blocks of 48 trials.



120  
121 **Fig. 2 | Experimental Virtual Reality Setup.** The ball in the serve followed a prespecified  
122 spline trajectory (left). The return trajectory was also prespecified and rotated according to the  
123 estimation error (right). The sign of the estimation error was positive if the sweet spot was not  
124 far enough and to the left of the ball at the time of the hit, which was proximal to the participant  
125 (in the example right, the estimation error is therefore negative). The participant's task was to  
126 return the ball toward the centre of the target on the opponent's court (left). If the ball was hit  
127 perfectly with the sweet spot (zero estimation error), the return was perfectly in the direction  
128 toward the centre of the target and the maximum score of 100 was displayed. Participants  
129 swung a real racket with an integrated Wii for haptic feedback vibration and placed markers to  
130 track the racket's position (center). A video of the experimental task is available on GitHub  
131 ([https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)).  
132

133 To examine whether participants' estimation error was biased by the bimodal prior as a  
134 function of the uncertainty condition, we compared the nonlinearity (i.e. the "jump") between  
135 the left and right sides of the distribution. We calculated multilevel regression analyses for all  
136 three uncertainty conditions (slow, moderate, and fast ball speeds). Based on the assumption  
137 that the acquired experience about the bimodal prior needs 24 hours to be sufficiently  
138 consolidated during one night of sleep (Körding & Wolpert, 2003), we considered all returns  
139 for each condition on the first day separately (see Figure 3, top) and all returns for each  
140 condition on the second and third days together (see Figure 3, bottom).

#### 141 ***Biomechanical effects on day 1***

142 There was a significant linear fixed effect of ball position on estimation error for all days and  
143 conditions (see Tables 1, 3, 5, 7, 9, and 11 in the Extended Data – except for the slow condition  
144 on day 1). At day 1, there was no significant bimodal prior fixed effect neither in the fast  
145 condition ( $N_{\text{subjects}} = 34$ ,  $N_{\text{measurements}} = 2913$ ,  $b$  (0 = left, 1 = right) =  $-0.49$  [ $-3.93$ ,  $2.86$ ],  $t(2887)$   
146 =  $-0.28$ , two-sided  $p = .781$ ), nor in the moderate condition ( $N_{\text{subjects}} = 34$ ,  $N_{\text{measurements}} = 3171$ ,  
147  $b$  (0 = left, 1 = right) =  $0.18$  [ $-3.65$ ,  $3.02$ ],  $t(3145) = 0.13$ , two-sided  $p = .899$ ). A significant  
148 bimodal prior fixed effect was observed in the slow condition ( $N_{\text{subjects}} = 34$ ,  $N_{\text{measurements}} = 6508$ ,  
149  $b$  (0 = left, 1 = right) =  $-2.37$  [ $-3.91$ ,  $-0.83$ ],  $t(4882) = -3.02$ , two-sided  $p = .003$ ). This effect  
150 is not expected. However, the effect should not be overestimated as the explained variance  
151 ( $R^2_{\text{marginal}} = .002$ , see Table 5) of this model is close to zero and much smaller than the models  
152 of the conditions moderate ( $R^2_{\text{marginal}} = .091$ , see Table 3) and fast ( $R^2_{\text{marginal}} = .124$ , see Table  
153 1); thus even weak multicollinearity (*variance inflation factor* = 1.30) can be relevant and lead  
154 to incorrect confidence intervals and p-values (Craney & Surles, 2002, p. 394). Overall, the  
155 results suggest that participants have not yet learned the bimodal prior to day 1. Further, data  
156 shows a positive linear trend between the estimation error and ball position, which can be  
157 explained by a biomechanical effect (i.e., a distance effect): When the ball is played close to  
158 the participants' body, they are likely to hit too far to the right, leading to negative errors,  
159 especially when balls are fast.

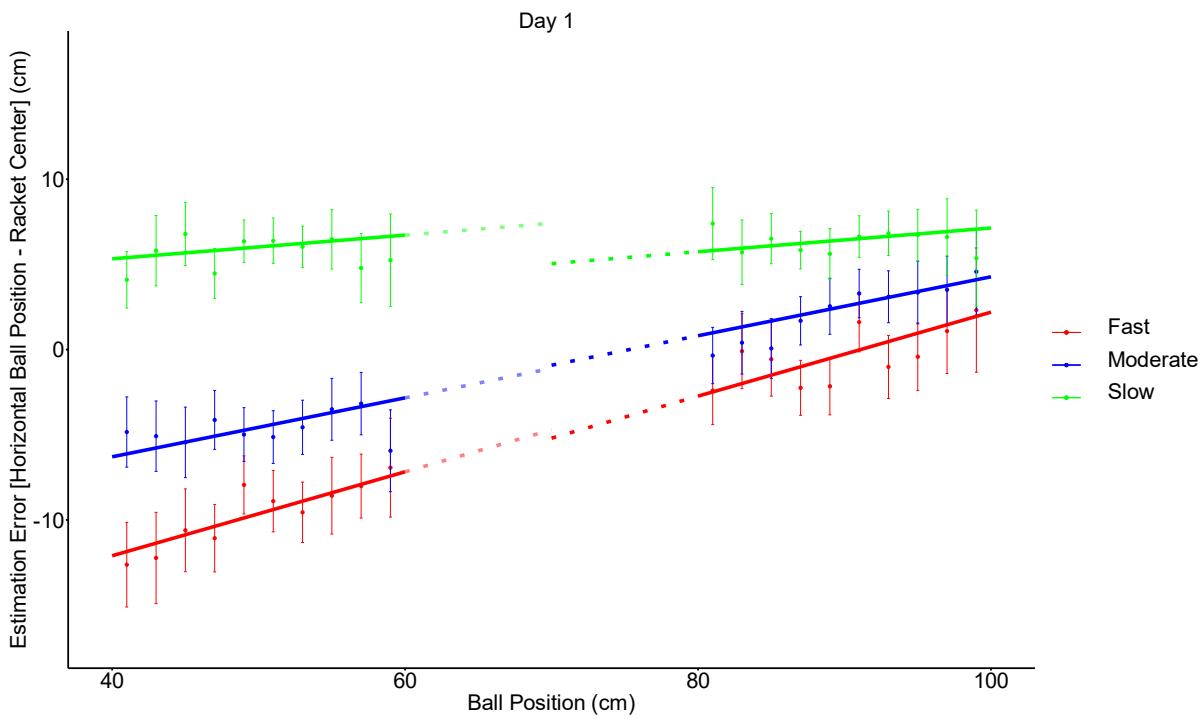
#### 160 ***Subjects learned and used the bimodal prior on days 2 and 3***

161 As predicted for days 2 and 3, we found a significant bimodal prior fixed effect in the fast  
162 condition ( $N_{\text{subjects}} = 34$ ,  $N_{\text{measurements}} = 6049$ ,  $b$  (0 = left, 1 = right) =  $-3.01$  [ $-5.09$ ,  $-0.93$ ],  
163  $t(6023) = -2.84$ , two-sided  $p = .005$ ), and in the moderate condition ( $N_{\text{subjects}} = 34$ ,  $N_{\text{measurements}}$   
164 =  $6791$ ,  $b$  (0 = left, 1 = right) =  $-2.50$  [ $-4.23$ ,  $-0.77$ ],  $t(6791) = -2.83$ , two-sided  $p = .005$ ).  
165 There was no such significant effect in the slow condition ( $N_{\text{subjects}} = 34$ ,  $N_{\text{measurements}} = 6520$ ,  $b$   
166 (0 = left, 1 = right) =  $-0.78$  [ $-2.27$ ,  $0.70$ ],  $t(6494) = -1.03$ , two-sided  $p = .302$ ). See full statistics

167 and model comparisons in Tables 1-12 in the Extended Data. This pattern of results aligns well  
168 with the core predictions derived from the Bayesian model, as the magnitude of the bimodal  
169 prior effect increases as a function of uncertainty, being more pronounced under conditions of  
170 fast serves compared to moderate and slow serves.

171

172



173

**Fig. 3 | Bimodal nonlinear prior effect on three different levels of visual uncertainty.** The graphs show the estimation errors in terms of the distance between the sweet spot and the ball hit positions on the racket in the conditions of slow, moderate, and fast ball speed. On the upper part, the data from day 1 is displayed, and on the lower part, the data from days 2 and 3 together. The data are divided into 10 bins on each side, and the arithmetic mean and 95% confidence interval are displayed for each bin. The multilevel regression model is computed with the

180 independent factors of ball position and bimodal segment factor (left 40–60 cm, right 80–100  
181 cm).

182 ***Subject prior knowledge of the bimodal distribution is implicit***

183 After the last experimental session, we asked the participants if they recognised a pattern in the  
184 opponent's serve distribution. On a schematic tennis court on paper, no participant was able to  
185 draw hit positions split into a left and right part, or anything similar to a bimodal distribution.  
186 In the following forced-choice question (see Appendix), we asked participants to choose  
187 between four potential distributions: uniform, unimodal, bimodal distribution or a scenario  
188 where the ball always landed in the same location. Only 6 out of 24 participants crossed the  
189 bimodal distribution; just as one would expect accidentally by chance with four answer choices.  
190 15 participants crossed the normal distribution with the highest probability in the centre where  
191 there was actually the lowest. This result suggests that participants integrated implicit prior  
192 knowledge of the bimodal distribution into their tennis return, without any explicit awareness  
193 of the pattern.

194

195 **Discussion**

196 In this study, we investigated whether humans can learn bimodal prior distributions and use  
197 them according to Bayesian principles in complex sensorimotor behaviour. Over three days,  
198 participants returned 1'440 tennis serves that followed a bimodal distribution. Our results show  
199 that, just through playing tennis, participants acquired a bimodal prior and used it in action.  
200 Specifically, after extensive experience on days 2 and 3, we observed a significant nonlinear  
201 relationship between the estimation error and the true ball position – a “bimodal prior effect”  
202 –, which increased with higher ball speeds (i.e., higher levels of uncertainty), as predicted by  
203 Bayesian theory (Körding & Wolpert, 2004). Remarkably, despite being exposed to the  
204 opponent's serving pattern over 1'440 trials and incorporating this information into their  
205 behaviour, participants were unable to report above chance level whether the opponent's serves  
206 followed a bimodal distribution when asked explicitly. This finding highlights that the  
207 sensorimotor system can utilise prior “knowledge” of environmental statistics to optimize  
208 behaviour without the need for explicit awareness of these patterns.

209 However, while our results align well with the core predictions derived from the Bayesian  
210 model (Ma et al., 2023), the data clearly shows that acquired prior information is not the only  
211 factor affecting the pattern of errors as a function of the true ball location. In addition to the  
212 bimodal prior effect, a positive linear relationship between the estimation error and the true  
213 ball location has been observed. This effect can be well explained by biomechanical constraints

and associated motor costs of potential movements (e.g., Griessbach et al., 2022). When the ball is close to the participant's body (e.g., a ball position of 40 cm), participants generally tend to hit too far to the right, leading to a negative error, particularly when balls are fast. Data from day 1 (without the bimodal prior effect) suggests that balls played at the right end of the scale are most naturally hit by swinging the racket with an almost stretched arm, i.e. a movement with low motor costs. When the ball gets closer to the body, participant had to flex their arm or make a small step to the left. The finding that movements are biased towards lower motor costs is well established in the literature (Cos et al., 2014; Gallivan et al., 2018; Morel et al., 2017; Shadmehr et al., 2016; Wolpert & Landy, 2012). Consequently, in contrast to experiments that test Bayesian integration in isolated tasks, examining behaviour in highly complex tasks – such as returning tennis serves – highlights that movements are not only biased by prior expectations but also by other, here: presumably biomechanical factors. Importantly, however, the nonlinear effects found in our data cannot be explained by those biomechanical factors and thus show that humans did actually learn a bimodal prior and combined it with sensory information in action. Together, participants' behaviour is well explained by a combined effect of the acquired bimodal prior and motor costs.

The results of the current study strengthen two decades of experimental lab-based work in perception, cognition and motor control (Körding & Wolpert, 2006; Tenenbaum et al., 2006; Yuille & Kersten, 2006) by demonstrating that Bayesian principles generalize to more complex cases including naturalistic movements and bimodal distributions. Specifically, regarding the learning of bimodal priors, the absence of any prior effect on day 1 is in line with previous studies suggesting that humans are, in principle, able to perform probabilistic inference with bimodal priors but require extensive experience to learn them (Acerbi et al., 2014; Körding & Wolpert, 2004). More generally, the study puts into practice current calls to test major theories in the field of complex, naturalistic behaviour (Cisek & Green, 2024; Maselli et al., 2023; Tsay et al., 2024). In this regard, our work demonstrates that Bayesian theory provides a principled explanation of how our sensorimotor system solves impressive challenges at the limits of human performance, such as returning an over 250 km/h tennis serve. This extension is particularly valuable for applied fields – from high-level sports to working environments or rehabilitation settings – suggesting that Bayesian theory provides a well-founded framework for addressing real-world challenges and, ultimately, advancing practice.

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336 **Methods**

337 ***Participants***

338 24 healthy right-handed participants (13 females and 11 males;  $M_{age} = 22.0$  years,  $SD = 2.2$ )  
339 with no distinctive tennis experience participated in the experiment. The study was approved  
340 by the ethics committee of the Faculty of Human Sciences at the University of Bern (Approval  
341 Number: 2017-12-00003) and was conducted in accordance with the Declaration of Helsinki.  
342 Written informed consent was obtained from all participants. In particular, the person shown  
343 in the video of the experimental task on GitHub  
344 ([https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)) provided  
345 written consent for publication.

346 ***Virtual Reality Setup***

347 Participants performed tennis returns in a custom life-sized virtual-reality (VR) CAVE  
348 environment, which has already been described in detail by Beck et al. (2024) (video on  
349 [https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)). The virtual  
350 tennis environment is displayed stereoscopically in real time and rendered in high resolution  
351 from the player's perspective on a  $6.00\text{ m} \times 3.75\text{ m}$  front wall, two  $11.00\text{ m} \times 3.75\text{ m}$  side  
352 walls, and a  $6.00\text{ m} \times 11.00\text{ m}$  floor. Participants only saw their real racket, while the virtual  
353 racket (of the same size) was not displayed. Furthermore, a Wii controller was built into the  
354 handle of the racket to provide haptic vibration feedback when the virtual ball was successfully  
355 hit (Figure 2, centre).

