Aus dem Zentrum für Neurologie der Universität Tübingen
Neurologische Klinik und Hertie-Institut für klinische Hirnforschung
Abteilung Kognitive Neurologie
Ärztlicher Direktor: Professor Dr. H.-P. Thier

Plastizität der Wahrnehmung eigener Bewegungen

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Carlo Arthur Magnus Wilke
aus
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Dekan: Professor Dr. I. B. Authenrieth

1. Berichterstatter: Professor Dr. H.-P. Thier

2. Berichterstatter: Professor Dr. C. Braun

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1. Einleitung

1.1. Selbst und fremd verursachte sensorische Afferenzen

Sensorische Afferenz kann ihre Ursache sowohl in externen Ereignissen (*Exafferenz*) als auch in unseren eigenen Bewegungen (*Reafferenz*) haben (von Holst und Mittelstaedt 1950). Jedoch unterscheiden sich Exafferenz und Reafferenz nicht intrinsisch (von Helmholtz 1867): Ein afferentes sensorisches Signal enthält als solches keine Information über die Ursache der Aktivierung der peripheren Sensoren unseres Körpers. Dennoch kann eine derartige Unterscheidung für das Verhalten eines Lebewesens wichtig sein: Wenn wir durch den Wald streifen, so kann das Rascheln des Laubs auf dem Boden von unseren eigenen Schritten stammen oder aber von einer Schlange, der wir besser ausweichen. Bedeutsam ist die Unterscheidung zwischen Exafferenz und Reafferenz auch für unsere visuelle Wahrnehmung: Wenn wir ein Objekt betrachten, dann kann sich eine Verschiebung der retinalen Projektion des Objekts sowohl aus Bewegungen des Objekts in der Welt als auch durch unsere Augenbewegungen ergeben. Um in der Welt ruhende Objekte auch als ruhend wahrzunehmen, ist es also notwendig, diejenigen Projektionsänderungen auf der Netzhaut auszugleichen, welche durch unsere eigenen Bewegungen entstehen (perzeptuelle Raumkonstanz, von Holst und Mittelstaedt 1950). Ohne eine solche aktive Kompensation der visuellen Reafferenz würde ein bewegtes Objekt, dem wir mit dem Blick folgen, fälschlicherweise als ruhend wahrgenommen, während der ortsfeste Hintergrund uns bewegt erscheinen würde.

Um selbst verursachte sensorische Signale auszugleichen, muss das Nervensystem aber in der Lage sein, die eigenen Bewegungen in eine Beziehung zu ihren sensorischen Folgen zu setzen: Eignen würde sich dazu ein internes Signal, das – unter Berücksichtigung der jeweils aktuellen motorischen Pläne und Befehle – die sensorischen Folgen der eigenen Bewegungen gleichsam vorwegnimmt. Schon Descartes (Leisegang 1954), von Graefe (1854) und von

Helmholtz (1867) beschrieben Grundzüge eines derartigen Mechanismus (für eine ausführliche Darstellung: Lindner et al. 2006b). So postulierte von Helmholtz (1867), dass die perzeptuelle Kompensation der visuellen Reafferenz durch eine interne Größe erfolge („Willensanstrengung“), welche die bevorstehende Muskelinnervierung abbilden würde.

Ein explizites Modell für die perzeptuelle Kompensation von Reafferenz durch interne Bezugssignale beschrieben erstmals von Holst und Mittelstaedt (1950) in Form des *Reafferenzprinzips*. Demnach verwende das Nervensystem eine interne Kopie der motorischen Befehle, die so genannte *Efferenzkopie*, um vorherzusagen, welche sensorischen Signale aus einer Bewegung folgen. Indem das Nervensystem die tatsächliche sensorische Afferenz und die vorhergesagte Afferenz vergleiche (Abb. 1), könne es dann auf die Ursache der sensorischen Afferenz zurückschließen (inferentielle Perzeption, Lindner et al. 2006b): Wenn die tatsächliche und die prädizierte Afferenz übereinstimmen, werde die Afferenz den eigenen Bewegungen zugeschrieben. Andernfalls, bei Nicht-Übereinstimmung, werde die Differenz zwischen der tatsächlichen Afferenz und der prädizierten Afferenz als Ergebnis eines externen Ereignisses wahrgenommen. (Jedoch sei bereits hier angemerkt, dass diese Differenz auch als *Prädiktionsfehler* gesehen werden kann, der als Fehlersignal für sensomotorisches Lernen dient, siehe Abschnitt 1.3.).

Experimentelle Belege hat das Reafferenzprinzip insbesondere in Hinblick auf die Kompensation der visuellen Reafferenz bei Augenbewegungen erhalten (von Holst und Mittelstaedt 1950, Sperry 1950). Tatsächlich nutzt das visuelle System efferente Information über die aktuellen Blickbewegungen, um die retinale sensorische Afferenz zu interpretieren (Haarmeier et al. 1997, Haarmeier et al. 2001, Lindner et al. 2006a, Sommer und Wurtz 2006). Auch andere Sinnesmodalitäten scheinen das Reafferenzprinzip zu berücksichtigen: So nutzen schwach elektrische Fische efferente Signale, welche auf motorischen Befehlen beruhen, um selbst verursachte Veränderungen des sie umgebenden elektrischen Felds perzeptuell abzumildern (Bell 1981). Das Reafferenzprinzip kann somit als allgemeine Herangehensweise an die Wahrnehmung eigener Bewegungen sowie die Unterscheidung von Exafferenz und Reafferenz verstanden werden (von Holst und Mittelstaedt 1950, Frith 1992, Crapse und Sommer 2008, Sommer und Wurtz 2008, Nelson et al. 2013).

Jedoch beantwortet das Reafferenzprinzip nach von Holst und Mittelstaedt (1950) nicht die Frage, auf welche Weise die motorischen Befehle in Beziehung zur Reafferenz gebracht werden. Laut von Holst (1954) ist eine Efferenzkopie nicht als bloße Kopie der motorischen Befehle zu verstehen, die unmittelbar mit der sensorischen Afferenz verglichen werden könnte. Vielmehr entspreche eine Efferenzkopie der prädizierten Reafferenz wie eine Fotografie ihrem Negativ (von Holst 1954, Seite 91). Wie durch diese Analogie deutlich wird, erfordert das Reafferenzprinzip eine Transformation des internen Bewegungssignals aus dem motorischen Kontext in den sensorischen Kontext, um die tatsächlichen sensorischen Bewegungsfolgen mit den erwarteten abgleichen und verrechnen zu können (Lindner 2004, Seite 17). Diese Transformation versuchen interne *Vorwärtsmodelle* des sensomotorischen Systems zu spezifizieren (Abschnitt 1.2. und Abb. 1).

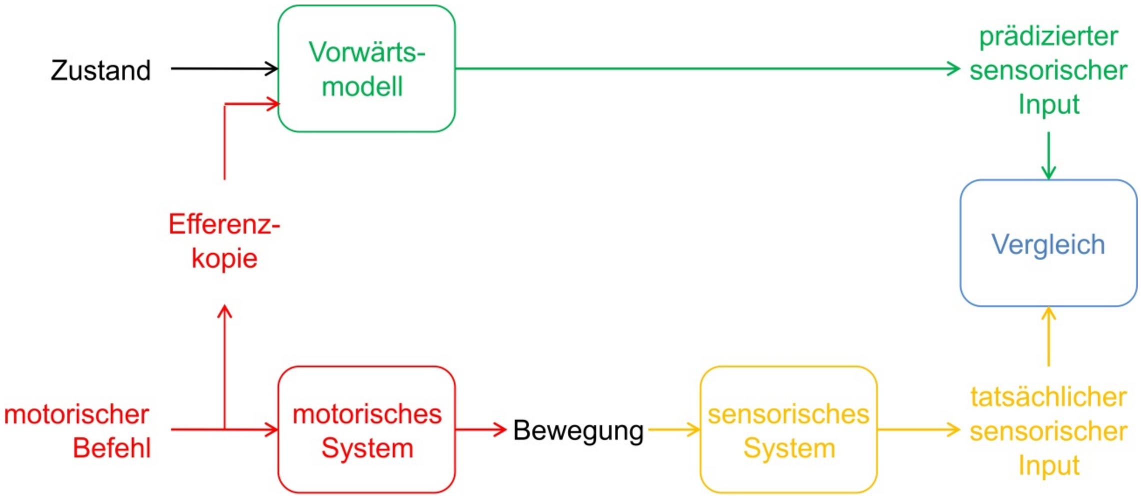

Abb. 1. Unterscheidung selbst und extern verursachter sensorischer Afferenz.

Sensorische Afferenz kann sowohl aus externen Ereignissen (Exafferenz) als auch aus unseren eigenen Bewegungen (Reafferenz) resultieren. Gemäß dem Reafferenzprinzip (von Holst und Mittelstaedt 1950) stellt das Nervensystem die Ursache der sensorischen Afferenz fest, indem es den tatsächlichen sensorischen Input mit dem prädizierten sensorischen Input vergleicht. Dazu prädiziert das sensomotorische System den sensorischen Input, der aus den eigenen Bewegungen resultieren wird, auf der Grundlage interner bewegungsbezogener Information, wie zum Beispiel einer Efferenzkopie des motorischen Befehls. Diese Prädiktion wird durch ein Vorwärtsmodell (Wolpert et al. 1995) berechnet, das zusätzlich den gegenwärtigen Zustand des motorischen Systems und des sensorischen Systems berücksichtigt. Das Nervensystem trifft dann einen Vergleich des tatsächlichen sensorischen Inputs mit dem prädizierten sensorischen Input. Im Fall einer Übereinstimmung sollte die sensorische Afferenz als intern verursacht gedeutet werden. Andernfalls, also bei Nicht-Übereinstimmung, sollte die Differenz zwischen dem tatsächlichen und dem prädizierten sensorischen Input als extern verursacht gedeutet werden. Wie Abb. 3 zeigt, kann diese Differenz zwischen den tatsächlichen und den intern prädizierten sensorischen Bewegungsfolgen auch als Prädiktionsfehler (Shadmehr et al. 2010) für sensomotorisches Lernen verstanden werden. Angepasste Abbildung (Wolpert und Miall 1996, Wilke et al. 2013).