356 An adaptation of the setup used by Beck et al. (2024) was that the ball trajectories in the Unreal  
357 Engine followed a prespecified serve spline trajectory (see Figure 2, left). The spline of the  
358 serve was rotated around the vertical axes to reach the manipulated impact positions on the  
359 ground plane; apart from this rotation, however, the ball always followed the exact same spline.  
360 The ball speed was related to how fast the ball followed the same spline trajectory, which does  
361 not reflect real physics but has the advantage that the visual input only varied in regard to the  
362 available time to accumulate information.

363 There was a target on the opponent's side of the tennis court ( $2.05\text{ m}$  in front of the service line  
364 and  $2.05\text{ m}$  from the centre line, see Figure 1, left). For the tennis return, a prespecified spline  
365 trajectory was scaled according to the deviation of the hit location from the racket's sweet spot,  
366 so that for a zero deviation of the ball from the sweet spot at impact on the axes parallel to the  
367 tennis ground line, the ball would hit the centre of the target perfectly (see Figure 2, right). The  
368 deviation of the ball from the sweet spot at the impact on the axes parallel to the tennis ground  
369 line resulted in a deviation of the minimum distance of the ball trajectory to the centre of the

370 target by a factor of 20. In other words, a 1 cm deviation on the racquet was equivalent to a 20  
371 cm deviation in the minimum distance to the target on the ground plane projection.  
372 Consequently, the deviation of the ball from the sweet spot at the impact on the axes parallel  
373 to the tennis ground line determined how many points were awarded for the return. After each  
374 return, the points were displayed on a scale from 0 to 100. For a deviation of 15.5 cm and more  
375 (over the racket edge), participants received 0 points; for a perfect hit, 100 points, and linearly  
376 scaled in between. The impact angle and direction of the racket had no effect on the return  
377 trajectory, but participants had to hit the ball at a minimum racket speed of 4 m/s. Below this  
378 threshold, the ball did not reach the opponent's court over the net and no points were thus  
379 scored.

380 To facilitate the return of fast serves (with initial speeds depending on the condition of 108  
381 km/h, 180 km/h, and 252 km/h, respectively), the timing demands were reduced and made  
382 equally hard for each speed condition. To this end, the ball actually to be struck was an invisible  
383 stationary ball that was located parallel to the ground line on the forehand side of the  
384 participants on the prespecified trajectory and could be hit 200 ms before until 200 ms after the  
385 visibly displayed ball passed the position of the invisible stationary ball.

### 386 ***Experimental Task***

387 In a within-subjects design, the participants had three sessions in the laboratory within one  
388 week, with a minimum of 24 hours between each session. During each of the 2-hour sessions,  
389 after having been fitted with 3D glasses and a racket, the players' task was to repeatedly return  
390 serves from the right side of the court and try to hit the centre of a target on the opponent's side  
391 of the court (Figure 2, left), thereby trying to gain as many points as possible (0 points if they  
392 missed the ball, 100 points if they hit the ball perfectly at the sweet spot in the centre of the  
393 racket). There was a financial incentive for the participants: the three participants with the  
394 highest scores among the top ten in each condition over all three sessions received book  
395 vouchers (30, 50, and 80 Swiss francs).

396 Participants were instructed to stand always in the same starting position at the beginning of a  
397 trial but were then free to move. The starting position was 1.2 m behind the ground line and  
398 3.0 m away from the mid-line so that participants could easily reach the stationary invisible  
399 ball. Before each trial, a red dot was displayed at the position of the serving avatar, and a short  
400 acoustic signal indicated the imminent start of the trial. After a random delay of 1–2 s duration,  
401 the simulation began. As the avatar always performed exactly the same serving motion, no  
402 information could be obtained from the movement kinematics. Despite the constant serving  
403 motion, the ball trajectories were manipulated according to a bimodal probability distribution

404 such that participants could hit the ball on their right forehand side in the range between 40 cm  
405 to 60 cm and 80 cm to 100 cm in relation to the fixed starting position (see Figure 2, right).  
406 Visual uncertainty was manipulated with three different speed conditions, slow, moderate, and  
407 fast, which always followed each other in the same order so that the participants knew in  
408 advance in which speed condition the next ball would be played. In each of the three sessions,  
409 participants played 480 returns divided into 10 blocks. There were 16 trials of each speed  
410 condition in each block of 48 trials and thus a total of 160 trials of each speed condition in a  
411 session. These 160 bimodally distributed trials were quasi-randomly divided into 10 blocks  
412 such that, in each half of the distribution, the mean of the 8 trials was no more than 1 cm away  
413 from one of the distribution peaks and their standard deviation was in the same range and  
414 maximum 2 cm higher as the overall standard deviation.

415 On the first day, the participants had additionally two warm-up blocks with only slow serves  
416 in which all serves were first played to the centre of the bimodal distribution at a distance of  
417 70 cm and then bimodally distributed as in a regular block. Further details of the experimental  
418 protocols are available on GitHub  
[https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)). To check  
419 whether participants were aware of the virtual reality manipulations, they were asked at the end  
420 of the third session whether they recognized any technical assistance and if they recognized the  
421 probability distribution (see Appendix).

### 423 ***Measures and Analyses***

424 We investigated whether the deviation of the sweet spot to the ball at racket hit (see Figure 2,  
425 right) was systematically biased by the learned prior (bimodal probability distribution) as a  
426 function of the reliability of the available visual sensory information (slow, moderate, fast ball  
427 speed). In order to make predictions, we ran a Bayesian simulation according to Ma et al.  
428 (2023), which is documented step by step on GitHub  
[https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)). As can be  
429 seen in Figure 1, the three levels of uncertainty (speed conditions) lead to different slopes and,  
430 therefore, different bimodal prior effects in the centre of the figure. For example, in the  
431 simulated fast condition the negative estimation error increases linearly to a positive value  
432 between the ball position at 40 cm and 60 cm and then “jumps” again to a negative value on  
433 the position 80 cm, from where the estimation error linearly increases again to a positive value  
434 at 100 cm (no balls were played in the range between 60 cm and 80 cm and therefore no data  
435 are available there).

437 However, besides the Bayesian simulation, it was also expected for the present return task that  
438 not every distance is reachable with equal effort. Balls close to the body or far away could be  
439 harder to hit with the racket's sweet spot, as a step to the right or left would be required.  
440 Consequently, it is reasonable to expect a distance effect in the dependent variable of estimation  
441 error from the 40–60 cm to the 80–100 cm ranges that are more pronounced for higher ball  
442 speeds and independent of any Bayesian priors. Nevertheless, it needs to be noted that this  
443 purely biomechanically effect should bridge the gap between the two hitting ranges in a linear  
444 manner that perfectly matches the slopes that can be calculated for the two ranges separately.  
445 In contrast, an eventually found nonlinear effect in the centre between the hitting ranges should  
446 solely be ascribed to the weighted integration of the bimodal prior under different levels of  
447 visual uncertainty (referred throughout the paper as “bimodal prior effect”). Therefore, we  
448 calculated regression models with two independent variables: ball position and a bimodal  
449 segment factor (left or right), where the bimodal segment factor is the indicator of the Bayesian  
450 effect. The dependent variable was the estimation error on the racket (see Figure 2, right).  
451 The following procedures were used to check assumptions and handle missing values and  
452 outliers. First, we had multiple data points for each participant, and the residuals were not  
453 independent. Therefore, we built and compared regression models in several steps in order to  
454 take the hierarchical structure of the data into account (Field et al., 2012). Second, we checked  
455 the multicollinearity of the two independent factors (ball position and bimodal segment factor)  
456 with the variance inflation factor (VIF). Third, we checked the homoscedasticity and normality  
457 of the residuals graphically. Fourth, under the assumption that missing values occur randomly,  
458 multilevel regression analyses can handle missing values (Field et al., 2012). Fifth, we detected  
459 outliers using Cook’s distance and removed them when values affected the intercept more than  
460 three times as much as the mean.  
461 In more detail to the first point, the following steps of the construction of the models have been  
462 taken: We started with an intercept-only model, then added the ball position factor, the random  
463 intercepts, the random slopes, and in the last step, the bimodal segment factor. Descriptively,  
464 we compared models using the Akaike Information Criterion (AIC), Bayesian Information  
465 Criterion (BIC), and log-likelihood (Tables 2,4,6,8,10,12 in the Extended Data). For inferential  
466 model comparisons, we used the log-likelihood ratio  $\chi^2$  test. This allowed us to conclude  
467 whether the last added bimodal segment factor was a relevant and significant model extension,  
468 according to the parsimony principle (Bates et al., 2015). Furthermore, we used the maximum  
469 likelihood for model estimations and tested regression coefficients with the Wald test for

470 significance. For all inferential tests, we chose an alpha level of 5%. For the required  
471 calculations, we applied the R-package ‘nlme’ (Pinheiro, 2009).

472 We aggregated all returns for each condition on the first day separately and all returns for each  
473 condition on the second and third days together, because the bimodal prior can be expected to  
474 be sufficiently consolidated over the first night’s sleep (Körding & Wolpert, 2003). Thus, on  
475 the first day, we predicted no effect of the bimodal segment factor, while on the second and  
476 third day, when the bimodal prior is consolidated, we expected no or a small effect of the  
477 bimodal segment factor in the slow condition and an increased effect in the moderate and fast  
478 conditions, as shown in Figure 1.

479

#### 480 **Data availability statements**

481 All raw data and data used for statistical analysis and figure generation, as well as a video of  
482 the experimental task, are available on GitHub  
483 ([https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)).

484

#### 485 **Code availability statements**

486 The Python script for preparing the raw data, the jupyter notebook for Bayesian simulations  
487 and all R-scripts used for statistical analysis and figure generation are available on GitHub  
488 ([https://github.com/DamianBeckUniBern/bimodal\\_prior\\_integration\\_vr\\_tennis](https://github.com/DamianBeckUniBern/bimodal_prior_integration_vr_tennis)).

489

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494

#### 495 **Author contributions**

496 As co-first authors, S.Z. and D.B. contributed equally to the work. S.Z. came up with the  
497 experimental idea. S.Z., D.B., E.-J.H., and K.K. collaborated on further conceptualization as  
498 well as on writing. D.B. and S.Z. developed the experimental setup. The experiment was led  
499 by D.B. and S.Z. D.B. analysed the data.

500

#### 501 **Competing Interest declaration**

502 There is no conflict of interest.

503

504    **Additional information**

505    Correspondence and requests for materials should be addressed to Stephan Zahno.

506 **Extended data**

Table 1. Multilevel regression model of error estimation on day 1 in the fast condition.

Fixed effects	B	SE B	95% CI	t(2887)	p two-sided
Intercept	-21.96	4.07	[-29.93, -13.99]	-5.40	< .001
Ball position	0.25	0.06	[0.12, 0.37]	3.82	< .001
Segment (0 = left, 1 = right)	-0.49	1.75	[-3.93, 2.86]	-0.28	.781

## Random effects

Intercept variance ( $\tau_{00}$ )	281.58	–	–	–	–
Slope variance ( $\tau_{11}$ )	0.06	–	–	–	–
Intercept-slope covariance ( $\rho_{01}$ )	-0.98	–	–	–	–
Level-1 residual ( $\sigma^2$ )	125.76	–	–	–	–
ICC	0.22	–	–	–	–

507 Note. B = unstandardized regression coefficients, SE = standard error, CI = confidence intervals, t(degrees of freedom).

508 ICC = Interclass correlation coefficient. Model statistics:  $N_{\text{participants}} = 24$ ,  $R^2_{\text{marginal}} = .124$ . Model comparison in Table 2.

509

510 Table 2. Model comparison for multilevel regression model of error estimation on day 1 in the fast condition.

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	2	23380.79	23392.74	-1688.40			
2 Base model	4	22974.49	22998.39	-11483.24	1 vs 2	410.307	< .001
3 Base model + RI	5	22842.44	22872.33	-11416.22	2 vs 3	134.041	< .001
4 Base model + RS	7	22462.67	22504.51	-11224.33	3 vs 4	383.774	< .001
5 Base model + RS + Bimodal segment factor	8	22464.59	22512.41	-11224.30	3 vs 4	0.077	.782

511 Note. df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-  
512 likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictor ball position.  
513

Table 3. Multilevel regression model of error estimation on day 1 in the moderate condition.

Fixed effects	B	SE B	95% CI	t(3145)	p two-sided
Intercept	-13.22	3.75	[-20.57, -5.86]	-3.52	< .001
Ball position	0.17	0.06	[0.06, 0.28]	3.11	.002
Segment (0 = left, 1 = right)	0.18	1.45	[-3.65, 3.02]	0.13	.899
Random effects					
Intercept variance ( $\tau_{00}$ )	261.30	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.04	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	-0.97	—	—	—	—
Level-1 residual ( $\sigma^2$ )	94.47	—	—	—	—
ICC	0.28	—	—	—	—

Note. B = unstandardized regression coefficients, SE = standard error, CI = confidence intervals, t(degrees of freedom).

ICC = Interclass correlation coefficient. Model statistics:  $N_{\text{participants}} = 24$ ,  $R^2_{\text{marginal}} = .091$ . Model comparison in Table 4.

Table 4. Model comparison for multilevel regression model of error estimation on day 1 in the moderate condition.

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	2	24690.94	24703.07	-12343.47			
2 Base model	4	24190.49	24214.74	-12091.25	1 vs 2	504.450	< .001
3 Base model + RI	5	23974.31	24004.62	-11982.16	2 vs 3	218.182	< .001
4 Base model + RS	7	23466.30	23508.73	-11726.15	3 vs 4	512.014	< .001
5 Base model + RS + Bimodal segment factor	8	23468.28	23516.78	-11726.14	3 vs 4	0.016	.900

Note. df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictor ball position.

Table 5. Multilevel regression model of error estimation on day 1 in the slow condition.

Fixed effects	B	SE B	95% CI	t(4882)	p two-sided
Intercept	2.54	3.05	[−3.44, 8.53]	0.83	.405
Ball position	0.07	0.04	[−0.01, 0.15]	1.76	.079
Segment (0 = left, 1 = right)	−2.37	0.78	[−3.91, −0.83]	−3.02	.003
Random effects					
Intercept variance ( $\tau_{00}$ )	192.25	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.03	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	−0.95	—	—	—	—
Level-1 residual ( $\sigma^2$ )	93.99	—	—	—	—
ICC	0.25	—	—	—	—

Note. B = unstandardized regression coefficients, SE = standard error, CI = confidence intervals, t(degrees of freedom).

ICC = Interclass correlation coefficient. Model statistics:  $N_{\text{participants}} = 24$ ,  $R^2_{\text{marginal}} = .002$ . Model comparison in Table 6.

Table 6. Model comparison for multilevel regression model of error estimation on day 1 in the slow condition.