1.2. Interne Prädiktionen der sensorischen Bewegungsfolgen

Für die Wahrnehmung der eigenen Bewegungen ist es notwendig, dass ein sensomotorisches System die Beziehung zwischen seinen motorischen Befehlen (oder Plänen) und den sensorischen Eigenschaften der Bewegungen repräsentieren kann. Eine solche Repräsentation kann durch *interne Modelle* beschrieben werden (Wolpert et al. 1995, Wolpert und Miall 1996, Wolpert und Kawato 1998, Wolpert et al. 1998, Ito 2000). Interne Modelle erfassen die Ursache-Wirkungs-Beziehung zwischen motorischen Efferenzen und sensorischen Reafferenzen (Wolpert und Ghahramani 2000, Wolpert und Flanagan 2001). Die Modelle werden anhand ihrer Input- und Outputvariablen in Vorwärtsmodelle und inverse Modelle unterschieden:

Vorwärtsmodelle (*forward models*, *predictors*, Abb. 1) verwenden motorische Befehle bzw. Handlungspläne als Input, um als Output die sensorischen Bewegungsfolgen vorherzusagen (Wolpert et al. 1995, Wolpert und Ghahramani 2000). Dabei berücksichtigen Vorwärtsmodelle den aktuellen Zustand des motorischen und des sensorischen Systems. Die Modelle beachten also die Tatsache, dass ein und dasselbe motorische Kommando in verschiedenen Situationen verschiedene sensorische Folgen haben kann. Zum Beispiel würde ein visuelles Vorwärtsmodell für Handbewegungen interne bewegungsbezogene Information über eine Handbewegung nutzen, um das visuelle Feedback der Bewegung zu prädizieren. Als interne bewegungsbezogene Information kommen Efferenzkopien (von Holst und Mittelstaedt 1950) oder *corollary discharge* von motorischen Befehlen in Frage (Sperry 1950). Den zu berücksichtigenden Zustand des motorischen Systems würde dabei u. a. die aktuelle Handstellung darstellen. Bedeutung haben Vorwärtsmodelle und die von ihnen ausgegebenen *sensorischen Prädiktionen* sowohl für die Wahrnehmung der eigenen Bewegungen als auch für deren motorische Kontrolle (Synofzik et al. 2006).

Inverse Modelle (*controller*) verwenden den erwünschten Zielzustand des motorischen Systems und den gegenwärtigen Körperzustand (Input), um daraus den motorischen Befehl zu berechnen (Output), durch welchen der angestrebte Zielzustand zu erreichen ist (Wolpert und Ghahramani 2000). Beispielsweise kann ein inverses Modell der Hand ein vorgegebenes (visuelles) Ziel in einen motorischen Plan umwandeln, durch den die Hand auf das Ziel geführt wird. Inverse Modelle sind wichtig für motorische Steuerung und Regelung. Auch werden inverse Modelle dazu herangezogen, um optimale Bewegungen zu erklären: Inverse Modelle wählen aus der Menge der möglichen Bewegungen, durch die ein vorgegebener Zustand erlangt werden kann, die für die aktuelle Situation optimale Bewegung aus (anhand eines Optimalitätskriteriums, beispielsweise nach dem Prinzip der Kostenkontrolle, Wolpert und Ghahramani 2000).

Beide Modelle spielen also eine wichtige Rolle bei der motorischen Planung und Kontrolle. Effektive Bewegungen erfordern, dass die notwendige Information über Körperposition und -bewegung dem Nervensystem schnell, akkurat und zuverlässig verfügbar ist. Sensorische Afferenz kann diese Anforderungen jedoch nur mit Einschränkungen erfüllen: Sensorisches Feedback unterliegt zeitlichen Verzögerungen (u. a. durch Reiztransduktion, Signalfortleitung und zentralnervöse Interpretation), kann externe Störeinflüsse erfahren (Abschnitt 1.1.) und ist nicht immer in vollem Umfang vorhanden (z. B. geringere visuelle Sehschärfe bei Nacht). Hier wird der biologische Nutzen der Vorwärtsmodelle deutlich (Synofzik 2008): Die sensorischen Prädiktionen, welche durch Vorwärtsmodelle ausgegeben werden, unterliegen keinen wesentlichen zeitlichen Verzögerungen, sind als solche frei von externen Störeinflüssen und bei aktiven Bewegungen stets vorhanden. Interne Prädiktionen über die sensorischen Konsequenzen der eigenen Bewegungen stellen damit wertvolle Signale für die motorische Kontrolle dar, insbesondere bei ballistischen Bewegungen, wie Sakkaden.

So können die sensorischen Prädiktionen der Vorwärtsmodelle (zusammen mit sensorischem Feedback) die inversen Modelle über den gegenwärtigen Körperzustand informieren, damit diese dann Bewegungsziele in motorische Befehle umrechnen können (Wolpert und Kawato 1998). Die Vorwärtsmodelle erlauben zudem eine Prädiktion der sensorischen Folgen der eigenen Bewegungen vor deren Ausführung (Flanagan et al. 2003). Damit wird eine Kontrolle der motorischen Befehle möglich, noch bevor sensorisches Feedback vorhanden ist oder sogar ohne eines sensorischen Feedbacks über die Konsequenzen der motorischen Befehle zu bedürfen. Für motorische Kontrolle können sensorische Prädiktionen also gleichsam als internes Feedback dienen bzw. dieses (teilweise oder vollständig) substituieren (Jordan und Rumelhart 1992, Wolpert und Flanagan 2001, Ariff et al. 2002).

Über den Bereich der Motorik hinaus könnten die sensorischen Prädiktionen der Vorwärtsmodelle als interne *Referenzsignale* für perzeptuelle Leistungen dienen: Um Exafferenz und Reafferenz zu unterscheiden, muss das Nervensystem die eigenen Bewegungen in Beziehung zu ihren sensorischen Folgen setzen können. Diese Anforderung erfüllen die internen sensorischen Prädiktionen der Vorwärtsmodelle: Interne Vorwärtsmodelle leisten diejenige Transformation eines internen Bewegungssignals aus dem motorischen Kontext in den sensorischen Kontext, welche durch das Reafferenzprinzip gefordert wird (Abschnitt 1.1.). Sensorische Prädiktionen würden sich insofern als interne Referenzsignale für die Wahrnehmung der eigenen Bewegungen und für die Unterscheidung zwischen Exafferenz und Reafferenz eignen.

Tatsächlich fließen interne sensorische Prädiktionen über unsere eigenen Bewegungen in unsere Wahrnehmung ein (Haarmeier et al. 2001, Synofzik et al. 2006, Voss et al. 2006). Insbesondere werden Exafferenz und Reafferenz verschieden wahrgenommen – und zwar gerade dann, wenn ihre afferente Information identisch ist (Abb. 2). Beispielsweise nehmen wir fremde und eigene Berührungen unserer Haut selbst dann unterschiedlich stark wahr, wenn sich ihre taktilen Eigenschaften und damit ihre afferenten Informationen nicht unterscheiden (Shergill et al. 2003). Insbesondere empfinden wir einen selbst aktiv verursachten Druck auf unsere Fingerkuppe gegenüber einem physikalisch gleich starken, jedoch passiv erfahrenen Druck als schwächer. Diese perzeptuelle Abschwächung der Reafferenz gegenüber einer identischen Exafferenz ist dadurch erklärbar, dass das aktive Erzeugen von Druck mit einer sensorischen Prädiktion des Drucks auf die Fingerkuppe verbunden ist, die mit der tatsächlich erfahrenen Afferenz verrechnet wird. Eine solche Prädiktion fehlt dagegen für extern verursachten Druck auf die Fingerkuppe (Abb. 2). Auch erklären sensorische Prädiktionen, weshalb sich Menschen nicht selbst kitzeln können (Weiskrantz et al. 1971, Blakemore et al. 1998): Unsere eigenen Bewegungen sind mit sensorischen Prädiktionen verbunden, welche die durch den Versuch des Kitzelns hervorgerufene Reafferenz sensorisch auslöschen (*cancellation*) oder stark abmildern (*attenuation*, Voss et al. 2006). Der Versuch, sich selbst zu kitzeln, ist erst dann erfolgreich, wenn die eigene Bewegung und die daraus entstehende taktile Reizung zeitlich oder räumlich dissoziiert werden (Blakemore et al. 1999, Wolpert und Flanagan 2001).

Angesichts der Tatsache, dass wir Exafferenz und Reafferenz verschieden wahrnehmen, könnten sensorische Prädiktionen über die eigenen Bewegungen auch diejenigen internen Referenzsignale sein, welche uns das Erleben vermitteln, unsere Handlungen zu verursachen und zu kontrollieren (Georgieff und Jeannerod 1998, Gallagher 2000, de Vignemont und Fourneret 2004). Dieses Erleben, das Gefühl der Urheberschaft (*feeling of agency*, allgemeiner auch: *sense of agency*), kann als eine grundlegende Form der Unterscheidung zwischen Selbst und Nicht-Selbst verstanden werden (für eine ausführliche Darstellung: Synofzik et al. 2008b), für die jedoch kein explizites Konzept eines Selbst notwendig ist. Eine Erklärung des Gefühls der Urheberschaft bietet das *Komparatormodell* nach Frith (1992), indem es das Gefühl der Urheberschaft aus eben jenem Rechenmechanismus ableitet, den das Reafferenzprinzip als Grundlage der perzeptuellen Kompensation von Reafferenz postuliert.