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	2	37575.36	37588.36	−18785.68			
2 Base model	4	36664.46	36690.46	−18328.23	1 vs 2	914.898	< .001
3 Base model + RI	5	36311.71	36344.20	−18150.85	2 vs 3	354.759	< .001
4 Base model + RS	7	35843.74	35889.23	−17914.87	3 vs 4	471.966	< .001
5 Base model + RS + Bimodal segment factor	8	35836.62	35888.61	−17910.31	3 vs 4	9.117	.003

Note. df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictor ball position.

Table 7. Multilevel regression model of error estimation on day 2+3 in the fast condition.

Fixed effects	B	SE B	95% CI	t(6023)	p two-sided
Intercept	-28.27	3.12	[-34.39, -22.16]	-9.06	< .001
Ball position	0.39	0.05	[0.29, 0.48]	8.23	< .001
Segment (0 = left, 1 = right)	-3.01	1.06	[-5.09, -0.93]	-2.84	.005
Random effects					
Intercept variance ( $\tau_{00}$ )	192.43	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.04	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	-0.97	—	—	—	—
Level-1 residual ( $\sigma^2$ )	98.83	—	—	—	—
ICC	0.21	—	—	—	—

527 Note. B = unstandardized regression coefficients, SE = standard error, CI = confidence intervals, t(degrees of freedom).

528 ICC = Interclass correlation coefficient. Model statistics:  $N_{\text{participants}} = 24$ ,  $R^2_{\text{marginal}} = .250$ . Model comparison in Table 8.

529

530 Table 8. Model comparison for multilevel regression model of error estimation on day 2+3 in the fast condition.

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	2	47847.56	47860.98	-23921.78			
2 Base model	4	45977.92	46004.75	-22984.96	1 vs 2	1873.639	< .001
3 Base model + RI	5	45689.80	45723.34	-22839.90	2 vs 3	290.125	< .001
4 Base model + RS	7	44944.45	44991.40	-22465.22	3 vs 4	749.350	< .001
5 Base model + RS + Bimodal segment factor	8	44938.37	44992.04	-22461.19	3 vs 4	8.073	.005

531 Note. df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-  
532 likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictor ball position.

Table 9. Multilevel regression model of error estimation on day 2+3 in the moderate condition.

Fixed effects	B	SE B	95% CI	t(6791)	p two-sided
Intercept	-18.38	2.98	[-24.22, -12.54]	-6.17	< .001
Ball position	0.29	0.04	[0.21, 0.37]	7.24	< .001
Segment (0 = left, 1 = right)	-2.50	0.88	[-4.23, -0.77]	-2.83	.005
Random effects					
Intercept variance ( $\tau_{00}$ )	184.61	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.03	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	-0.97	—	—	—	—
Level-1 residual ( $\sigma^2$ )	76.73	—	—	—	—
ICC	0.24	—	—	—	—

Note. B = unstandardized regression coefficients, SE = standard error, CI = confidence intervals, t(degrees of freedom).

ICC = Interclass correlation coefficient. Model statistics:  $N_{\text{participants}} = 24$ ,  $R^2_{\text{marginal}} = .181$ . Model comparison in Table 10.

Table 10. Model comparison for multilevel regression model of error estimation on day 2+3 in the moderate condition.

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	2	51909.13	51922.77	-25952.56			
2 Base model	4	50084.12	50111.42	-25038.06	1 vs 2	1829.003	< .001
3 Base model + RI	5	49596.43	49630.55	-24793.22	2 vs 3	489.688	< .001
4 Base model + RS	7	48647.55	48695.31	-24316.78	3 vs 4	952.884	< .001
5 Base model + RS +	8	48641.54	48696.12	-24312.77	3 vs 4	8.015	.005

Bimodal segment factor

Note. df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictor ball position.

Table 11. Multilevel regression model of error estimation on day 2+3 in the slow condition.

Fixed effects	B	SE B	95% CI	t(6494)	p two-sided
Intercept	-1.03	2.40	[-5.73, 3.67]	-0.43	.667
Ball position	0.10	0.04	[0.03, 0.17]	2.78	.005
Segment (0 = left, 1 = right)	-0.78	0.76	[-2.27, 0.70]	-1.03	.302

---

Random effects

Intercept variance ( $\tau_{00}$ )	116.55	—	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.02	—	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	-0.96	—	—	—	—	—
Level-1 residual ( $\sigma^2$ )	55.64	—	—	—	—	—
ICC	0.24	—	—	—	—	—

540 Note.  $B$  = unstandardized regression coefficients,  $SE$  = standard error,  $CI$  = confidence intervals,  $t$ (degrees of freedom).

541 ICC = Interclass correlation coefficient. Model statistics:  $N_{\text{participants}} = 24$ ,  $R^2_{\text{marginal}} = .034$ . Model comparison in Table 12.

542

543 Table 12. Model comparison for multilevel regression model of error estimation on day 2+3 in the slow condition.

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	2	46592.44	46606.01	-23294.22			
2 Base model	4	45832.60	45859.73	-22912.30	1 vs 2	763.842	< .001
3 Base model + RI	5	45429.21	45463.13	-22709.61	2 vs 3	405.387	< .001
4 Base model + RS	7	44516.16	44563.64	-22251.08	3 vs 4	917.049	< .001
5 Base model + RS +	8	44517.10	44571.36	-22250.55	3 vs 4	1.066	.302

Bimodal segment factor

544 Note. df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-  
545 likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictor ball position.

546

## 547 Appendix

548 At the end of the experiment, participants were asked some questions about the experiment.

549 The questionnaire contained the following questions (translated from German):

550 1. did you notice a pattern to where the balls were played?

551 2. Draw where you hit the balls with a cloud of dots.

552 3. Circle the most appropriate answer:

553 a. The serves were evenly distributed.

554 b. The serves were normally distributed.

555 c. The serves were bimodally distributed.

556 d. The serves always came to the same place.

557 4. Indicate as a percentage how sure you are of your answer:

558 5. Playback has been made technically easier. Have you noticed how? Please write down  
559 everything you have noticed:



561 1. Ist dir ein Muster aufgefallen, wo die Bälle hin gespielt wurden?

562

563

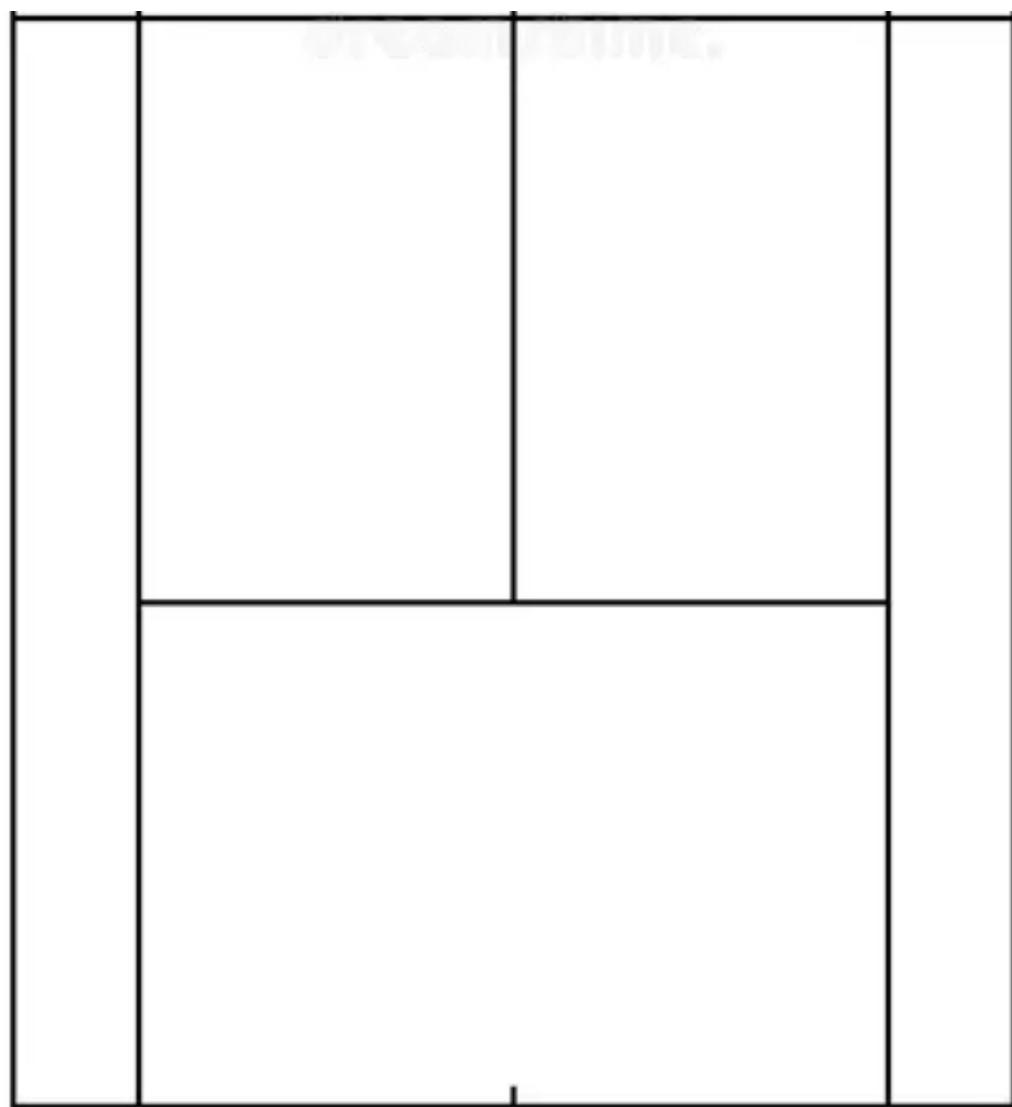
564

565

566

567

568 2. Zeichne mit einer Punktewolke ein, wo du die Bälle getroffen hast.

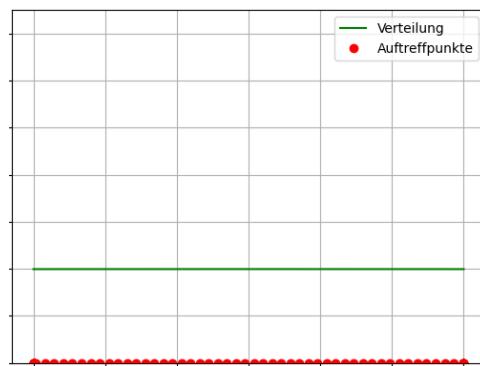


569

570

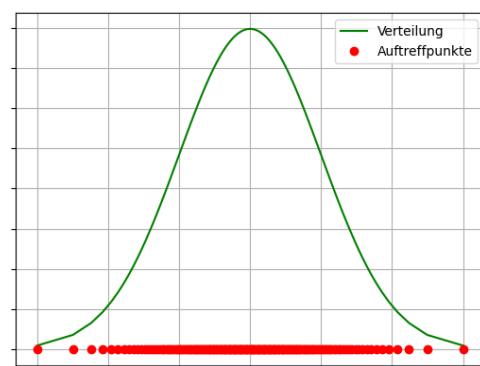
571        3. Umkreise die am ehesten zutreffende Antwort:

572        a) Die Aufschläge waren gleichverteilt.



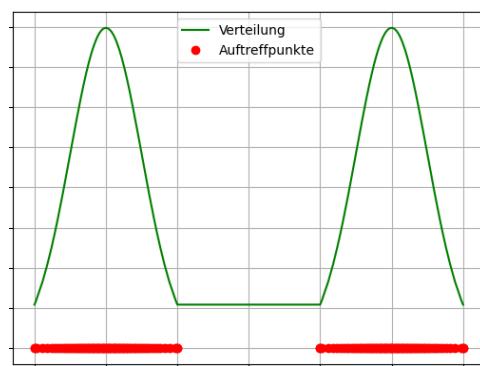
573

574        b) Die Aufschläge waren Normalverteilt.



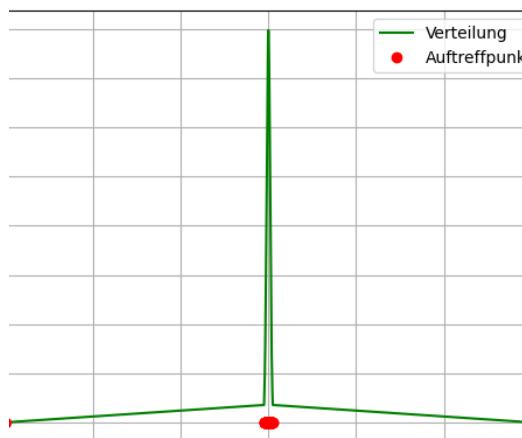
575

576        c) Die Aufschläge waren bimodal Normalverteilt.



577

578        d) Die Aufschläge kamen immer an den gleichen Ort.



579

580        4. Gib in Prozenten an, wie sicher du dir deiner Antwort bist:

581 Das Zurückspielen wurde technisch erleichtert. Ist dir aufgefallen wie? Bitte schreibe alles auf,  
582 was dir dazu aufgefallen ist:  
583  
584

**Tennis players exploit prior information to improve performance:  
Evidence for continuous anticipatory decision-making under  
uncertainty**

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1   **Abstract**

2   Leading theories of sensorimotor control propose that humans cope with uncertainty by  
3   integrating prior and sensory information in a Bayesian manner and continuously make  
4   predictions to evaluate action options in online decision-making. However, most empirical  
5   evidence is based on simple lab tasks, and it remains unclear if humans actually use prior  
6   information in complex, naturalistic behavior. Here, we study a task that pushes the human  
7   sensorimotor system to its limits: returning fast tennis serves. This task is particularly  
8   informative to gain insights into the dynamics of unfolding decisions in action due to a  
9   peculiarity of the return movement: the split-step – a preparatory movement with a small jump  
10   to increase initial speed into the desired direction. In the experiment, experienced tennis players  
11   returned serves in an immersive virtual reality setup with unconstrained movements and task  
12   demands matching real tennis. We manipulated the distributions of the opponent's preferred  
13   serve locations (80% to the right vs. 20% to the left of the service box and vice versa in a  
14   second session). Results show that, over the experiment, participants increasingly relied on an  
15   acquired prior of expected serve distribution and exploited it to improve performance. Over the  
16   split step, participants continuously adjusted their weight shift with incoming sensory  
17   information, while a bias toward the expected direction was observed already before the serve.  
18   Using tennis as an exemplary case, our finding provides evidence that humans use prior and  
19   sensory information to probabilistically optimize online decision-making in complex  
20   sensorimotor behavior.

21  
22   **Keywords**

23   Bayesian inference, decision-making, anticipatory behavior, spatiotemporal control, virtual  
24   reality, tennis

25

## 1. Introduction

26 Returning a fast tennis serve is a spatiotemporal task that pushes the human sensorimotor  
27 system to its limits. High-speed serves are particularly successful (Gillet, 2009) as they force  
28 the returning player to act under extremely high sensory uncertainty arising from noise and  
29 delays in incoming sensory signals (Faisal et al., 2008; van Beers et al., 2002). Additionally,  
30 the high time constraints force the returning player to move fast, leading to further uncertainty  
31 in motor outcomes due to signal-dependent noise (Franklin & Wolpert, 2011; Harris &  
32 Wolpert, 1998). Tennis players are, therefore, challenged to handle these sensorimotor  
33 uncertainties to be successful.

34 How humans successfully cope with uncertainty is a fundamental question in sensorimotor  
35 behavior research, central to leading theories in the field, such as the theory of internal models  
36 (Wolpert et al., 1995), optimal feedback control (Todorov & Jordan, 2002), active inference  
37 (Friston, 2010), and affordance competition (Cisek, 2007). While differences between these  
38 theories exist (Friston, 2011), they converge on the core concept that humans continuously  
39 predict future states of the sensorimotor system in order to deal with uncertainties arising from  
40 noisy and delayed signal processing. These internal predictions not only refer to expected  
41 changes in the external environment but include sensory consequences of one's own actions  
42 (Wolpert & Flanagan, 2001). Based on such online predictions, multiple options for actions are  
43 continuously evaluated (Gallivan et al., 2018; Selen et al., 2012; Thura & Cisek, 2014). In  
44 contrast to traditional sequential-stages models (e.g., Sternberg, 1969), where decision-making  
45 and motor control are thought to operate serially, contemporary theories such as the affordance  
46 competition hypothesis suggest that multiple potential actions are specified in parallel and  
47 continuously compete against each other, biased by the desirability of their predicted outcomes  
48 (Pezzulo & Cisek, 2016). In this perspective, both decision-making and sensorimotor  
49 coordination are an integral part of online behavioral control (Wolpert & Landy, 2012).  
50 Accordingly, predicting the next state of the system is fundamental to behavioral control and  
51 not a specific feature of actions that require "anticipation" due to high temporal demands – as  
52 is the case of the tennis return. The difference between tasks with low and high time pressure  
53 then is that in the first case, sufficient time is available to wait for the confirmation of one's  
54 prediction by incoming reafferent signals, whereas in the second case of "anticipation", one  
55 must rely on the currently usable predictions to initiate one's motor response. In both cases,  
56 however, behavioral control constitutes an ongoing process of predictive and thus anticipatory  
57 online decision-making (Gallivan et al., 2018; Gordon et al., 2021).

58 As a further commonality, the theories cited above suggest that both prior expectations and  
59 sensory information from multiple sources are used to form predictions and make inferences  
60 about current to be expected states of the world in a probabilistic manner, referring to Bayesian  
61 inference as an overarching framework (Ernst & Banks, 2002; Kording & Wolpert, 2004).  
62 There is good empirical evidence from fundamental perception (Kersten et al., 2004) and motor  
63 control research (Kording & Wolpert, 2006) that humans integrate information from different  
64 sources in a Bayesian, reliability-based manner. In sport science research, a recent review by  
65 Beck et al. (2023) reports an increasing number of studies showing that prior knowledge  
66 improves performance or influences perception and action in more complex, sport-related  
67 tasks. Focusing on our case of tennis, there is good empirical evidence that anticipatory  
68 judgments are affected by the integration of auditory and visual information (Cañal-Bruland et  
69 al., 2018; Sinnott & Kingstone, 2010; Takeuchi, 1993) and that players generally benefit from  
70 prior knowledge on contextual information or situational probabilities (Farrow & Reid, 2012;  
71 Loffing & Hagemann, 2014; Loffing et al., 2016; Murphy et al., 2016; Murphy et al., 2018).  
72 In a recent study, Beck et. al. (2024) show that, when returning tennis serves, participants  
73 generate predictive saccades based on both prior knowledge of the opponent's preferred serve

74 locations (acquired through experience) and incoming sensory information in a Bayesian  
75 manner. Converging evidence for Bayesian integration in anticipatory gaze behavior is  
76 provided in similar racket sports tasks (Arthur & Harris, 2021; Harris et al., 2022).

77 However, while these studies provide clear evidence that expert tennis players are able to  
78 extract situational probabilities about the opponent's action outcomes, empirical support for  
79 the idea that prior knowledge is used in online decision-making is still largely lacking. On the  
80 contrary, Avilés et al. (2019, p. 17) came to the following conclusion in their systematic review  
81 on the anticipatory behavior of expert tennis players:

82 After 40 years of research, evidence has not yet been found that expert tennis players  
83 move to either side before the ball is hit in representative task conditions. Hence, players  
84 do not demonstrate observable anticipatory behavior towards the ball direction on the  
85 first serve in tennis, but guide their actions upon the information unfolding around the  
86 server's action and first moments of the ball flight.

87 Thus, studies capturing real-world task demands and dynamics of the unfolding decision-  
88 making process appear to be highly desirable, not only for our case of tennis but to further our  
89 understanding of complex sensorimotor behavior in general (Maselli et al., 2023). Above, there  
90 have been increasing calls in psychology and neuroscience in recent years to advance human  
91 behavior research from simple, reductionist tasks to complex, naturalistic tasks, aiming to  
92 capture human behavior in situational demands the sensorimotor system has evolved to  
93 function in (Cisek & Green, 2024; Maselli et al., 2023; Tsay et al., 2024). For this purpose, the  
94 tennis return situation can be considered a particularly informative task, not only because of  
95 the high time pressure that facilitates the experimental detection of predictive "anticipatory"  
96 behavior but also because of a peculiarity of the return movement that may reflect the time  
97 course of online decision-making: the split step.

98 In elite tennis, the split step is regularly performed as a preparatory movement for the return as  
99 a small jump and landing with the feet wider than shoulder-width apart, exploiting  
100 neuromuscular mechanisms and biomechanical elastic energy to increase the initial speed into  
101 the desired direction (e.g., Nieminen et al., 2013; Uzu et al., 2009). In perfect agreement with  
102 this explanation, Navia et al. (2022) report in their analyses of real tennis matches that in 60 %  
103 of cases, players landed from the split step with the contralateral foot in relation to the serve  
104 direction, which in turn correlated with a faster onset of the trunk movement towards the ball.  
105 However, due to the design of the study in the field, we can not disentangle whether this  
106 anticipatory behavior is based solely on the kinematic information obtained online of the  
107 serving player and the approaching ball or whether prior knowledge also plays a decisive role.  
108 Navia et al. (2022, p. 7), therefore, call for further investigations into "whether awareness of  
109 information pertaining to an opponent's serving pattern impacts upon the spatiotemporal  
110 control of the return".

111 Consequently, the present study has two goals. First, we aim to respond to the call by Navia et  
112 al. (2022) and investigate whether participants actually exploit accumulated prior knowledge  
113 of the opponent's preferred serve direction – a T-serve vs. a wide-serve as the most common  
114 first serves in professional tennis (Tea & Swartz, 2022) – to improve performance under  
115 representative conditions. Specifically, we will take a closer look at the temporal evolution of  
116 the weight shift over the split step, making a potential early use of prior knowledge observable,  
117 and examine whether this explains performance. Second, using tennis returns as an exemplary  
118 case, we aim to contribute to the fundamental understanding of how humans use prior and  
119 sensory information in online decision-making in complex, full-body naturalistic behavior  
120 (Gordon et al., 2021; Maselli et al., 2023). To do so, we extend the immersive virtual reality  
121 setup from Beck et al. (2024) allowing the study of movements with spatial and temporal

123 constraints that match real tennis for high ecological validity while simultaneously ensuring  
124 full experimental control.

125 Based on the theoretical standpoint that prior knowledge is incorporated into anticipatory  
126 online decision-making and motor control in a Bayesian manner, we hypothesize that (1) split  
127 steps are regularly performed by experienced participants, (2) over the split step, participants  
128 continuously adjust their weight shift with incoming sensory information, while a bias toward  
129 the expected direction can be detected in the early phases, (3–4) prior knowledge increasingly  
130 affects performance in congruent vs. incongruent trials in terms of initiating a movement in the  
131 correct direction and successfully hitting the ball, and (5) the resulting performance can be  
132 predicted by the extent to which prior knowledge is integrated already in early phases of the  
133 split step. Finally, we would like to consider the investigated tennis-return task as an exemplary  
134 case for the integration of prior knowledge into complex behavioral control in general and will  
135 thus draw conclusions that clearly go beyond our case of tennis.

136 **2. Method**

137 **2.1 Participants**

138 Fourteen right-handed male tennis players ( $M_{\text{age}} = 23.7$  years,  $SD_{\text{age}} = 4.7$  years) participated  
139 in the experiment. All players were licensed and actively competing with a minimum rating of  
140 R7 ( $M = 5.5$ ,  $SD = 1.3$ ) on the Swiss Tennis regional scale. On average, they trained 3.3 hours  
141 per week ( $SD = 1.4$  hours) and had 9.5 years ( $SD = 5.5$  years) of competitive experience. The  
142 experiment was approved by the Ethics Committee of the Faculty of Human Science at the  
143 University of Bern (approval number: 2017-12-00003) and conducted in accordance with the  
144 Declaration of Helsinki. All players gave written informed consent to participate. In particular,  
145 the player shown in Figure 1 and Figure 2, as well as in the video of the experimental task  
146 (<https://tube.switch.ch/videos/2otCdMkJpF>), provided written consent for publication.

147 **2.2 Virtual Reality Tennis Setup**

148 The tennis players performed returns in a custom-built life-size virtual reality CAVE  
149 environment, which has already been described in detail by (Beck et al., 2024) (Figure 1 and  
150 video <https://tube.switch.ch/videos/2otCdMkJpF>). The virtual tennis environment is displayed  
151 in real time and rendered in high resolution from the player's perspective on a  $6.00 \text{ m} \times 3.75$   
152 m front wall, two  $11.00 \text{ m} \times 3.75 \text{ m}$  side walls and a  $6.00 \text{ m} \times 11.00 \text{ m}$  floor. In a further  
153 improvement of the setup used by Beck et al., 2024, the players wore 3D glasses, which  
154 allowed to display the virtual tennis environment stereoscopically. The data was processed in  
155 real time to ensure accurate rendering from the participant's perspective. To track the tennis  
156 strokes, the participants held a custom-made real racket with a marker cluster and a Wii  
157 controller built into the handle (Figure 1, middle). A brief vibration of the Wii controller  
158 provided haptic feedback of the racket's contact with the virtual ball. The players only saw  
159 their real racket whilst the virtual racket (of the same size) was not displayed.



160

161        >>> Please insert Figure 1 about here <<<

162 *Figure 1. Participants were equipped with 3D glasses and six rigid marker bodies (left) as well as with a custom-made tennis*  
 163 *racket with an integrated Wii controller and further markers (middle). Their task was to return virtual serves to either the*  
 164 *forehand or backhand, following one of two possible ball trajectories, with the aim to hit the center of the target on the*  
 165 *opponent's side of the court (right).*

166

167 The markers attached to the racket were tracked with an Optitrack 3D motion capture system  
 168 at a rate of 200 Hz. Beyond, six marker clusters were placed on the head, back, left and right  
 169 hand and left and right foot to calculate a full body skeleton in Motive software (Figure 1, left).  
 170 The racket position data from the Optitrack system was streamed in real time to the virtual  
 171 tennis scene using Unreal Engine 4.27 to dynamically calculate interactive elements. Within  
 172 the Motive software, the racket and head movements were smoothed and predicted forward to  
 173 overcome a small delay optimized for the moment of ball contact with the racket. All the  
 174 systems were coordinated simultaneously using Streamix, an in-house software development  
 175 (<https://tpf.philhum.unibe.ch/portfolio/streamix>) based on the theoretical work of Maurer  
 176 (2018).

177 After a consistently identical serve motion of the displayed avatar, the ball followed one of two  
 178 possible trajectories (Figure 1, right). However, the return trajectory was calculated according  
 179 to the impact of the racket swing on the basis of simulated physics in the Unreal engine. In  
 180 more detail, gravity, friction (air resistance), and collision were turned on, but radial  
 181 momentum was turned off to avoid spin effects. We also used continuous collision detection  
 182 to prevent the ball from tunneling through the racket.

183 **3.3 Experimental Task**

184 In a within-subjects design, the participants had two sessions in the laboratory at the same time  
 185 of day, with a break of one-week in between. During each of the 1-hour sessions, after having  
 186 been fitted with 3D glasses and markers, the players' task was to repeatedly return serves from

187 the right side of the court and try to hit the center of a target on the opponent's side of the court.  
188 Players were free to position themselves to cover the entire field. Before each trial, a red dot  
189 was displayed at the position of the serving avatar, and a short acoustic signal indicated the  
190 imminent start of the trial. After a random delay of 1–2 s duration, the simulation began. As  
191 the avatar always performed exactly the same serving motion, no information could be obtained  
192 from the movement kinematics.

193 Despite the constant serving motion, two distinct ball trajectories were possible, namely, either  
194 to the left side for backhand returns or to the right side for forehand returns. All the displayed  
195 serves had exactly the same characteristics in terms of flight distance and speed. In more detail,  
196 serves were hit at 144 km/h, the bounce came after 0.446 s, and the ball reached the return area  
197 after exactly 1 s. The bounce location in the virtual space of the tennis court was always either  
198 38 cm behind the service line and 61 cm right to the center line or 80 cm behind the service  
199 line and 89 cm left to the sideline, respectively. Participants were not informed about these  
200 regularities.

201 Both sessions began with four blocks of 20 warm-up trials in which the ball was constantly  
202 played to the same – i.e., either the left or the right – side, followed by a fifth warm-up block  
203 in which 10 serves to the left and 10 serves to the right side were presented in random order.  
204 Before the fifth block, the players were told that from now on, the ball could go to the right or  
205 to the left side, however, without providing them with explicit information about the respective  
206 probabilities. Additionally, they were reminded to perform a split step as usual.

207 After the warm-up trials, players were faced with two blocks of 20 trials each, again with a  
208 50% chance for each side (neutral condition). Without any further instructions, the probabilities  
209 then changed to 80% for one side and 20% for the other side for the last four blocks of again  
210 20 trials each (biased condition). In compliance with this specification, individual random  
211 sequences were created for each participant (for details, see protocols on GitHub  
212 [https://github.com/DamianBeckUniBern/anticipatoryBehaviour\\_in\\_vr\\_tennis\\_a\\_bayesian\\_perspective](https://github.com/DamianBeckUniBern/anticipatoryBehaviour_in_vr_tennis_a_bayesian_perspective)).  
213 The experiment was insofar intraindividual counterbalanced as half of the players  
214 had an 80% chance of receiving serves to the left in the first session and an 80% chance of  
215 receiving serves to the right in the second session, and vice versa for the other half of the  
216 players. Consequently, in comparison to the first session, all trials were exactly mirrored in the  
217 second session.