Demnach entstehe das Gefühl der Urheberschaft für ein Ereignis aufgrund eines Vergleichs (Abb. 1) der tatsächlichen sensorischen Afferenz mit den vorhergesagten sensorischen Folgen der eigenen Bewegungen. Bei Übereinstimmung erfolge eine Selbstzuschreibung der Afferenz (bzw. des durch die Afferenz vermittelten Ereignisses). Andernfalls, wenn sich tatsächliche und prädizierte Afferenz unterscheiden, werde die Afferenz nicht der eigenen Urheberschaft zugeschrieben. Im Rahmen des Komparatormodells sind die sensorischen Prädiktionen, welche die Vorwärtsmodelle ausgeben, also interne Referenzsignale für die kausale Attribution der sensorischen Afferenz. Folglich können interne Vorwärtsmodelle als implizite Selbstrepräsentation gedeutet werden.

Jedoch ist das Erleben, die eigenen Handlungen zu verursachen und zu kontrollieren, nicht selbstverständlich. Störungen des Gefühls der Urheberschaft finden sich u. a. bei psychotischen Erkrankungen, zum Beispiel in Form von Ich-Störungen bei Schizophrenie. Die Betroffenen erleben dabei ihre eigenen Handlungen nicht als selbst verursacht, sondern als extern kontrolliert. Solche Symptome könnten sich durch Störungen der internen Referenzsignale oder Störungen ihres Vergleichs mit den tatsächlichen sensorischen Bewegungsfolgen erklären lassen (Feinberg 1978, Frith 1992, Frith et al. 2000b). Wenn nämlich die internen Referenzsignale über die eigenen Handlungen unpräzise sind, dann ist nach dem Komparatormodell zu erwarten, dass die perzeptuelle Trennung zwischen selbst und fremd verursachten Ereignissen weniger zuverlässig erfolgen wird. Tatsächlich zeigen Experimente, dass die gestörte Wahrnehmung der eigenen Handlungen bei Schizophrenie-Kranken mit unpräzisen Prädiktionen der sensorischen Konsequenzen der eigenen Bewegungen verbunden ist (Lindner et al. 2005, Shergill et al. 2005, Synofzik et al. 2010, Voss et al. 2010).

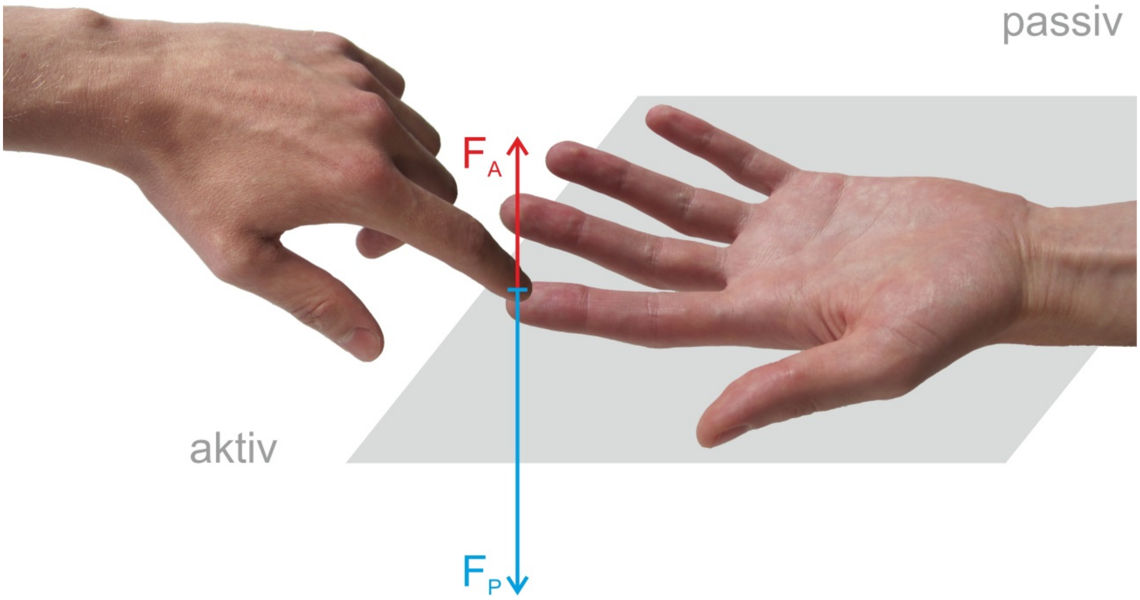

Abb. 2. Perzeptuelle Attenuierung selbst generierter sensorischer Afferenz.

Selbst generierte Kräfte werden als schwächer wahrgenommen als extern generierte Kräfte des gleichen Betrags (Shergill et al. 2003). Wenn eine Person mit ihrer Fingerspitze aktiv auf die Fingerspitze einer anderen drückt, dann sind die Kräfte, welche physikalisch auf die peripheren Drucksensoren der beiden Personen einwirken, identisch (Actio-et-Reactio-Prinzip, Newton 1687). Die taktilen Afferenzen vermitteln also den gleichen Druck. Trotzdem wird die aktiv generierte Kraft (F_A) als rund die Hälfte der passiv erfahrenen Kraft (F_P) wahrgenommen. Diese Beobachtung deutet auf einen zentralen Mechanismus, durch den die sensorischen Folgen der eigenen Bewegungen vorweggenommen und perzeptuell attenuiert werden.

1.3. Aktualisierung der internen Prädiktionen

Wie die Störungen der Selbstwahrnehmung bei schizophrenen Patienten verdeutlichen, benötigen wir für die Wahrnehmung unserer eigenen Bewegungen akkurate interne Referenzsignale. Jedoch ändern sich die Eigenschaften des motorischen Systems ständig: Wachstum, Ermüdung und Erkrankung ändern die Beziehung zwischen unseren motorischen Befehlen und den verursachten Bewegungen (Abb. 3). Folglich wird ein und derselbe motorische Befehl verschiedene sensorische Folgen haben – welche jedoch stets unserer eigenen Bewegung zugeordnet werden sollten und nicht externen Ereignissen (Synofzik et al. 2006). Darum muss die Prädiktion der sensorischen Folgen der eigenen Bewegungen plastisch erfolgen.

Die veränderlichen Eigenschaften des motorischen Systems (Abb. 3) erfordern insbesondere eine Anpassung der internen Vorwärtsmodelle, damit stets akkurate Prädiktionen über die sensorischen Folgen der eigenen Bewegungen ausgegeben werden (Haarmeier et al. 2001, Flanagan et al. 2003, Synofzik et al. 2006, Cameron et al. 2012). Eine wesentliche Information für diese Anpassung sind sensorische *Prädiktionsfehler* (Shadmehr et al. 2010): Wenn sich die Beziehung zwischen einem Motorkommando und dessen sensorischen Folgen ändert, wird eine Differenz zwischen der tatsächlichen und der prädizierten Reafferenz entstehen, welche einen Prädiktionsfehler darstellt. Diese Differenz ist, wenn ihre Ursache innerhalb des sensomotorischen Systems liegt, durch Anpassung des Vorwärtsmodells zu korrigieren (Abb. 3). Denn ohne eine solche Anpassung würden die allfälligen Veränderungen des motorischen Systems zu einer fehlerhaften Wahrnehmung führen: Reafferenzen würden unsere Wahrnehmung der Welt verzerren und sensorisches Feedback könnte nicht mehr den eigenen Bewegungen zugeschrieben werden.

Jedoch entstehen Prädiktionsfehler nicht nur aus *internen* Ursachen, sondern auch aus *externen* Ursachen: Nach dem Reafferenzprinzip bewirken externe Ereignisse eine Differenz zwischen der tatsächlichen Afferenz und der prädizierten Afferenz (Abschnitt 1.1.). Eine derartige extern verursachte Differenz sollte das Nervensystem aber nicht durch Anpassung eines internen Vorwärtsmodells korrigieren, sondern externen Ursachen zuschreiben. Andernfalls würde auch hier eine fehlerhafte Wahrnehmung von Selbst und Welt entstehen. Zusammenfassend sollte die Anpassung der internen Referenzsignale, welche der Wahrnehmung der eigenen Bewegungen zu Grunde liegen, also die *Ursache* eines Prädiktionsfehlers berücksichtigen (Abb. 3).

Das fundamentale Problem der plastischen Wahrnehmung der eigenen Bewegungen ist nun, dass sich intern und extern verursachte Prädiktionsfehler nicht als solche unterscheiden.

Dieses Problem, Fehlerinformation kausal zuzuschreiben, ist ein allgemeines Problem des *sensomotorischen Lernens*. Verschiedene Studien legen nahe (Franck et al. 2001, Farrer et al. 2003, Wei und Körding 2009, Marko et al. 2012), dass unser sensomotorisches System kausale Annahmen über Fehlersignale vornehmen würde, welche in Adaptationsvorgänge einfließen. So sollte auch motorische Adaptation berücksichtigen, ob ein Fehler internen Veränderungen unseres Körpers oder aber externen Störeinflüssen zugeschrieben wird (Wei und Körding 2009): Ein Fußballspieler sollte seine Schusstechnik genau dann anpassen, wenn er den Misserfolg seines Torschusses der eigenen Schusstechnik zuschreibt (Abb. 4). Das Prinzip, Fehlerinformation in Abhängigkeit der Ursachenzuschreibung für das sensomotorische Lernen zu nutzen (Abb. 3), mag insofern plausibel sein (Körding und Wolpert 2004, Berniker und Körding 2008). Jedoch fehlen Experimente, welche die *kausale Attribution* eines Fehlersignals messen und diese Attribution in Bezug zum Lernen setzen.