### 218 **3.4 Measures and Analyses**

219 For our investigation, it was crucial (1) to check whether a split step had actually been  
220 performed and to determine (2) the weight-shift dynamics over the split step, (3) the movement  
221 direction after the split step, and (4) the percentage of trials in which players went to the side  
222 played (correct response rate) and the ball was successfully hit (hit rate), respectively. In turn,  
223 the weight-shift dynamics, response and hit rates were required for drawing comparisons as a  
224 function of a more or less developed prior (neutral vs. biased) and, in the biased case, as a  
225 function of confirmed or non-confirmed expectations (congruent vs. incongruent). Finally, (5)  
226 we found it interesting to investigate the extent to which the weight shift dynamics predict later  
227 performance in terms of conducting a lateral movement in the direction of the serve and  
228 successfully hitting the ball.

#### 229 **3.4.1 Split-step detection**

230 For determining whether and, if applicable, when a split step has actually been performed, the  
231 analyses started with the calculation of the participant's center of mass (COM). To this end, a  
232 full-body model with 21 body segments (Figure 4 in Appendix A) was computed from the six

235 rigid motion-capture bodies (head, back, left hand, right hand, left foot, right foot) and exported  
236 from the Motive software. Based on the anthropometric data from Shan and Bohn (2003), we  
237 assigned relative weights to the body segment positions to calculate a raw COM value. The  
238 data for each body segment was finally calculated using a Savitzky-Golay filter of a third  
239 polynomial order with a window length of 99 to obtain COM data in 3D space for each time  
240 frame.

241 The subsequently conducted algorithmic detection of the split step involved several steps. First,  
242 we set the time in relation to the serve. Starting from the maximum COM height in the time  
243 interval of -0.2 s to 1 s around the moment of serve, it was iteratively checked frame by frame  
244 in both directions whether the following frame had a lower COM height. The identified local  
245 minima were taken as the beginning and end of a potentially performed split step, respectively.  
246 A split step was confirmed if the difference between the maximum COM value and the COM  
247 value at the end of the calculated split-step interval was greater than 5 cm. The median was  
248 used as a robust estimate to calculate the average time for the initiation of the split step.  
249

### 250 3.4.2 Weight-shift dynamics

251 The COM was also used to calculate the weight shift. To this end, we compared the lateral  
252 distances of the left and right ankles to the COM, respectively, and defined the weight shift as  
253 the difference between these distances. If the smaller distance was on the same side as the more  
254 probable serve side in the biased condition, we considered the weight shift to be positive in the  
255 direction of the prior and, otherwise, to be negative. In the neutral condition, positive values  
256 were assigned to the weight-shift difference if the side of the smaller distance matched the side  
257 of the actually played serve.

258 For analyzing weight-shift dynamics, we calculated each participant's mean values for the time  
259 interval from 0.1 s before to 1.0 s after the serve, that is, to the moment when the ball reached  
260 the return area. These curves were aggregated from the two blocks of the neutral condition as  
261 well as from the last two blocks of the biased condition per session, separately for correct and  
262 incorrect trials and for the biased condition additionally for congruent and incongruent trials.  
263 To investigate whether the weight shift is drawn towards the prior in the biased condition, we  
264 conducted multilevel regression analyses at three different points in time relative to the serve  
265 onset that precede the average initiation of the lateral movement, namely at -0.1 s, 0.2 s, and  
266 0.5 s. For these points in time, we tested if the overall mean deviates from zero. On the basis  
267 of all individual measurements over the last two blocks of the biased condition, we had multiple  
268 data points for each participant, and the residuals were not independent. Therefore, we built  
269 and compared regression models in several steps in order to take the hierarchical structure of  
270 the data into account (Field et al., 2012). Descriptively, we compared models considering the  
271 Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and log-likelihood  
272 (Tables 4–9 in Appendix B). For the purpose of inferential model comparisons, we used the  
273 log-likelihood ratio  $\chi^2$  test. Only the best model according to the parsimony principle will be  
274 reported. Further, in the case of a singular model fit, we took the one less complex model before  
275 (Bates et al., 2015). The following procedures were used for missing values, outlier detection  
276 and checking prerequisites: Under the assumption that missing values occur randomly,  
277 multilevel regression analyses can handle missing values (Field et al., 2012). We detected  
278 outliers using Cook's distance and removed them when values affected the intercept more than  
279 three times as much as the mean. We checked the homoscedasticity and normality of the  
280 residuals graphically. Further, we used the maximum likelihood for model estimations, and we  
281 tested intercept coefficients with the Wald test for significance. For all inferential tests, we  
282 chose an alpha level of 5%. For the required calculations, we applied the R-package 'nlme'  
283 (Pinheiro, 2009).

285

## 286 3.4.3 Lateral movement direction

287

288 The algorithmic detection of lateral movement initiation was also based on the COM and  
 289 carried out in the following steps. First, the initial lateral COM position was defined as the  
 290 average position over the time interval between 0.2 s and 0.1 s before the serve. Next, the  
 291 algorithm searched for the first instance when the average lateral position of the COM over ten  
 292 consecutive frames deviated by at least 0.2 m from this initial position. The algorithm then  
 293 iterated backwards frame by frame until the lateral velocity of the COM fell below 0.4 m/s,  
 294 and the identified frame was taken as the moment of lateral movement initiation. The median  
 295 was used as a robust estimate to calculate the average time of lateral movement initiation.

296 In addition to the derivation of temporal marker's position, the sign of the difference between  
 297 initial lateral COM position and COM position at the moment of lateral movement initiation  
 298 unambiguously allowed the movement direction either to the left or to the right side to be  
 299 clearly determined. These directions were, in turn, used to calculate the correct response rate  
 300 as the percentage of trials in which the players initiated their movement in the direction of the  
 301 actual serve. This variable was computed separately for congruent and incongruent trials of the  
 302 four blocks of the biased condition.

303 To analyze the development of the correct response rate over the four blocks of the biased  
 304 condition, we conducted a multiple regression analysis with the independent predictors: trial  
 305 number and the dummy coded (in)congruency of the respective trial as well as their interaction,  
 306 thereby, in accordance with the exponential law of practice (Heathcote & Brown, 2000), taking  
 307 the root of the trial number rather than its raw value. As we were able to calculate a correct  
 308 response rate for each trial, we had no missing values in the analysis. Outliers were detected  
 309 using Cook's distance and were removed if they affected the regression more than three times  
 310 than the mean. For all inferential tests, we chose an alpha level of 5%.

311

## 312 3.4.4 Hitting performance

313

314 As an additional performance measure to the correct response rate, the hit rate was calculated  
 315 as the percentage of trials in which the players were able to successfully hit the served ball, as  
 316 was the case in the correct response-rate variable, again separately for congruent and  
 317 incongruent trials of the four blocks of the biased condition. For the analysis of the  
 318 development of the hit rate over the four blocks of the biased condition, the same regression  
 319 approach was chosen as already been described for the variable of correct response rate.

320 Given the relatively high serve speed, it was a difficult task for the participants to hit the ball  
 321 successfully at all. As a result, in the vast majority of cases the players failed to hit the target  
 322 disc on the opponent's half of the court. Consequently, we refrained from calculating another  
 323 performance measure that would reflect target accuracy.

324

## 325 3.4.5 Performance predictions

326

327 To investigate the extent to which the weight-shift variable predicts later performance, we  
 328 conducted multilevel logistic regression analyses, again at three different time points relative  
 329 to the serve onset (-0.1 s, 0.2 s, 0.5 s). As already described in Section 3.4.2 for weight-shift  
 330 dynamics above, we considered the hierarchical structure of the data. Therefore, we built and  
 331 compared models similarly (Tables 10–25 in Appendix B). In contrast to the analyses described  
 332 in the section 3.4.2, regression coefficients were tested for significance using the log-likelihood  
 333 ratio  $\chi^2$  test. For all inferential tests, we chose again an alpha level of 5%. We applied the R-  
 334 package 'lme4' (Bates et al., 2015).

335 **3. Results**

336 Results were obtained for (1) the detection of actually performed split steps, (2) the weight-  
337 shift dynamics over the split step, (3) the subsequent actual movement direction, (4) the hit  
338 rate, and (5) the prediction of the two performance variables (movement direction and hit rate)  
339 from the split-step characteristics.

340

341 **3.5.1 Split-step detection**

342

343 In 90.6% of the trials, a clear split step could be detected based on the specified criterion of a  
344 definite raising and lowering of the COM around the opponent's serve. Consequently, it can  
345 be inferred that the participants definitely performed a split step in the vast majority of cases.  
346 However, as weight-shift data can also be computed for vertical COM displacements of a lesser  
347 extent than 5 cm, all trials were included in the analysis.

348 On average, the split step was initiated quite exactly at the moment of serve ( $M = -0.01$  s) in a  
349 neutral forward direction. The resulting lateral movement initiation started on average about  
350 half of a second later ( $M = 0.62$  s), and in successful trials, as prespecified by the experimentally  
351 manipulated serve speed, the ball was hit about one second after the serve ( $M = 1.00$  s).

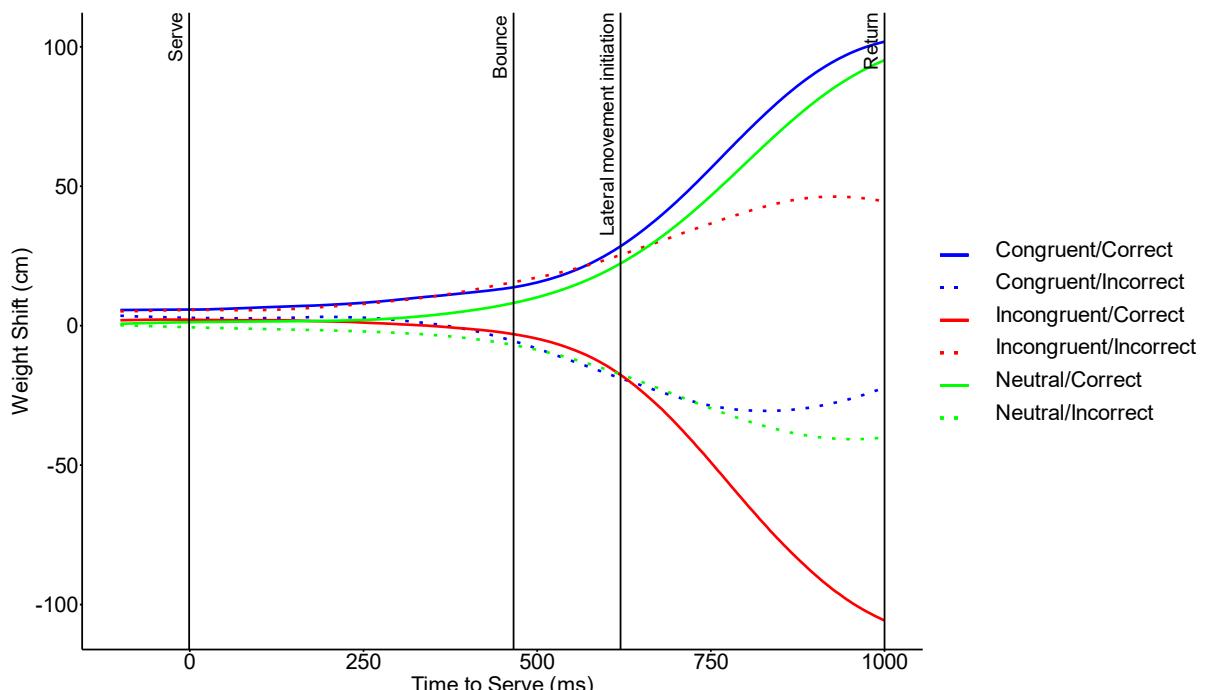
352

353 **3.4.2 Weight-shift dynamics over the split step**

354

355 Figure 2 shows the players' average weight shifts in the last two blocks of the biased condition,  
356 separated according to the (in)congruence between the to-be-expected and actual serve  
357 direction (blue vs. red lines) and to the correctness of the response, determined as an initiation  
358 of the movement in or against the serve direction (solid vs. dotted lines). Please note that the  
359 weight-shift data is plotted relative to the prior, i.e., positive values reflect a behavior in which  
360 the opponent's preferred serve direction is clearly taken into account. For comparison purposes,  
361 Figure 2 also includes the weight-shift data for the neutral condition (green lines), in this case,  
362 as no prior exists, plotted relative to the correct movement direction.

363



364

365

366 >>> Please insert Figure 2 about here <<<

367 *Figure 2. Weight shift over the split step in congruent vs. incongruent trials with correct vs. incorrect responses in the final*  
368 *blocks of biased condition with serve-direction probabilities of 80:20, plotted relative to the developed prior, in comparison*  
369 *to the weight-shift dynamics for the neutral condition with serve-direction probabilities of 50:50, plotted relative to the correct*  
370 *movement direction*

371

372 Analyzing the overall mean weight shift for the biased condition shows that the weight is  
373 already shifted towards the more probable side 100 ms before the serve ( $N_{\text{players}} = 14$ ,  $B = 2.49$ ,  
374  $\text{CI} = [0.37, 4.61]$ ,  $t(1037) = 2.30$ , two-sided  $p = .022$ ), namely on average by 2.49 cm. This  
375 effect increases when considering the weight-shift data 200 ms ( $M = 3.35 \text{ cm}$ ;  $N_{\text{players}} = 14$ ,  $B$   
376  $= 3.35$ ,  $\text{CI} = [1.36, 5.35]$ ,  $t(1044) = 3.29$ , two-sided  $p = .001$ ) and 500 ms ( $M = 5.02 \text{ cm}$ ;  $N_{\text{players}}$   
377  $= 14$ ,  $B = 5.02$ ,  $\text{CI} = [2.06, 7.97]$ ,  $t(1026) = 3.33$ , two-sided  $p = .001$ ) after the serve,  
378 respectively (see full statistics in Appendix B, Tables 4–9). In the neutral condition, the mean  
379 weight shift cannot be calculated in relation to the prior as there is a 50:50 chance for each side.  
380 Accordingly, the overall means of the weight shift directed towards the ball played were all  
381 close to zero and did not significantly deviate from this neutral value.

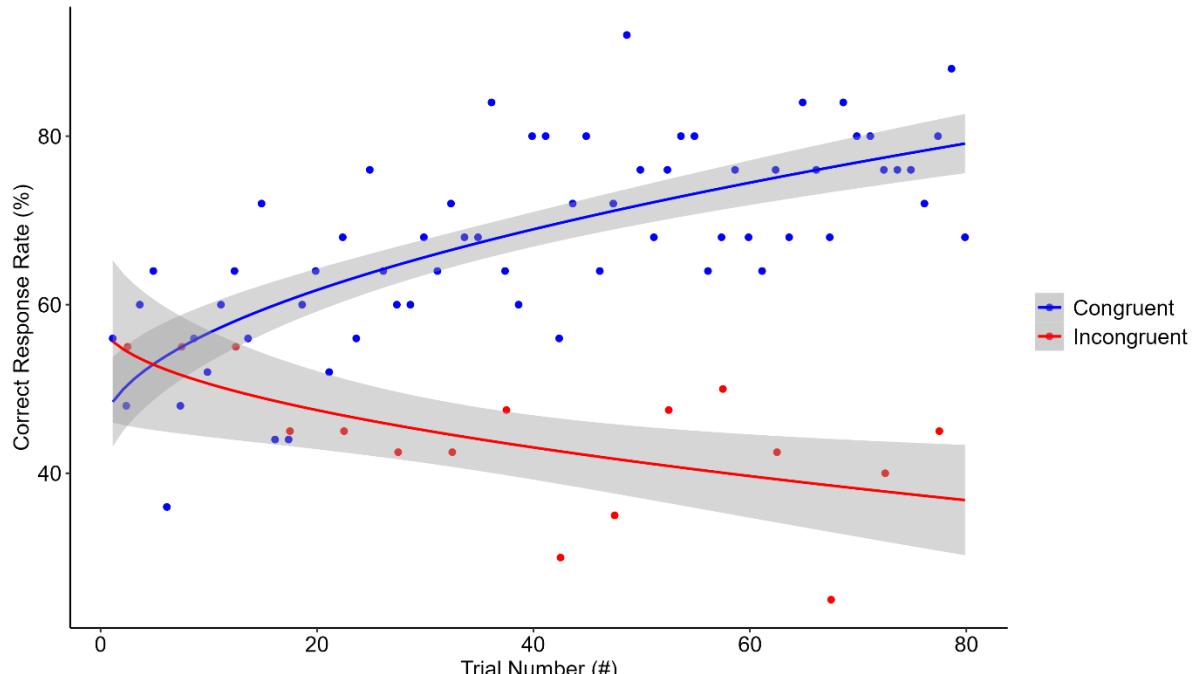
382

### 383 3.4.3 Correctness of lateral movement direction

384

385 To examine the effect of accumulated prior knowledge on performance over the experiment,  
386 we analyzed the response correctness (i.e., players' movement initiation in the direction of the  
387 actual serve) over the experiment in congruent vs. incongruent trials (Figure 3). Overall, due  
388 to high serve speeds, the perceptual-motor demands were high, resulting in an overall response  
389 correctness of 57.2% only (56.8% for left/backhand, 57.6% for right/forehand). In the neutral  
390 condition after the warm-up trials, the overall correct response rate was 49.5 %. However, in  
391 the biased condition with an 80% probability to one side and a 20% probability to the other  
392 side, the players learned the probabilities quickly. Accordingly, they were able to increase their  
393 correct response rate in the congruent trials to 79.1%, while the corresponding value for the  
394 incongruent trials fell to 36.8% (Figure 3), resulting in an overall correct response rate of 70.6%  
395 at the end of the practice blocks in the biased condition. The regression model was significant  
396 with a large effect ( $N_{\text{players}} = 14$ ,  $F(3,76) = 62.49$ , two-sided  $p < .001$ ,  $R^2_{\text{adjusted}} = .700$ ,  $f^2 = 2.33$ ),  
397 and all coefficients were significant (Table 1).

398



399  
400

401 >>> Please insert Figure 3 about here <<<

402 *Figure 3. Development of tennis players' performance in congruent vs. incongruent trials in the blocks of the biased condition*  
 403 *with serve-direction probabilities of 80:20 in terms of correct response rate. The uncertainty area represents a 95% confidence*  
 404 *interval of the regression lines.*

Table 1 Regression model for correct response rate

Predictors	B	95% CI	t(76)	p two-sided
Intercept	58.17	[46.17, 70.17]	9.66	< .001
sqrt(trial number)	-2.39	[-4.29, -0.49]	-2.51	.014
condition (0 = incongruent, 1 = congruent)	-13.84	[-27.28, -0.39]	-2.05	.044
sqrt(trial number) × condition	6.28	[4.16, 8.40]	5.89	< .001

405 Note. B = unstandardised regression coefficients, CI = confidence intervals, sqrt = square root function.  
 406 Model statistics  $N_{\text{players}} = 14$ ,  $F(3,76) = 62.49$ , two-sided  $p < .001$ ,  $R^2_{\text{adjusted}} = .700$ ,  $f^2 = 2.33$ .

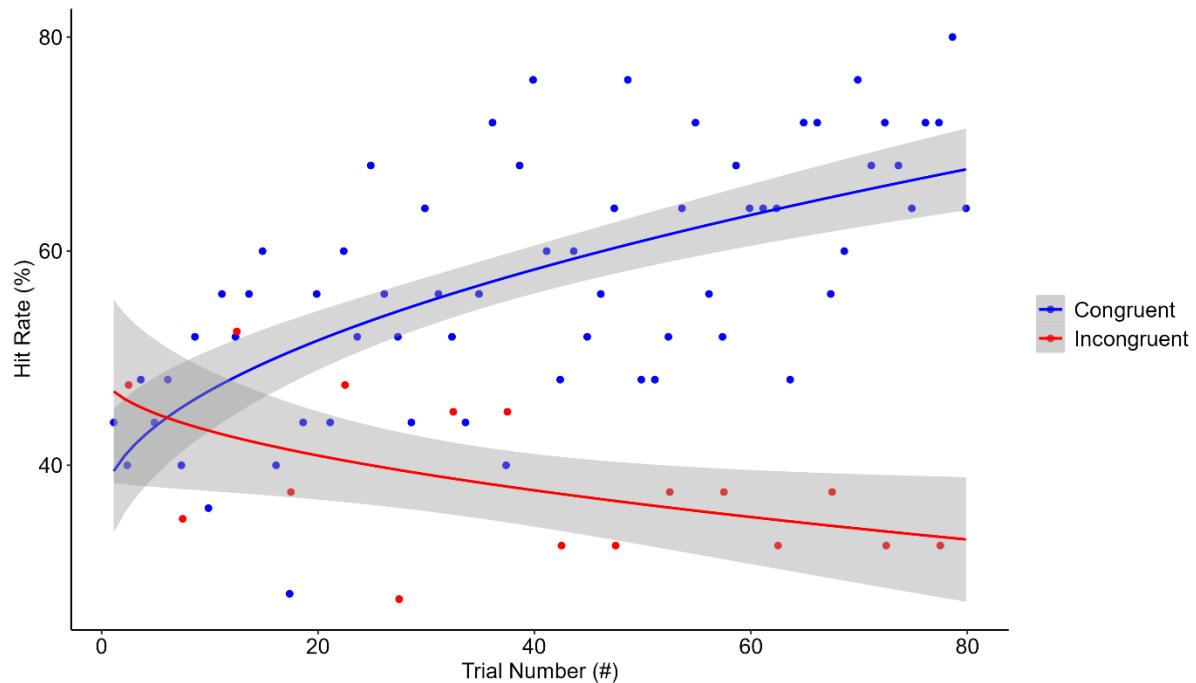
407  
 408 >>> Please insert Table 1 about here <<<

409

#### 410 3.4.4 Hitting performance

411

412 Since hitting the ball is even harder compared to initiating a movement in the correct direction,  
 413 the overall hit rate was no more than 35.5% in the neutral condition after the warm-up trials.  
 414 However, the participants managed to increase this value to 67.7% in congruent trials at the  
 415 end of the biased condition with, at the same time, a decrease to 33.1% in incongruent trials  
 416 (Figure 4), which comes down to an overall final hit rate of 60.8%. The corresponding  
 417 regression model reaches significance with a large effect ( $N_{\text{players}} = 14$ ,  $F(3,76) = 39.04$ , two-  
 418 sided  $p < .001$ ,  $R^2_{\text{adjusted}} = .591$ ,  $f^2 = 1.44$ ), and again all coefficients were significant (Table 2).



419  
420

421 >> Please insert Figure 4 about here <<<

422 *Figure 4. Development of tennis players' performance in congruent vs. incongruent trials in the blocks of the biased condition*  
 423 *with serve-direction probabilities of 80:20 in terms of hit rate. The uncertainty area represents a 95% confidence interval of*  
 424 *the regression lines.*

Table 2 Regression model for hit rate

Predictors	B	CI	t(76)	p two-sided
Intercept	48.75	[36.04, 61.47]	7.64	<.001
sqrt(trial number)	-1.75	[-3.77, 0.26]	-1.74	.086
condition dummy code	-13.09	[-27.34, 1.17]	-1.83	.071
sqrt(trial number) × condition dummy code	5.33	[3.08, 7.58]	4.72	<.001

425 *Note. B = unstandardised regression coefficients, CI = confidence intervals, sqrt = square root function.*  
 426 *Model statistics N<sub>players</sub> = 14, F(3,76) = 39.04, two-sided p < .001, R<sup>2</sup> adjusted = .591, f<sup>2</sup> = 1.44.*  
 427

428 >>> Please insert Table 2 about here <<<

429  
430 3.4.5 Performance prediction

431  
432 It was shown above that in the last two blocks of the biased condition, the established prior  
 433 affects weight-shift dynamics over the split step already at the starting position at rest before  
 434 the serve (Figure 2). Interestingly, however, it also appears that the weight shift tends towards  
 435 the less likely side for correct responses in incongruent trials as well as for incorrect responses  
 436 in congruent trials early in the split step, which in turn implies that the direction of the weight

shift predicts the direction of the later initiated movement. Inferentially, this can already be proven for the starting position at rest before the serve since the odds ratio for initiating a movement in the same direction as the direction of the weight shift turns out to be significantly higher than one ( $N_{\text{players}} = 14$ ,  $OR = 1.02$ ,  $CI = [1.01, 1.03]$ ,  $z(1067) = 4.97$ , two-sided  $p < .001$ ), and this value increases further for the time points of 200 ms ( $N_{\text{players}} = 14$ ,  $OR = 1.03$ ,  $CI = [1.02, 1.04]$ ,  $z(1085) = 8.22$ , two-sided  $p < .001$ ) and 500 ms ( $N_{\text{players}} = 14$ ,  $OR = 1.25$ ,  $CI = [1.20, 1.30]$ ,  $z(1055) = 10.09$ , two-sided  $p < .001$ ) after the serve (see full statistics in Tables 10–13 in Appendix B).

As the overall weight shift is towards the prior and the weight shift increases the probability of taking the same side as the weight shift, there is also an interaction between condition (incongruent/congruent) and weight shift towards the prior in increasing the odds of a correct response. These interaction effects are significant with increasing odds ratios (all higher than one) 100 ms before the serve ( $N_{\text{players}} = 14$ ,  $OR = 1.03$ ,  $CI = [1.01, 1.06]$ ,  $z(1074) = 2.64$ , two-sided  $p = .008$ ) as well as 300 ms after the serve ( $N_{\text{players}} = 14$ ,  $OR = 1.07$ ,  $CI = [1.04, 1.09]$ ,  $z(1086) = 5.17$ , two-sided  $p < .001$ ) and 500 ms after the serve ( $N_{\text{players}} = 14$ ,  $OR = 1.25$ ,  $CI = [1.20, 1.30]$ ,  $z(1055) = 10.09$ , two-sided  $p < .001$ ) (see full statistics in Tables 14–19 in Appendix B).

Furthermore, there is a significant interaction between condition (incongruent/congruent) and weight shift directed towards the prior in increasing the odds to hit the ball. These interaction effects are significant with increasing odds ratios (all higher than one) 100 ms before the serve ( $N_{\text{players}} = 14$ ,  $OR = 1.05$ ,  $CI = [1.02, 1.08]$ ,  $z(1062) = 3.77$ , two-sided  $p < .001$ ) as well as 300 ms after the serve ( $N_{\text{players}} = 14$ ,  $OR = 1.05$ ,  $CI = [1.02, 1.07]$ ,  $z(1065) = 3.44$ , two-sided  $p < .001$ ) and 500 ms after the serve ( $N_{\text{players}} = 14$ ,  $OR = 1.14$ ,  $CI = [1.10, 1.18]$ ,  $z(1071) = 7.40$ , two-sided  $p < .001$ ) (see full statistics in Tables 20–25 in Appendix B).

#### 4. Discussion

This study had two aims. First, we aimed to understand how tennis players exploit prior knowledge in tennis returns with high spatiotemporal demands and thus make a contribution to the applied field of sports science. Second, taking tennis as an informative exemplary case, we aimed to contribute to the general understanding of how humans use prior and sensory information in online decision-making and motor control in complex, naturalistic movements. To this end, we investigated a preparatory movement for the tennis return under real-world task demands in virtual reality: the split step. We showed that experienced tennis players (1) regularly performed a split step and (2) continuously adjusted their weight shifts over the split step based on an ongoing weighting of prior knowledge on situational probabilities regarding the serve direction and accumulated sensory evidence for one proposition or the other (Figure 2). Furthermore, over the course of the experiment, participants learned situational probabilities of the opponent's serve directions and increasingly exploited this information to improve performance in terms of (3) initiating a movement in the correct direction and (4) successfully hitting the ball (Figures 3 and 4). As predicted based on a Bayesian framework, participants increasingly relied on prior information, resulting in enhanced performance in congruent and thus frequent trials (80%) whilst accepting degraded performance in incongruent and thus rare trials (20%) – a functional strategy that optimizes overall performance in a Bayesian way. Finally, we showed that (5) players' performance can be explained by the extent to which prior knowledge is integrated in the early phase of the split step. Specifically, players' weight shifts were already biased towards the more probable side *before* the serve, which in turn increased the likelihood of a subsequent movement in the same direction and the achievement of a good position for a successful return.