Ein erstes Experiment wird deshalb die Hypothese testen, dass die Aktualisierung der Wahrnehmung der eigenen Bewegungen von der kausalen Attribution sensorischer Prädiktionsfehler an interne Ursachen abhängig ist (Abb. 3). Das Experiment soll dazu die kausale Attribution sensorischer Prädiktionsfehler an interne versus externe Ursachen messen und anhand dieser gemessenen Fehlerattribution die Aktualisierung der Wahrnehmung der eigenen Bewegungen charakterisieren (Abschnitt 3.1.).

Welche Faktoren aber bestimmen die kausale Attribution sensorischer Prädiktionsfehler, wenn sich intern und extern verursachte Prädiktionsfehler nicht als solche unterscheiden? Die alltäglichen Kontexte unserer Bewegungen bieten zahlreiche Informationen, welche Rückschlüsse auf die eigenen Bewegungen erlauben (Synofzik et al. 2008b). So zeigt ein einfaches Beispiel, dass die Ergebnisse unserer Bewegungen (*action outcomes, Handlungsergebnisse*) einen Einfluss auf unsere eigene Bewegungswahrnehmung haben könnten: Wenn ein Fußball unerwartet so abgefälscht wird, dass der Ball ins Tor fliegt, dann mag sich ein Fußballspieler das Ergebnis selbst zuschreiben – auch wenn sein tatsächlicher Schuss das Tor deutlich verfehlt hätte. Gemäß dem Phänomen der *selbstwertdienlichen Verzerrung* (*self-serving bias*) neigen Individuen dazu, Erfolg an interne Ursachen und Misserfolg an externe Ursachen zu attribuieren (Johnson et al. 1964, Beckman 1970, Wolosin et al. 1973, Miller und Ross 1975, Tetlock und Levi 1982). Der Fußballspieler könnte sich den Treffer also deshalb selbst zuschreiben, weil er gern den Treffer als Folge der eigenen Bewegung sehen würde – auch wenn die tatsächlichen und die prädizierten sensorischen Bewegungsfolgen nicht übereinstimmen (Wegner und Sparrow 2004, Johansson et al. 2005, Synofzik et al. 2008b).

Ausgehend von diesen Überlegungen ist zu erwarten, dass Handlungsergebnisse die kausale Attribution sensorischer Prädiktionsfehler an interne versus externe Ursachen ändern können. Insbesondere ist zu erwarten, dass sensorische Prädiktionsfehler, die mit *positiven* Handlungsergebnissen verbunden sind, eher an interne Ursachen attribuiert werden als solche Prädiktionsfehler, welche mit *negativen* Handlungsergebnissen verbunden sind. Diese spezifische Hypothese wird ein zweites Experiment testen (Abschnitt 3.2.). Weitere Einflussfaktoren auf die kausale Attribution sensorischer Prädiktionsfehler werden diskutiert (Abschnitt 4.5.).

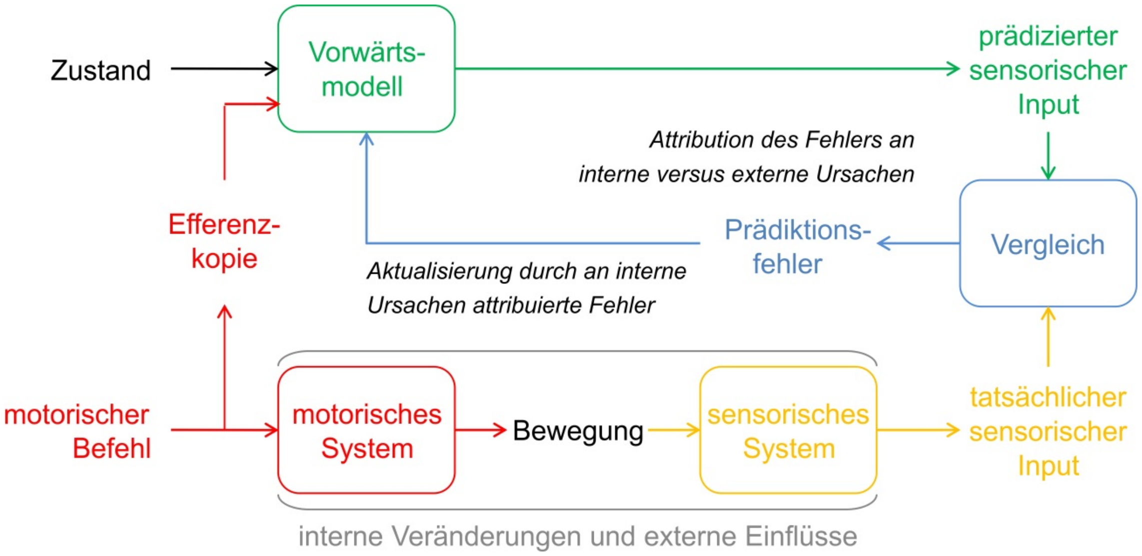

Abb. 3. Aktualisierung interner sensorischer Prädiktionen durch Prädiktionsfehler.

Wie in Abb. 1 beschrieben, stellt das Nervensystem die Ursache der sensorischen Afferenz fest, indem es den tatsächlichen sensorischen Input mit dem prädizierten sensorischen Input vergleicht. Gemäß dem Reafferenzprinzip soll die Differenz zwischen dem tatsächlichen und dem prädizierten sensorischen Input als extern verursacht gedeutet werden. Jedoch können derartige Differenzen – welche Prädiktionsfehler darstellen – auch aus internen Veränderungen resultieren, nämlich aus Veränderungen innerhalb des sensomotorischen Systems, wie Wachstum, Ermüdung oder Erkrankung. Deshalb benötigen interne sensorische Prädiktionen eine kontinuierliche Aktualisierung. Wie frühere Forschungsarbeiten nahelegen, sollte diese Aktualisierung nur diejenigen Prädiktionsfehler kompensieren, welche aus internen Ursachen resultieren. Jedoch unterscheiden sich intern und extern verursachte Prädiktionsfehler nicht als solche. In Hinblick auf dieses Problem zeigt die vorliegende Dissertation, dass die Aktualisierung der internen sensorischen Prädiktionen durch Prädiktionsfehler auf der Attribution des Prädiktionsfehlers an interne Ursachen beruht. Angepasste Abbildung (Wolpert und Miall 1996, Wilke et al. 2013).

Er lernt‘s nie

Abb. 4. Fehlersignal, kausale Fehlerattribution und sensomotorisches Lernen.

Ein Junge hat seinen Fußball nicht, wie beabsichtigt und intern vorhergesagt, in das Tor geschossen, sondern mit dem Ball eine Fensterscheibe getroffen, die dadurch zu Bruch gegangen ist. Jedoch leugnet der Junge, den Ball dorthin geschossen zu haben und die Ursache des Schadens zu sein. Wenn ein Prädiktionsfehler aber nicht dem eigenen sensomotorischen System ursächlich zugeschrieben wird, dann sollte – so die stark vereinfachte Hypothese – der Fehler auch nicht zu adaptiven Veränderungen des eigenen Systems führen. Zu den Faktoren, welche die Zuschreibung des Fehlers an interne versus externe Ursachen bestimmen, könnten das Ergebnis einer Bewegung und seine affektive Verarbeitung gehören, wie hier das Erschrecken über den verursachten Schaden. (Die Abbildung wurde wegen ihrer Anschaulichkeit gewählt. Die vorliegende Dissertation untersucht primär nicht die motorische Kontrolle der eigenen Bewegungen, sondern unsere Wahrnehmung der eigenen Bewegungen. Die spezifischen Fragestellungen ergeben sich insbesondere aus der Überlegung, dass interne Prädiktionen über die eigenen Bewegungen der Unterscheidung von Exafferenz und Reafferenz als Grundlage dienen und eine Aktualisierung der internen Prädiktionen diese Unterscheidung nicht verzerren darf, vergleiche Abschnitt 1.3.). Die Reproduktion der Abbildung erfolgte mit der freundlichen Genehmigung von Wolfgang Neumann (Copyright: VG Bild-Kunst, Bonn, 2012).

1.4. Fragestellung

Auf der Grundlage des dargelegten Wissensstands untersucht die vorliegende Dissertation die Wahrnehmung der eigenen Handbewegungen in Hinblick auf ihre Plastizität.

A. Ein erstes Experiment soll die Hypothese testen, dass die Aktualisierung der Wahrnehmung der eigenen Bewegungen auf der kausalen Attribution sensorischer Prädiktionsfehler an interne Ursachen beruht. Dazu wird das Experiment die kausale Attribution sensorischer Prädiktionsfehler messen (im Sinne einer Attribution an interne versus externe Ursachen) und die Aktualisierung der internen Prädiktionen über die sensorischen Konsequenzen der eigenen Bewegungen anhand der gemessenen Fehlerattribution charakterisieren (Abschnitt 3.1.).

B. Ein zweites Experiment soll untersuchen, ob Handlungsergebnisse die kausale Attribution sensorischer Prädiktionsfehler an interne versus externe Ursachen modulieren. Insbesondere soll das Experiment die Hypothese testen, dass diejenigen sensorischen Prädiktionsfehler, die mit positiven Handlungsergebnissen verbunden sind, eher an interne Ursachen attribuiert werden als solche Prädiktionsfehler, welche mit negativen Handlungsergebnissen verbunden sind (Abschnitt 3.2.).