Regarding the first goal, we followed the call of Avilés et al. (2019) and Navia et al. (2022) to investigate the effect of prior knowledge on anticipatory behavior and performance in a tennis return under real-world spatial and temporal task demands to maximize representativeness and ecological validity. To study participants' naturalistic, unconstrained behavior while maintaining experimental control (in this case: disentangling kinematic information and situational probabilities), we developed an experimental setup in which tennis players performed returns in a life-size CAVE environment, where they could freely move in space, swing a real racket to return virtual balls with an initial speed of 144 km/h, thereby facing a task difficulty similar to the challenge ATP/WTA players encounter, where they achieve a successful return rate around 50–80% on first serves (Gillet et al., 2009; Mecheri et al., 2019). With this representative experimental design, we have obtained results that can claim practical relevance for the world of sports, in particular for sports situations that are classically studied under the label of "anticipation research". First, the results reconcile and put into context the seemingly incompatible positions that anticipation is, on the one hand, key to returning tennis serves (Williams & Jackson, 2019) and, on the other hand, no overt anticipatory behavior can be observed when players actually return serves (Avilés et al., 2019). In this regard, we show that tennis players are not only able to extract situational probabilities (Farrow & Reid, 2012; Loffing & Hagemann, 2014; Loffing et al., 2016; Murphy et al., 2016; Murphy et al., 2018) but actually actively exploit predictive information by optimizing their weight shifts during and even before initiating the split step. These weight shifts are optimized for the more likely trials and thus improve overall performance. Second, confirming previous studies (Jackson et al., 2020; Mann et al., 2014), our results show that players increasingly rely on acquired prior information with exposure to an opponent's action tendencies, leading to performance increases in congruent trials and, conversely, performance decreases in incongruent trials. Importantly, however, this should not be taken as a "bug" of the system; accepting the costs of incorrect decisions in cases only occurring at low frequency should rather be regarded as a functional strategy to improve overall performance – as predicted by Bayesian theory. Third, on a theoretical level, putting sports-related anticipation research in the context of state-of-the-art theories of sensorimotor behavior suggests that using predictions to guide action is fundamental to behavioral control and not a specific feature of actions that require "anticipation" due to high temporal demands. The difference between tasks with low and high time pressure then comes down to the fact that in the first case, sufficient time is available to wait for the confirmation of one's prediction by incoming sensory information, whereas in the second case of "anticipation", one must rely on the currently usable predictions to initiate action. In both cases, however, behavioral control constitutes an ongoing process of anticipatory online decision-making. Our empirical findings on continuous weight-shift adjustments over the split step based on prior knowledge and accumulated sensory evidence is perfectly in line with such a theoretical position of a Bayesian online integration in decision-making and motor control.

In relation to the second goal, aiming beyond the field of behavioral control and performance enhancement in sports, we see three major indications for a continuous predictive decision-making process in action (Figure 2), thereby especially referring to the theoretical concept of the affordance competition hypothesis (Cisek, 2007). First, it should be noted that weight shifts of the congruent/correct and incongruent/incorrect responses develop similarly over the early phase of the split step until the players, based on incoming sensory evidence, seem to realize in the incongruent/incorrect cases that they are wrong. The same – but mirrored – development in the weight shift can be seen in the congruent/incorrect in comparison to the incongruent/correct returns, which also suggests that players are constantly evaluating the costs of the two response options and stop pushing as soon as they realize that they are moving in the wrong direction. A second point regards the fact that in incongruent/correct and

534 congruent/incorrect trials, the weight shift even in the very early phase of the split step does  
535 not tend to the more likely side but remains close to zero (Figure 2). Admittedly, this pattern  
536 could also be attributed to pre-decisions and consequently pre-planned movement initiations,  
537 for instance due to the in cognitive psychology well-known phenomenon of the gambler's  
538 fallacy, which implies that players expect an incongruent serve from time to time if there have  
539 previously been several congruent serves in a row (e.g., described for soccer goalkeepers by  
540 Misirlisoy & Haggard, 2014). However, as negative rather than zero values for the weight-shift  
541 would be expected on this basis, we would like to take our finding as further evidence in favor  
542 of our interpretation that players are constantly evaluating the two response options. Since the  
543 weight shifts are distributed around a mean value in early phases of the split step, it can be  
544 predicted that players sometimes start with a less pronounced weight shift to the congruent  
545 side, which in turn increases the attractiveness of the incongruent side. This random deviation  
546 is then reflected in a higher probability of initiating a movement in the right direction in  
547 incongruent trials, but also of moving incorrectly in response to congruent serves. Third – and  
548 entirely in line with this explanation –, it should be noted that the weight shifts in  
549 congruent/correct and neutral/correct trials develop almost in parallel over the split step (Figure  
550 2), which again means that if one is already inclined towards a particular option, this option  
551 becomes even more attractive as, due to biomechanically justifiable motor costs (Griessbach  
552 et al., 2022), alternatives become increasingly difficult to achieve. And consequently, the  
553 advantage of integrating prior knowledge at an early stage of an action is retained throughout  
554 the entire process of integrated online decision-making and sensorimotor control.

555 In conclusion, this study builds a bridge between current theories in fundamental research and  
556 applied questions in sport science. For future research, this work shows how contributions to  
557 both fields can be simultaneously made by leveraging virtual reality technologies to investigate  
558 complex, naturalistic behavior while keeping high experimental control (e.g., Cisek & Green,  
559 2024; Mangalam et al., 2023). The current study provides evidence that tennis players exploit  
560 prior knowledge in continuous anticipatory decision-making – which was controversially  
561 debated in sports (Avilés et al., 2019) – and show that they do it in a Bayesian way, in line with  
562 leading approaches of sensorimotor behavior such as the theories of internal models (Wolpert  
563 et al., 1995), optimal feedback control (Todorov & Jordan, 2002), active inference (Friston,  
564 2010), and affordance competition (Cisek, 2007). Specifically, we show that players  
565 continuously optimize their weight shifts during the split step based on online predictions.  
566 Using tennis as an exemplary case, the current finding demonstrates that predictive control and  
567 Bayesian integration provide a powerful framework to explain human behavior in complex,  
568 naturalistic tasks in sports and beyond.

569

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576 obtained.

## 577 Declaration of interest statement

578 The authors report no conflict of interest.

## 579 Data availability statement

580 All data and code used for statistical analysis and figure generation, a video of the experimental  
581 task, the experimental protocols, and the c3d files of the full body model of each trial are  
582 available at GitHub  
583 ([https://github.com/DamianBeckUniBern/anticipatoryBehaviour\\_in\\_vr\\_tennis\\_a\\_bayesian\\_perspective](https://github.com/DamianBeckUniBern/anticipatoryBehaviour_in_vr_tennis_a_bayesian_perspective)). Full raw data will be provided upon reasonable request.  
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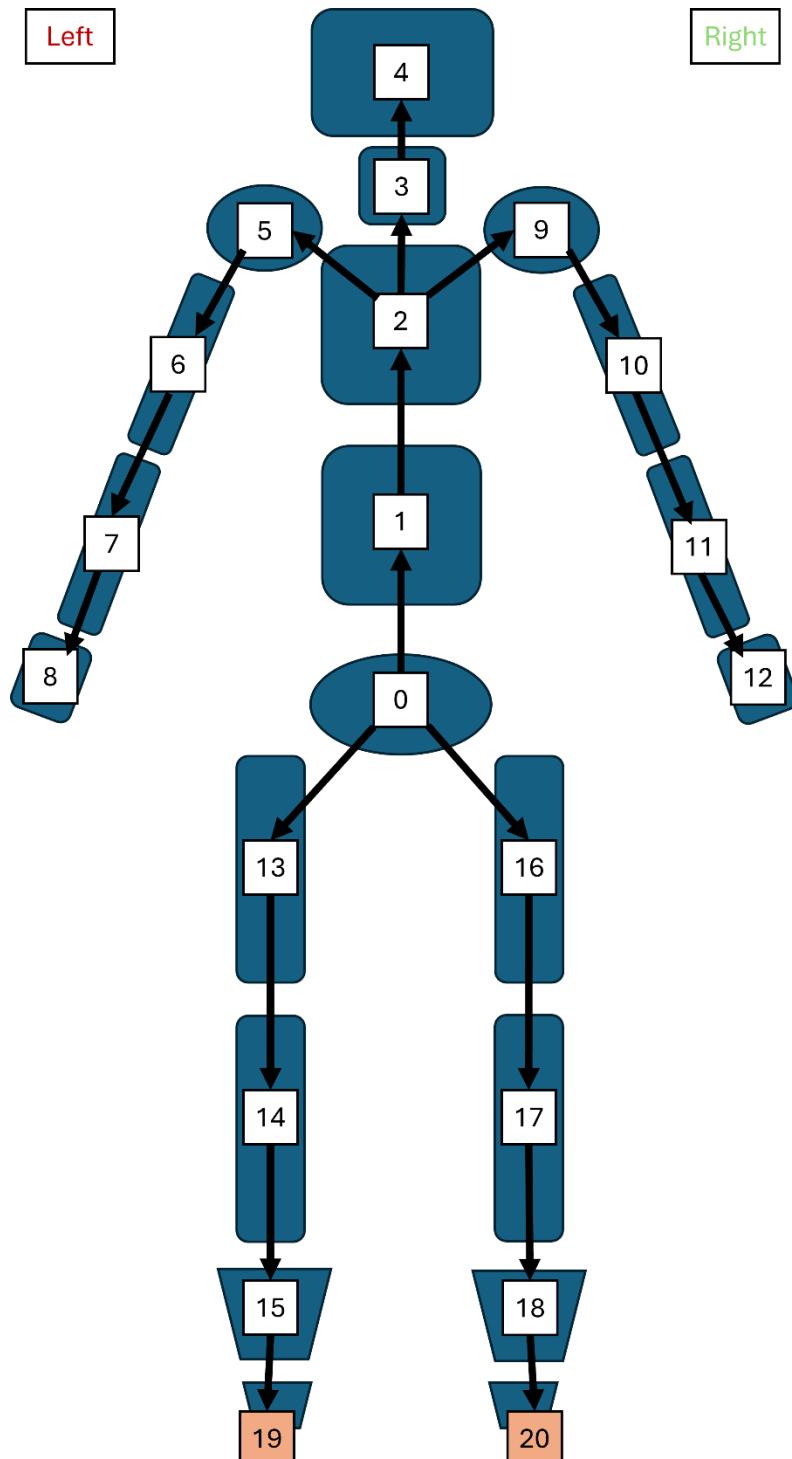
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752 Appendix A.



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754 >>> Please insert Figure 5 about here <<<

755 *Figure 5* Body segments of the full body model exported from Motive software.  
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*Table 3 Relative weights of the body segments to calculate the centre of mass*

Body segments (Shan & Bohn, 2003)	Relative weights	Motive body segments	Relative weights
Head	0.07	Head	0.07
Upper torso	0.18	Neck	0.18/4
		Left shoulder	0.18/4
		Right shoulder	0.18/4
		Upper torso	0.18/4
Middle torso	0.12	Middle torso	0.12
Lower torso	0.13	Lower torso	0.13
Tigh	0.14	Left thigh	0.14
		Right thigh	0.14
Shank	0.05	Left shank	0.05
		Right shank	0.05
Foot	0.01	Left ankle	0.01/2
		Left foot	0.01/2
		Right ankle	0.01/2
		Right foot	0.01/2
Upper arm	0.03	Left upper arm	0.03
		Right upper arm	0.03
Forearm	0.01	Left forearm	0.01
		Right forearm	0.01
Hand	0.01	Left hand	0.01
		Right hand	0.01

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&gt;&gt;&gt; Please insert Table 18 about here &lt;&lt;&lt;

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761 **Appendix B.**762 *Table 4. Weight shift directed to the prior at 100 ms before the serve*

Fixed effects	B	95% CI	SE B	t(1037)	p two-sided
Intercept	2.49	[0.37, 4.61]	1.08	2.30	.022
<hr/>					
Random effects					
Intercept variance ( $\tau_{00}$ )	13.18	—	—	—	—
Level-1 residual ( $\sigma^2$ )	231.18	—	—	—	—
ICC	0.05	—	—	—	—

763 Note.  $B$  = unstandardized regression coefficient, CI = confidence intervals,  $SE$  = standard error,  $t$ (degrees of freedom). ICC =  
 764 Interclass correlation coefficient. Weight shift is positive in the direction of the prior. Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{marginal}}$   
 765 < .001. Multilevel model comparison in Table 5.

766 *Table 5. Model comparison for multilevel regression of the weight shift in the direction of the prior at 100 ms before the serve*

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	2	8766.824	8776.738	-4381.412			
2 Random intercepts	3	8732.574	8747.446	-4363.287	1 vs 2	36.250	< .001

767 Note. df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-  
 768 likelihood.  
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771*Table 6. Weight shift directed to the prior at 200 ms after the serve*

Fixed effects	B	95% CI	SE B	t(1044)	p two-sided
Intercept	3.35	[1.36, 5.35]	1.02	3.29	.001

Random effects

Intercept variance ( $\tau_{00}$ )	11.10	–	–	–	–
Level-1 residual ( $\sigma^2$ )	252.68	–	–	–	–
ICC	0.04	–	–	–	–

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*Note.* B = unstandardized regression coefficient, CI = confidence intervals, SE = standard error, t(degrees of freedom). ICC = Interclass correlation coefficient. Weight shift is positive in the direction of the prior. Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{marginal}} < .001$ . Multilevel model comparison in Table 7.

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*Table 7. Model comparison for multilevel regression of the weight shift in the direction of the prior at 200 ms after the serve (biased condition)*

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	2	8905.439	8915.367	-4450.719			
2 Random intercepts	3	8881.836	8896.728	-4437.918	1 vs 2	25.603	< .001

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*Note.* df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-likelihood.

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*Table 8. Weight shift directed to the prior at 500 ms after the serve*

Fixed effects	B	95% CI	SE B	t(1026)	p two-sided
Intercept	5.02	[2.06, 7.97]	1.51	3.33	.001

Random effects

Intercept variance ( $\tau_{00}$ )	22.13	–	–	–	–
Level-1 residual ( $\sigma^2$ )	370.83	–	–	–	–
ICC	0.06	–	–	–	–

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*Note.*  $B$  = unstandardized regression coefficient, CI = confidence intervals,  $SE$  = standard error,  $t$ (degrees of freedom). ICC = Interclass correlation coefficient. Weight shift is positive in the direction of the prior. Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{marginal}} < .001$ . Multilevel model comparison in Table 9.

*Table 9. Model comparison for multilevel regression of the weight shift in the direction of the prior at 200 ms after the serve*

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	2	9033.488	9048.329	-4513.744			
2 Random intercepts	3	9024.690	9044.478	-4508.345	1 vs 2	10.80	.001

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*Note.* df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-likelihood.

Table 10. Logistic regression model of the weight shift in the direction of the side played for predicting direction taken 100 ms before the serve

Fixed effects	<i>B</i>	<i>SE B</i>	<i>z</i> (1067)	<i>p</i> two-sided	<i>OR</i>	95% CI
Intercept	-0.05	0.06	-0.81	.417	0.95	[0.84, 1.07]
Weight shift	0.02	0.00	4.97	< .001	1.02	[1.01, 1.03]

790 Note. *B* = unstandardised regression coefficients, *SE* = standard error, *z*(degrees of freedom), *OR* = Odds Ratio, CI =  
 791 confidence intervals. Weight shift is positive in the direction of the prior. Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{Tjur}} = .024$ . No  
 792 multilevel model comparison due to singularities in their model fits.

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Table 11. Logistic regression model of the weight shift in the direction of the side played for predicting direction taken 100 ms before the serve

Fixed effects	<i>B</i>	<i>SE B</i>	<i>z</i> (1086)	<i>p</i> two-sided	<i>OR</i>	95% CI
Intercept	-0.13	0.06	-1.98	.047	0.88	[0.78, 1.00]
Weight shift	0.03	0.00	8.15	< .001	1.03	[1.02, 1.04]

Note. *B* = unstandardised regression coefficients, *SE* = standard error, *z*(degrees of freedom), *OR* = Odds Ratio, CI = confidence intervals. Weight shift is positive in the direction of the prior. Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{Tjur}} = .080$ . No multilevel model due to worse model fits, see Tab 12.

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799 Table 12. Model comparison for logistic regression of the weight shift in the direction of the side played for predicting  
800 direction taken probability 200 ms after the serve

Model	<i>df</i>	AIC	BIC	logLik	Comparison	$\chi^2$	<i>p</i>
1 Intercept	1	1510.108	1515.100	-754.05			
2 Base model	2	1415.037	1425.021	-705.52	1 vs 2	97.072	< .001
3 Base model + RI	3	1414.927	1429.904	-704.46	2 vs 3	2.11	.146
4 Base model + RS	5	–	–	–	3 vs 4	–	–

801 Note. *df* = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-  
802 likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictor weight shift  
803 directed to the side played.  
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Table 13. Logistic regression model of the weight shift in the direction of the side played for predicting direction taken 500 ms after the serve

Fixed effects	<i>B</i>	<i>SE B</i>	<i>z</i> (1088)	<i>p</i> two-sided	<i>OR</i>	95% CI
Intercept	-0.13	0.06	-2.09	.037	0.88	[0.77, 0.99]
Weight shift	0.02	0.00	7.92	< .001	1.02	[1.02, 1.03]

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808 Note. *B* = unstandardised regression coefficients, *SE* = standard error, *z*(degrees of freedom), *OR* = Odds Ratio, CI =  
confidence intervals. Weight shift is positive in the direction of the prior. Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{Tjur}} = .068$ . No  
multilevel model comparison due to singularities in their model fits.

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Table 14. Multilevel logistic regression model of the weight shift in the direction of the prior for predicting correct response probability 100 ms before the serve

Fixed effects	<i>B</i>	SE <i>B</i>	<i>z</i> (1074)	<i>p</i> two-sided	<i>OR</i>	95% CI
Intercept	-0.61	0.32	-1.89	.058	0.54	[0.29, 1.02]
Weight shift	-0.02	0.01	-1.73	.084	0.98	[0.95, 1.00]
Condition (0 = incongruent, 1 = congruent)	1.91	0.20	9.77	< .001	6.73	[4.59, 9.86]
Weight shift × Condition	0.03	0.01	2.64	.008	1.03	[1.01, 1.06]

Random effects

Intercept variance ( $\tau_{00}$ )	1.11	—	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.00	—	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	0.20	—	—	—	—	—
Level-1 residual ( $\sigma^2$ )	3.29	—	—	—	—	—
ICC	0.33	—	—	—	—	—

Note. *B* = unstandardised regression coefficients, *SE* = standard error, *z*(degrees of freedom), *OR* = Odds Ratio, CI = confidence intervals. ICC = Interclass correlation coefficient. Weight shift is positive in the direction of the prior. Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{marginal}} = .154$ . Multilevel model comparison in Table 15.

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*Table 15. Model comparison for logistic regression of the weight shift in the direction of the prior for predicting correct response probability 100 ms before the serve*

Model	df	AIC	BIC	logLik	Comparison	$\chi^2$	p
1 Intercept	1	1401.346	1406.331	-699.67			
2 Base model	4	1264.726	1284.668	-628.36	1 vs 2	142.620	< .001
3 Base model + RI	5	1146.668	1171.596	-568.33	2 vs 3	120.058	< .001
4 Base model + RS	7	1139.357	1174.257	-562.68	3 vs 4	11.311	.003

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Note. df = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictors weight shift, condition, and weight shift  $\times$  condition.

Table 16. Multilevel logistic regression model of the weight shift in the direction of the prior for predicting correct response probability 200 ms after the serve

Fixed effects	<i>B</i>	SE <i>B</i>	<i>z</i> (1086)	<i>p</i> two-sided	<i>OR</i>	95% CI
Intercept	-0.59	0.33	-1.75	.080	0.56	[0.29, 1.07]
Weight shift	-0.05	0.01	-3.55	< .001	0.95	[0.93, 0.98]
Condition (0 = incongruent, 1 = congruent)	1.77	0.20	8.92	< .001	5.87	[3.98, 8.66]
Weight shift × Condition	0.07	0.01	5.17	< .001	1.07	[1.04, 1.09]

Random effects

Intercept variance ( $\tau_{00}$ )	1.20	—	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.00	—	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	0.02	—	—	—	—	—
Level-1 residual ( $\sigma^2$ )	3.29	—	—	—	—	—
ICC	0.33	—	—	—	—	—

Note. *B* = unstandardised regression coefficients, SE = standard error, *z*(degrees of freedom), *OR* = Odds Ratio, CI = confidence intervals. ICC = Interclass correlation coefficient. Weight shift is positive in the direction of the prior. Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{marginal}} = .190$ . Multilevel model comparison in Table 17.

Table 17. Model comparison for logistic regression of the weight shift in the direction of the prior for predicting correct response probability 200 ms after the serve

Model	<i>df</i>	AIC	BIC	logLik	Comparison	$\chi^2$	<i>p</i>
1 Intercept	1	1417.875	1420.771	-707.94			
2 Base model	4	1267.921	1290.993	-629.96	1 vs 2	155.95	< .001
3 Base model + RI	5	1139.966	1172.613	-564.98	2 vs 3	129.95	< .001
4 Base model + RS	7	1129.159	1171.764	-557.58	3 vs 4	14.81	.001

Note. *df* = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictors weight shift, condition, and weight shift × condition.

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Table 18. Multilevel logistic regression model of the weight shift in the direction of the prior for predicting correct response probability 500 ms after the serve

Fixed effects	<i>B</i>	<i>SE B</i>	<i>z</i> (1055)	<i>p</i> two-sided	<i>OR</i>	95% CI
Intercept	-0.53	0.40	-1.32	.188	0.59	[0.27, 1.29]
Weight shift	-0.15	0.02	-7.36	<.001	0.86	[0.82, 0.89]
Condition (0 = incongruent, 1 = congruent)	1.73	0.27	6.46	<.001	5.65	[3.34, 9.56]
Weight shift × Condition	0.22	0.02	10.09	<.001	1.25	[1.20, 1.30]

Random effects

Intercept variance ( $\tau_{00}$ )	1.55	—	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.00	—	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	0.01	—	—	—	—	—
Level-1 residual ( $\sigma^2$ )	3.29	—	—	—	—	—
ICC	0.42	—	—	—	—	—

831 Note. *B* = unstandardised regression coefficients, *SE* = standard error, *z*(degrees of freedom), *OR* = Odds Ratio, CI =  
832 confidence intervals. ICC = Interclass correlation coefficient. Weight shift is positive in the direction of the prior. Model  
833 statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{marginal}} = .682$ . Multilevel model comparison in Table 19.

834 Table 19. Model comparison for logistic regression of the weight shift in the direction of the prior for predicting correct  
835 response probability 500 ms after the serve

Model	<i>df</i>	AIC	BIC	logLik	Comparison	$\chi^2$	<i>p</i>
1 Intercept	1	1368.695	1549.624	-683.35			
2 Base model	4	946.972	1453.351	-469.49	1 vs 2	427.724	<.001
3 Base model + RI	5	822.651	1280.728	-406.33	2 vs 3	126.321	<.001
4 Base model + RS	7	818.754	1285.899	-402.38	3 vs 4	7.897	.019

836 Note. *df* = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-  
837 likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictors weight shift,  
838 condition, and weight shift × condition.

Table 20. Multilevel logistic regression model of the weight shift in the direction of the prior for predicting hit probability 100 ms before the serve

Fixed effects	<i>B</i>	<i>SE B</i>	<i>z</i> (1062)	<i>p</i> two-sided	<i>OR</i>	95% CI
Intercept	-1.14	0.35	-3.21	.001	0.32	[0.16, 0.64]
Weight shift	-0.03	0.01	-1.76	.079	0.97	[0.95, 1.00]
Condition (0 = incongruent, 1 = congruent)	1.80	0.21	8.62	< .001	6.03	[4.01, 9.07]
Weight shift × Condition	0.05	0.01	3.77	< .001	1.05	[1.02, 1.08]

Random effects

Intercept variance ( $\tau_{00}$ )	1.32	—	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.00	—	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	-0.08	—	—	—	—	—
Level-1 residual ( $\sigma^2$ )	3.29	—	—	—	—	—
ICC	0.36	—	—	—	—	—

840 Note. *B* = unstandardised regression coefficients, *SE* = standard error, *z*(degrees of freedom), *OR* = Odds Ratio, CI =  
841 confidence intervals. ICC = Interclass correlation coefficient. Weight shift is positive in the direction of the prior.  
842 Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{marginal}} = .168$ . Multilevel model comparison in Table 21.

843 Table 21. Model comparison for logistic regression of the weight shift in the direction of the prior for predicting hit probability  
844 100 ms before the serve

Model	<i>df</i>	AIC	BIC	logLik	Comparison	$\chi^2$	<i>p</i>
1 Intercept	1	1475.848	1480.822	-736.92			
2 Base model	4	1363.833	1383.731	-677.92	1 vs 2	118.015	< .001
3 Base model + RI	5	1194.925	1219.798	-592.46	2 vs 3	170.908	< .001
4 Base model + RS	7	1184.875	1219.696	-585.44	3 vs 4	14.051	< .001

845 Note. *df* = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-  
846 likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictors weight shift,  
847 condition, and weight shift × condition.

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Table 22 Multilevel logistic regression model of the weight shift in the direction of the prior for predicting hit probability 200 ms after the serve

Fixed effects	<i>B</i>	SE <i>B</i>	<i>z</i> (1061)	<i>p</i> two-sided	<i>OR</i>	95% CI
Intercept	-1.27	0.36	-3.54	< .001	0.28	[0.14, 0.57]
Weight shift	-0.03	0.01	-2.64	.008	0.97	[0.94, 0.99]
Condition (0 = incongruent, 1 = congruent)	1.89	0.22	8.68	< .001	6.64	[4.33, 10.18]
Weight shift × Condition	0.04	0.01	3.44	.001	1.05	[1.02, 1.07]

Random effects

Intercept variance ( $\tau_{00}$ )	1.31	—	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.00	—	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	0.28	—	—	—	—	—
Level-1 residual ( $\sigma^2$ )	3.29	—	—	—	—	—
ICC	0.34	—	—	—	—	—

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*Note.* *B* = unstandardised regression coefficients, SE = standard error, *z*(degrees of freedom), *OR* = Odds Ratio, CI =  
confidence intervals. ICC = Interclass correlation coefficient. Weight shift is positive in the direction of the prior. Model  
statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{marginal}} = .189$ . Multilevel model comparison in Table 23.

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Table 23. Model comparison for logistic regression of the weight shift in the direction of the prior for predicting hit probability  
200 ms after the serve

Model	<i>df</i>	AIC	BIC	logLik	Comparison	$\chi^2$	<i>p</i>
1 Intercept	1	1479.854	1479.943	-738.93			
2 Base model	4	1369.016	1389.741	-680.51	1 vs 2	116.839	< .001
3 Base model + RI	5	1197.478	1215.237	-593.74	2 vs 3	173.538	< .001
4 Base model + RS	7	1194.064	1220.430	-590.03	3 vs 4	7.414	.025

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*Note.* *df* = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictors weight shift, condition, and weight shift × condition.

Table 24. Multilevel logistic regression model of the weight shift in the direction of the prior for predicting hit probability 500 ms after the serve

Fixed effects	<i>B</i>	<i>SE B</i>	<i>z</i> (1071)	<i>p</i> two-sided	<i>OR</i>	95% CI
Intercept	-1.34	0.49	-2.73	.006	0.26	[0.10, 0.69]
Weight shift	-0.11	0.02	-6.10	< .001	0.89	[0.86, 0.93]
Condition (0 = incongruent, 1 = congruent)	1.84	0.25	7.28	< .001	6.27	[3.83, 10.28]
Weight shift × Condition	0.01	0.02	7.40	< .001	1.14	[1.10, 1.18]

Random effects

Intercept variance ( $\tau_{00}$ )	2.68	—	—	—	—	—
Slope variance ( $\tau_{11}$ )	0.00	—	—	—	—	—
Intercept-slope covariance ( $\rho_{01}$ )	-0.15	—	—	—	—	—
Level-1 residual ( $\sigma^2$ )	3.29	—	—	—	—	—
ICC	0.52	—	—	—	—	—

Note. *B* = unstandardised regression coefficients, *SE* = standard error, *z*(degrees of freedom), *OR* = Odds Ratio, CI = confidence intervals. ICC = Interclass correlation coefficient. Weight shift is positive in the direction of the prior. Model statistics:  $N_{\text{players}} = 14$ ,  $R^2_{\text{marginal}} = .410$ . Multilevel model comparison in Table 25.

Table 25. Model comparison for logistic regression of the weight shift in the direction of the prior for predicting hit probability 500 ms after the serve

Model	<i>df</i>	AIC	BIC	logLik	Comparison	$\chi^2$	<i>p</i>
1 Intercept	1	1483.919	1488.902	-740.96			
2 Base model	4	1296.260	1316.191	-644.13	1 vs 2	193.659	< .001
3 Base model + RI	5	1107.124	1132.038	-548.56	2 vs 3	191.136	< .001
4 Base model + RS	7	1088.760	1123.640	-537.38	3 vs 4	22.364	< .001

Note. *df* = degrees of freedom, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion, logLik = log-likelihood, RI = random intercepts, RS = random intercept and slopes. The base model includes the predictors weight shift, condition, and weight shift × condition.

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