2. Methoden

Ziel dieses Kapitels ist es, die Operationalisierung der wesentlichen Konzepte dieser Dissertation darzustellen. Beschrieben werden hier die untersuchten Handbewegungen, die Generierung der sensorischen Prädiktionsfehler und die Quantifizierung der Wahrnehmung dieser Prädiktionsfehler. Beschrieben wird auch, wie das Konzept der internen Prädiktionen über sensorische Bewegungskonsequenzen (interne sensorische Prädiktionen) und die Quantifizierung der Aktualisierung dieser Prädiktionen experimentell verwirklicht wurden. Die Reproduzierbarkeit der Versuche gewährleisten die Methodenabschnitte der Originalmanuskripte (Abschnitte 3.1.2. und 3.2.2.)

Wir testeten die Hypothesen (Abschnitt 1.4.) mittels einer *virtuellen Umgebung* (Abb. 5), in der die Probanden mit ihrem rechten Zeigefinger horizontale *Zeigebewegungen* ausführten. Um die visuellen Konsequenzen der Bewegungen in Echtzeit manipulieren zu können, maßen wir kontinuierlich die Position der Fingerspitze und präsentierten diese Position den Probanden über eine Bildschirm-Spiegel-Anordnung als *visuelles Feedback* (Synofzik et al. 2006). Dabei erschien das Feedback in derselben horizontalen Ebene, in der die Probanden ihre Bewegungen ausführten. Die Fingerposition wurde mit einem auf Ultraschall basierenden Motion-Tracking-System gemessen (Zebris CMS 70 P, Isny im Allgäu, Sampling- und Feedback-Rate des Gesamtsystems: 60 Hz). Für die Zeigebewegungen erhielten die Probanden keine externen Ziele vorgegeben, sondern wurden instruiert, selbst verschiedene *motorische Zeigerichtungen* innerhalb eines definierten Bereichs zu wählen (oberes rechtes Kreisviertel in Abschnitt 3.1.2. bzw. obere Kreishälfte in 3.2.2.). Nur die Zeigeamplitude wurde durch eine Kreislinie vorgegeben, deren Mittelpunkt taktil in der Bewegungsebene markiert war und dem Start- und Endpunkt der Bewegungen entsprach. Wir instruierten die Probanden, ihre Bewegungen so schnell und so geradlinig wie möglich auszuführen und mit dem Zeigefinger nach der Auswärtsbewegung sogleich wieder auf den Startpunkt zurückzukehren.

Um visuelle Prädiktionsfehler zu generieren, verwendeten wir *Feedback-Durchgänge* (Abb. 6A). Hier erhielten die Probanden visuelles Feedback über ihre Bewegungen in Echtzeit. Dieses Feedback wurde entweder wahrheitsgetreu präsentiert (also in Übereinstimmung mit der tatsächlichen Bewegung) oder alternativ um den Startpunkt der Bewegungen rotiert. Für die einzelnen Durchgänge wurden die Rotationswinkel zufällig gewählt. Über alle Durchgänge hinweg war die Verteilung des Feedbacks jedoch symmetrisch zur tatsächlichen Zeigebewegung. Aufgrund dieser symmetrischen Verteilung der Feedback-Manipulation nahmen wir an, dass die internen Prädiktionen der Probanden über die visuellen Konsequenzen ihrer Zeigebewegungen im Mittel der tatsächlich durchgeführten Bewegung entsprachen. Daher sollte jegliches manipuliertes Feedback von der intern prädizierten visuellen Bewegungsrichtung abweichen. Deshalb interpretierten wir die Feedback-Manipulationen als visuelle Prädiktionsfehler (Abschnitt 3.1.2.).

Um die Wahrnehmung der visuellen Prädiktionsfehler durch die Probanden zu quantifizieren, instruierten wir diese, nach jeder Bewegung ihre tatsächliche Zeigerichtung visuell zu schätzen. Hierzu rotierten die Probanden nach jeder Bewegung einen Trackball-gesteuerten Cursor mit der linken Hand in diese Richtung (ähnlich einem Uhrzeiger, Abb. 6A). Angemerkt sei, dass die Probanden ihre Bewegung nicht reproduzierten. Stattdessen wurde die Rotation des Trackballs in eine zirkuläre Bewegung des Cursors um den Startpunkt umgesetzt. Die so *geschätzte Zeigerichtung* ergab – relativ zur tatsächlichen motorischen Zeigerichtung – ein Maß für die Bewegungswahrnehmung der Probanden. Insbesondere ließ sich so diejenige Komponente der Feedback-Manipulation bzw. des Prädiktionsfehlers abschätzen, welche die Probanden kausal an interne Ursachen attribuierten (Abschnitte 3.1.2. und 4.1. für eine ausführliche Darstellung). Der in Abschnitt 3.2.2. beschriebene Versuch verwendete anstelle der hier beschriebenen analogen Messung der geschätzten Zeigerichtung eine two-alternative forced-choice Abfrage, aus welcher auf die wahrgenommene Zeigerichtung zurückgeschlossen werden kann.

In den Feedback-Durchgängen flossen in die geschätzte Zeigerichtung der Probanden sowohl visuelle Informationen als auch interne bewegungsbezogene Informationen ein. Um diese internen Informationen experimentell zu isolieren, verwendeten wir *Wahrnehmungstest-Durchgänge* (Abb. 6B). Hier erhielten die Probanden keinerlei visuelles (oder anderweitiges externes) Feedback über ihre Zeigebewegungen. Deshalb und da kein externes visuelles Ziel für die Bewegungen vorgegeben war, musste die Schätzung der Zeigerichtung in den Wahrnehmungstest-Durchgängen vollständig auf internen Signalen beruhen, welche die tatsächliche Bewegung abbilden, wie beispielsweise Efferenzkopien motorischer Befehle (für eine ausführlichere Diskussion, siehe Abschnitt 4.2.). Daher nahmen wir an, dass die visuell geschätzte Zeigerichtung in den Wahrnehmungstest-Durchgängen eine Prädiktion der visuellen Bewegungskonsequenzen erfassen würde, die ausschließlich auf internen Informationen beruht, also eine interne sensorische Prädiktion (Synofzik et al. 2006).

Wir erwarteten, dass die internen sensorischen Prädiktionen der Probanden durch die Prädiktionsfehler eine Aktualisierung erfahren würden. Um die Aktualisierung der internen sensorischen Prädiktionen durch *einzelne* Prädiktionsfehler zu untersuchen, präsentierten wir den Probanden abwechselnd Feedback-Durchgänge und Wahrnehmungstest-Durchgänge. Das Ziel war es dabei, (1) visuelle Prädiktionsfehler zu generieren und deren kausale Attribution an interne versus externe Ursachen zu quantifizieren (Feedback-Durchgänge, Abb. 6A) und (2) anhand dieser kausalen Attribution der Prädiktionsfehler die Aktualisierung der internen Prädiktionen zu charakterisieren (Wahrnehmungstest-Durchgänge, Abb. 6B).

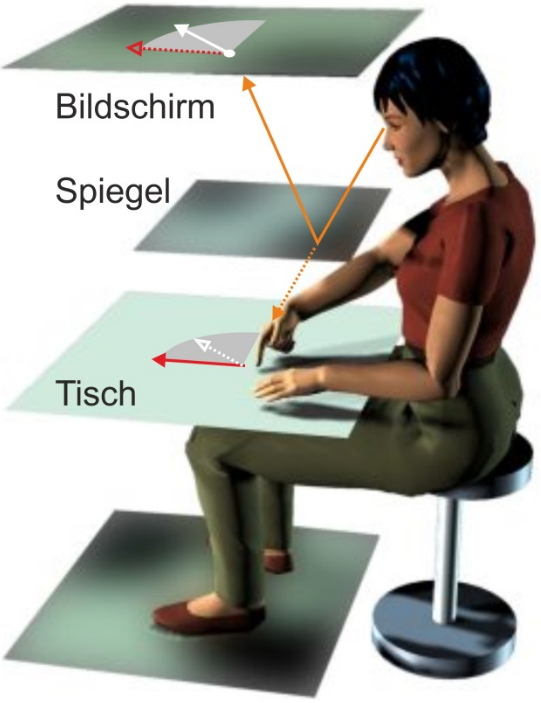

Abb. 5. Experimentelles Setup.

Die Probanden führten mit ihrem rechten Zeigefinger horizontale Zeigebewegungen aus. Dabei sahen sie über einen Spiegel (oranger Pfeil) ein virtuelles Abbild ihres Fingers auf dem Feedback-Bildschirm. Aufgrund der Geometrie der Anordnung erschien dieses virtuelle Abbild in der Ebene der horizontalen Zeigebewegungen. Das visuelle Feedback über die Zeigebewegungen wurde entweder wahrheitsgetreu präsentiert (also in Übereinstimmung mit der tatsächlichen Bewegung) oder alternativ (wie in diesem Beispiel) durch Rotation um den Startpunkt der Bewegungen manipuliert (roter Pfeil: tatsächliche Bewegung, weißer Pfeil: rotiertes visuelles Bewegungsfeedback, gepunktete Pfeile entsprechen den Projektionen dieser Bewegungsvektoren in die Ebene des Bildschirms bzw. der Zeigebewegungen). Angepasste Abbildung (Wilke et al. 2013).

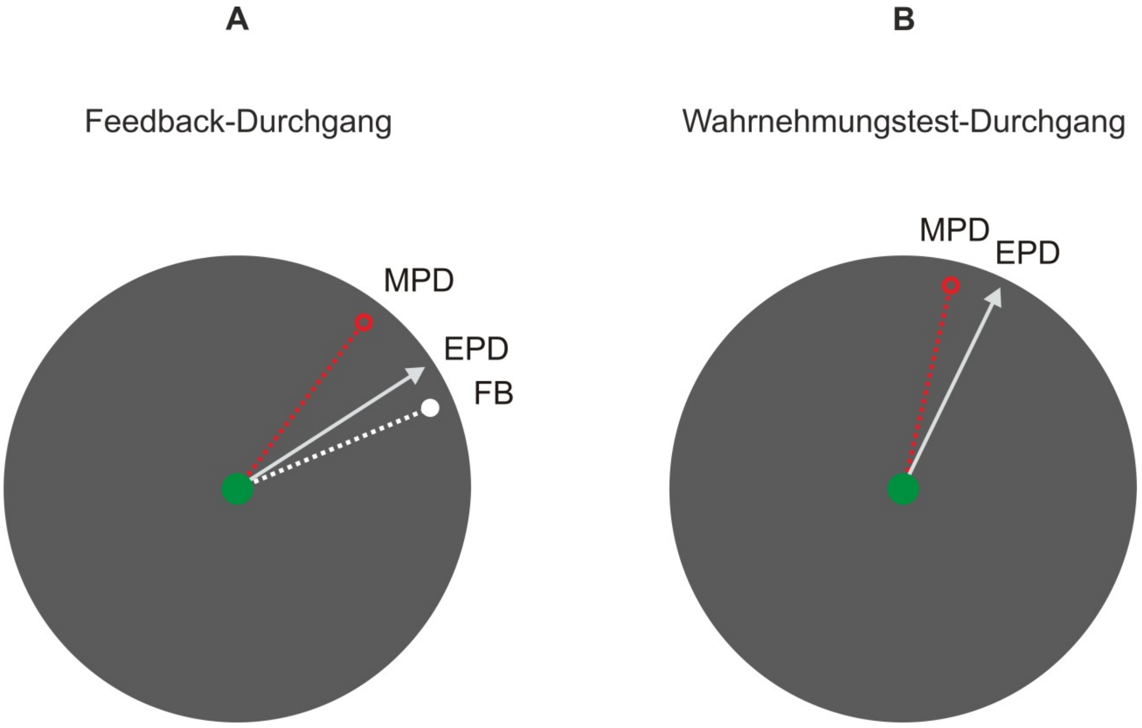

Abb. 6. Experimentelles Prozedere.

Für die Zeigebewegungen erhielten die Probanden keine externen Ziele vorgegeben, sondern wurden instruiert, selbst verschiedene motorische Zeigerichtungen (MPD) innerhalb eines definierten Bereichs zu wählen (oberes rechtes Kreisviertel in Abschnitt 3.1. bzw. obere Kreishälfte in 3.2.). Visuelle Prädiktionsfehler wurden in Feedback-Durchgängen (A) generiert. Dazu wurde das visuelle Feedback (FB) über die Bewegungen zufällig um den Startpunkt (grün) der Bewegungen rotiert, entweder im Uhrzeigersinn (wie in diesem Beispiel) oder alternativ gegen den Uhrzeigersinn. Nach Abschluss jeder Bewegung schätzten die Probanden visuell die tatsächliche Richtung der Bewegung (EPD), indem sie einen Trackball-gesteuerten Cursor mit der linken Hand in diese Richtung rotierten (ähnlich einem Uhrzeiger). Die geschätzte Zeigerichtung diente dazu, die Komponente der Feedback-Manipulation bzw. des visuellen Prädiktionsfehlers zu messen, welche die Probanden kausal an interne Ursachen attribuierten. Die Aktualisierung der internen visuellen Prädiktionen wurde in Wahrnehmungstest-Durchgängen (B) gemessen, bei denen die Probanden keinerlei visuelles Feedback über ihre Zeigebewegung erhielten. Folglich beruhte in diesen Durchgängen die geschätzte Zeigerichtung (EPD) ausschließlich auf internen bewegungsbezogenen Informationen und reflektierte somit eine interne Prädiktion der visuellen Bewegungskonsequenzen. Angepasste Abbildung (Wilke et al. 2013).

3. Ergebnisse

3.1. Aktualisierung der Wahrnehmung eigener Bewegungen durch kausale Attribution sensorischer Prädiktionsfehler

Grundlage dieses Abschnitts ist die folgende Publikation: Wilke C, Synofzik M, Lindner A. (2013). Sensorimotor recalibration depends on attribution of sensory prediction errors to internal causes. *PLoS One* 8(1):e54925. Ergänzend finden sich in diesem Abschnitt auch die supplementären Informationen, welche online erschienen sind.

3.1.1. Zusammenfassung und Bezug zur Fragestellung

Unsere Wahrnehmung der eigenen Bewegungen wird fortlaufend anhand von Wahrnehmungsfehlern aktualisiert, welche aus dem Vergleich der tatsächlichen und der intern prädizierten sensorischen Bewegungsfolgen hervorgehen. Die These, dass die Aktualisierung der Wahrnehmung der eigenen Bewegungen durch eine kausale Zuschreibung von sensorischen Prädiktionsfehlern erfolge (Attribution der Fehler an interne versus externe Ursachen), mag angesichts des dargelegten Wissensstands plausibel erscheinen (Abschnitt 1.3.). Jedoch fehlen Studien, welche die kausale Attribution von Prädiktionsfehlern messen und diese Attribution in Bezug zur Aktualisierung der Wahrnehmung bringen.

Deshalb untersuchte die vorliegende Studie die Plastizität der Wahrnehmung eigener Bewegungen, indem die kausale Attribution sensorischer Prädiktionsfehler gemessen wurde: Anhand der gemessenen Fehlerattribution wurde die Aktualisierung dieser Wahrnehmung charakterisiert. Als experimentelles Paradigma diente die Wahrnehmung der eigenen Handbewegungen, die psychophysisch gemessen wurde (Abschnitt 2. für einen methodischen Überblick). Dazu führten die Probanden Zeigebewegungen in einer virtuellen Umgebung aus. Diese erlaubte eine Dissoziation der visuellen Bewegungskonsequenzen von den tatsächlichen Zeigebewegungen durch die Rotation des visuellen Feedbacks über die Zeigebewegungen. Experimentell wurden dadurch zufällige, unvorhersehbare Diskrepanzen zwischen den tatsächlichen und den intern prädizierten visuellen Bewegungsfolgen geschaffen, also visuelle Prädiktionsfehler.

Diese Prädiktionsfehler bewirkten eine Aktualisierung der internen Prädiktionen über die visuellen Bewegungskonsequenzen im jeweils nachfolgenden Durchgang. Dabei war diese Aktualisierung nicht proportional zur absoluten Größe des *extern* generierten Fehlers. Stattdessen korrelierte die Aktualisierung mit der Fehlerkomponente, welche die Probanden an *interne* Ursachen attribuierten. Diese an interne Ursachen attribuierte Fehlerkomponente erklärte die Plastizität der internen visuellen Prädiktionen auf der Ebene der einzelnen Prädiktionsfehler: Je mehr ein Prädiktionsfehler in einem Durchgang an interne Ursachen attribuiert wurde, desto mehr Adaptation war im Folgedurchgang zu beobachten. Dieser Zusammenhang galt auch für Prädiktionsfehler einer und derselben Fehlergröße. Zusätzlich wurde eine Adaptation des motorischen Verhaltens der Probanden gefunden, welche ihre aktualisierten visuellen Prädiktionen reflektierte.

Zusammenfassend war die kausale Attribution sensorischer Prädiktionsfehler wesentlich für die Plastizität der Wahrnehmung eigener Bewegungen und für sensomotorisches Lernen im weiteren Sinne.

Zusätzlich zeigten die Ergebnisse, dass die Probanden die Fehlersignale nicht dichotom an entweder interne oder externe Ursachen attribuierten, wie frühere Studien angenommen hatten. Vielmehr erfolgte die kausale Fehlerattribution kontinuierlich auf der Ebene der einzelnen Fehler: Die Probanden attribuierten die Fehlersignale also sowohl an interne Ursachen als auch an externe Ursachen, wobei der an interne Ursachen attribuierte Anteil mit zunehmenden Fehlergrößen abnahm. Eine derartige teilweise, kontinuierliche Attribution von

Prädiktionsfehlern an interne Ursachen würde mit der These übereinstimmen, dass die Wahrnehmung der eigenen Bewegungen auf einer Integration interner und externer bewegungsbezogener Signale beruht.

In Hinblick auf die Unterscheidung von Exafferenz und Reafferenz wirft das Experiment insbesondere neues Licht auf die internen Prädiktionen über die sensorischen Folgen der eigenen Bewegungen. Diese sensorischen Prädiktionen sind keine absoluten Referenzsignale, sondern stattdessen plastische und relative Größen: Sensorische Prädiktionen sind interne Referenzsignale, die – wie das Komparatormodell fordert – eine kausale Attribution der sensorischen Afferenz erlauben und die wiederum selbst – wie die vorliegende Studie nahelegt – durch eine kausale Fehlerattribution anhand der sensorischen Afferenz aktualisiert werden (Abschnitt 4.4.). Die Wahrnehmung der eigenen Bewegungen ist also *nicht* hinreichend durch den Vergleich der tatsächlichen und der prädizierten sensorischen Bewegungskonsequenzen bestimmt, sondern ist auf weitere Information angewiesen. Die Studie wirft damit die Frage auf, welche Faktoren die kausale Attribution sensorischer Prädiktionsfehler an interne oder externe Ursachen bestimmen. Daher wird ein weiteres Experiment (Abschnitt 3.2.) exemplarisch testen, ob Handlungsergebnisse die kausale Attribution eines Prädiktionsfehlers ändern. Weitere Einflussfaktoren werden diskutiert (Abschnitt 4.5.).

3.1.2. Originalpublikation

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Sensorimotor Recalibration Depends on Attribution of Sensory Prediction Errors to Internal Causes

Carlo Wilke[1], **Matthis Synofzik**[2,3], **Axel Lindner**[1]*

1 Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany, **2** Department of Neurodegeneration, Hertie Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany, **3** German Centre for Neurodegenerative Diseases, University of Tübingen, Tübingen, Germany

Abstract

Sensorimotor learning critically depends on error signals. Learning usually tries to minimise these error signals to guarantee optimal performance. Errors can, however, have both *internal* causes, resulting from one's sensorimotor system, and *external* causes, resulting from external disturbances. Does learning take into account the *perceived cause* of error information? Here, we investigated the recalibration of internal predictions about the sensory consequences of one's actions. Since these predictions underlie the distinction of self- and externally produced sensory events, we assumed them to be recalibrated only by prediction errors attributed to internal causes. When subjects were confronted with experimentally induced visual prediction errors about their pointing movements in virtual reality, they recalibrated the predicted visual consequences of their movements. Recalibration was not proportional to the externally generated prediction error, but correlated with the error component which subjects attributed to *internal* causes. We also revealed adaptation in subjects' motor performance which reflected their recalibrated sensory predictions. Thus, causal *attribution* of error information is essential for sensorimotor learning.

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* E-mail: a.lindner@medizin.uni-tuebingen.de

Introduction

Sensory information results from both external events and our own actions [1]. To distinguish between *externally* and *internally caused* sensory information [2,3], the nervous system predicts the sensory consequences of one's actions on the basis of internal action-related information, such as efference copies [4] or corollary discharge [5] of motor commands. These *internal sensory predictions* are likely issued by forward models [6,7] which take into account the current states of the motor and the sensory system. By comparing the actual and the predicted sensory afference, the nervous system can infer the cause of the afference [2,3]. In case of a match, the afference should be interpreted as internally caused. Otherwise, the difference between the actual and the predicted afference – i.e. the *prediction error* – should be interpreted as the result of an external event (compare Figure 1).

However, as the properties of the motor system continuously change (e.g. due to growth, fatigue or disease), one and the same motor command will have various sensory consequences [8]. Such changes will likewise produce prediction errors – unlike in the first case, however, these errors result not from external events, but from internal causes. In order to maintain a reliable distinction between externally and internally caused sensory afference, internal sensory predictions therefore need continuous *recalibration* [8,9,10,11,12] to compensate for internally caused prediction errors. Such recalibration constitutes a fundamental problem since internally and externally caused prediction errors do not differ per se.

Given this uncertainty about the cause of prediction errors, we here asked whether the recalibration of internal sensory predictions depends on the *attribution* of prediction errors to internal causes (i.e. causes within the sensorimotor system). We therefore designed a sensorimotor recalibration paradigm and estimated the component of the prediction error which subjects attributed to internal causes. Our findings demonstrate that this *internally attributed component* determines the recalibration of internal sensory predictions.

Results

Causal Attribution of Sensory Prediction Errors

We tested our hypothesis in a virtual-reality setup (Figure 2A, [8]) in which subjects ($n = 11$) performed horizontal pointing movements in freely chosen directions. To generate visual prediction errors and to manipulate the component of these errors which subjects attributed to internal causes, we used trials with online visual feedback – referred to as *feedback trials* (Figure 2B). Here, subjects were provided with a visual marker which moved in an experimentally controlled relation to the tip of their right index finger. This visual feedback (FB) was either veridical, i.e. in spatiotemporal correspondence with the fingertip, or rotated relative to the actual movement by various angles. For each trial, the manipulation angle was randomly drawn from a discrete uniform distribution over the values 5°, 10°, 20°, 40° (counter-clockwise rotation), $-5°$, $-10°$, $-20°$, $-40°$ (clockwise rotation)

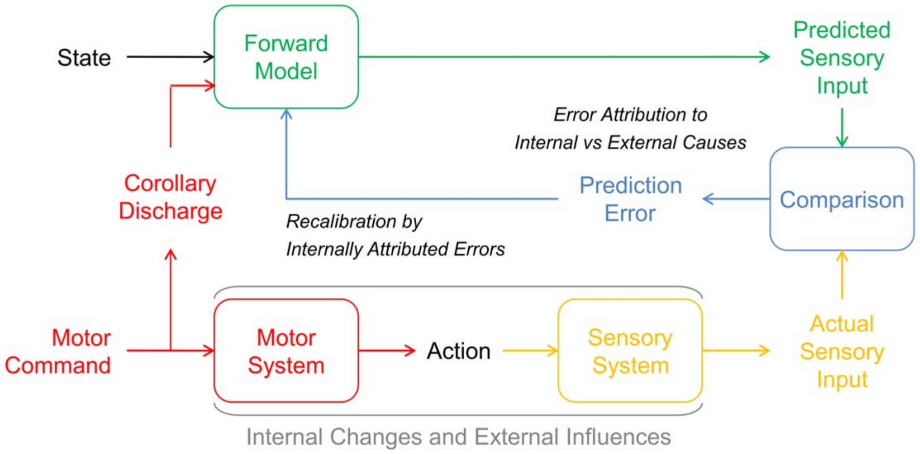

Figure 1. Recalibration of internal sensory predictions. Sensory afference can result both from external events (exafference) and, as this figure illustrates, from our own actions (reafference) [1]. According to the comparator model, the nervous system establishes the cause of the sensory afference by comparing the *actual sensory input* with the *predicted sensory input* [2,3]. To this end, the sensorimotor system predicts the sensory input which will result from one's actions on the basis of internal action-related information, such as *corollary discharge* [5] of the *motor command*. This prediction is computed by a *forward model* [6,7] which additionally takes into account the current *state* of the *motor system* and the *sensory system* [34,64]. The nervous system then makes a *comparison* between the *actual sensory input* and the *predicted sensory input*. In case of a match, the sensory afference should be interpreted as internally caused. Otherwise, in case of a mismatch, the difference between the actual and the predicted input should be interpreted as externally caused. This difference between the actual and the internally predicted sensory consequences of one's actions constitutes a *prediction error*. However, such errors arise not only from *external influences*. Prediction errors can also result from *internal changes*, i.e. changes within the sensorimotor system such as growth, fatigue or disease. Thus, one's internal sensory predictions need continuous *recalibration*. As previous research suggests [16,43,65], this recalibration should compensate only for those prediction errors which result from internal causes. However, internally and externally caused prediction errors do not differ per se. Addressing this issue, we here demonstrate that the recalibration of internal sensory predictions by prediction errors depends on the attribution of the prediction error to internal causes. Figure adapted from Wolpert and Miall, 1996 [66].
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and 0° (veridical feedback). Subjects were informed in advance that the visual feedback would be either veridical or rotated relative to their movements by various angles. Given the unpredictability and the distribution of the visual manipulation, subjects' internal prediction of the visual pointing direction should on average have corresponded to the direction of the actually performed movement. Accordingly, any manipulated feedback should have deviated from this internal prediction, which means that *feedback manipulations* should constitute visual prediction errors which are externally caused.

After each movement, subjects visually estimated their pointing direction by means of a trackball-guided cursor (Figure 2B). For each trial, the difference between the *estimated* pointing direction (EPD) and the *motor* pointing direction (MPD) – which we will refer to as the *perceived pointing direction* (PPD = EPD – MPD) – provided us with a relative measure of subjects' perception of their movements. Importantly, the perceived pointing direction captured any component of the feedback manipulation and thus of the visual prediction error which subjects attributed to internal causes. By way of illustration, the perceived pointing direction should match the feedback manipulation if subjects entirely attributed the prediction error to internal causes (red line in Figure 3A). Vice versa, subjects' perceived pointing direction should equal 0° (i.e. the estimated and the motor pointing direction should be identical) if subjects entirely attributed the prediction error to external causes (green line in Figure 3A).

The *internally attributed component* of the prediction error should – among other factors – depend on the *absolute error size*. Specifically, the results of earlier studies suggest that subjects should perceive large prediction errors less likely as internally caused than small prediction errors [13,14,15,16,17]. Accordingly, the share of the internally attributed component in relation to the absolute error size should decrease if the absolute error size increases. If true, this would allow us to gradually manipulate subjects' causal attribution of prediction errors.

Indeed, when plotting the perceived pointing direction versus the manipulation applied to the visual feedback (blue curve in Figure 3A), we obtained an s-shaped curve, with clockwise manipulations changing the perceived pointing direction in a clockwise manner and, vice versa, counterclockwise rotations inducing a counterclockwise change. For manipulations as small as ±5° and ±10°, subjects' perceived pointing direction strongly reflected the feedback manipulation (red line in Figure 3A). In contrast, if manipulations were as large as ±20° and ±40°, the estimated pointing direction resembled rather the motor pointing direction (green line in Figure 3A) than the visual feedback direction. This indicated a subproportional relationship between large prediction errors and the internally attributed error component.

To quantify the *internally attributed share* of the prediction error, we defined the *relative weight of visual information* in subjects' perceptual estimates [18], namely by dividing subjects' offset-corrected perceived pointing direction by the manipulation applied to the visual feedback in the same trial (Figure 3B, also compare Methods and Figure S1A). This quotient equals 1 if and only if the perceived pointing direction matches the angle of feedback rotation (red line in Figure 3A), which would correspond to an entirely internal attribution of the prediction error. The quotient equals 0 if and only if the estimated pointing direction and the motor pointing direction are identical (green line in

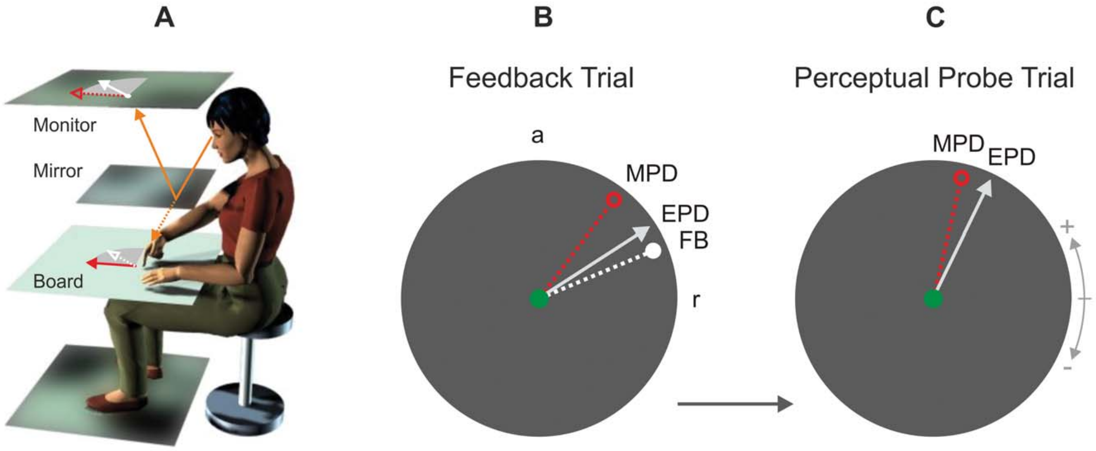

Figure 2. Experimental design. *(A) Setup.* Subjects viewed the virtual image of their finger (white disc) on the feedback monitor via a mirror (solid orange arrow) while performing horizontal pointing movements. For geometric reasons, the virtual image appeared in the same plane as subjects' finger movements (dotted orange arrow). Visual feedback could be either veridical, i.e. in spatiotemporal correspondence with subjects' fingertip, or manipulated online by rotation around the starting point of the movements (solid red arrow: actual movement vector, solid white arrow: rotated visual feedback vector, dotted arrows correspond to projections of these vectors into the monitor or the movement plane, respectively). *(B) and (C) Procedure.* Feedback trials (B) and perceptual probe trials (C) followed on each other alternately. In both conditions, subjects were instructed to freely choose various motor pointing directions between the subjective directions of *right* (r = 0°) and *anterior* (a = 90°). In feedback trials (B), visual feedback (FB, dotted white line) about the pointing movement (MPD, dotted red line) was provided in real time. Feedback could be rotated around the starting point (green disc) of the movements by various angles, either in a clockwise (as in this example) or in a counterclockwise manner. When having completed a movement, subjects visually estimated the direction of their movement (referred to as the estimated pointing direction, EPD, solid grey arrow) by placing a trackball-guided cursor in the respective direction. The perceived pointing direction, defined as the difference PPD = EPD – MPD, allowed to us to estimate the component of the feedback manipulation – and thus of the visual prediction error – which subjects attributed to internal causes. In perceptual probe trials (C), subjects did not receive any visual feedback about their pointing movement (MPD). Consequently, they needed to rely entirely on internal action-related information when estimating their pointing direction (EPD). By analysing subjects' perceived pointing direction (PPD = EPD – MPD) in perceptual probe trials as a function of the visual manipulation applied in the preceding feedback trial, we assessed how subjects' internal sensory predictions recalibrated in response to visual prediction errors (see Figure 1 for background information).
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Figure 3A), which would correspond to an entirely external attribution of the prediction error.

As expected, the relative weight of visual information – representing the internally attributed share of the prediction error – decreased with increasing prediction error size. Specifically, for manipulations of ±5° and ±10°, the relative weight of visual information was 0.54 and 0.57, respectively. This means that if the prediction error was small, subjects attributed comparable shares of this error to internal and external causes. However, for manipulations of ±20° and ±40°, the visual weight decreased to 0.38 and 0.19, respectively. Here, subjects rather attributed the prediction error to external than to internal causes.

In order to analyse the influence of feedback manipulations on the relative weight of visual information statistically, we conducted a repeated-measures ANOVA with the factors *orientation* (counterclockwise, clockwise) and *amount* of manipulation (5°, 10°, 20°, 40°). We found a significant main effect of amount of manipulation (F(3, 30) = 16.66, P<.001). There were no significant main effect of orientation (F(1, 10) = 1.84, P = .205) and no significant interaction (F(1.26, 12.56) = 0.09, P = .828). We therefore pooled the data across counterclockwise (original data values) and clockwise manipulations (data values multiplied by −1) of the same amount (see Figure 3B).

Additional post-hoc tests showed that the internally attributed share – as measured by the relative weight of visual information – decreased significantly if the amount of visual manipulation increased from 10° via 20° to 40° (P = .007, r = 0.35 and P<.001, r = 0.39 respectively, planned paired one-tailed t-tests to verify the assumption that weight(5°)>weight(10°)>weight(20°)>‴ weight(40°), Bonferroni-corrected for multiple comparisons). However, no significant difference could be found between amounts of manipulation of 5° and 10° (P≥.10). Note that, for all amounts of manipulation, the relative visual weight differed significantly from 0 (one-sample one-tailed t-tests, Bonferroni-corrected for multiple comparisons, see Figure 3B). These findings indicate that the internally attributed share was significant for all prediction errors – despite the fact that these errors were experimentally and, therefore, externally caused – and that the internally attributed share decreased significantly with increasing error size. Note that the internally attributed share of the prediction error across trials showed a density distribution which supports no dichotomous attribution to either internal or, alternatively, external causes, but which rather suggests a continuous attribution mechanism (for details, see Figure 4).

Feedback trials thus allowed us to gradually manipulate the internally attributed component of visual prediction errors – which, according to our hypothesis, should explain the recalibration of subjects' internal predictions about the visual consequences of their actions.

Recalibration of Internal Sensory Predictions

To study the recalibration of internal sensory predictions on a *trial-by-trial* basis [19,20], we used *perceptual probe trials* (Figure 2C), which we presented in alternation with the feedback trials. Perceptual probe trials were identical to feedback trials apart from the fact that subjects received *no* visual feedback about their

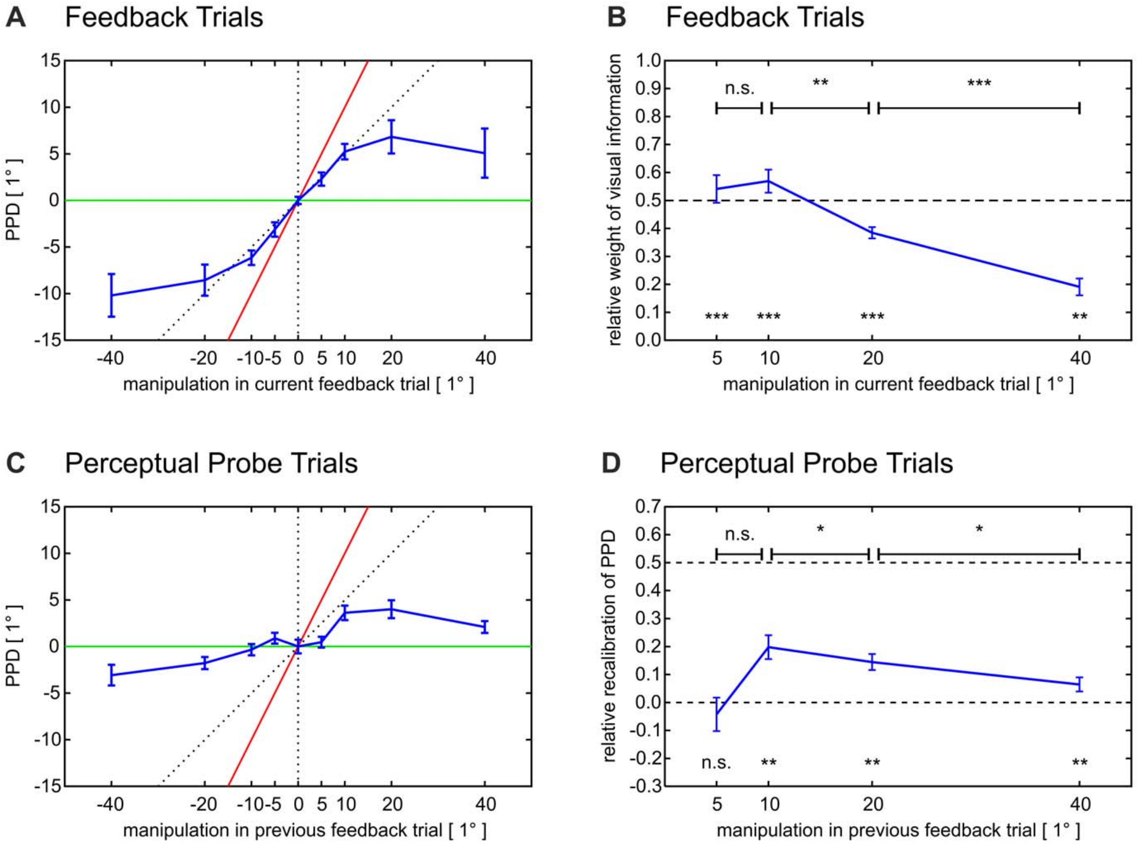

Figure 3. Error attribution and recalibration of internal sensory predictions. *(A) Perceived pointing direction in feedback trials.* Subjects' perceived pointing direction (PPD, blue curve), which is here plotted versus the manipulation applied to the visual feedback, allowed us to estimate the component of the feedback manipulation – and thus of the visual prediction error – which subjects attributed to internal causes. The PPD strongly reflected the size of the feedback manipulation (red line) if these manipulations were small. If manipulations were large, vice versa, subjects' estimated pointing direction rather resembled the motor pointing direction (green line). By varying the size of the feedback manipulations, we thus gradually manipulated the error component which subjects attributed to internal causes. *(B) Relative weight of visual information.* We captured the internally attributed share of the prediction error by the relative weight which visual feedback obtained in subjects' PPD. The relative weight of visual information was defined as the quotient of subjects' offset-corrected PPD (compare A) and the manipulation applied to the visual feedback. Relative visual weights of 1 and 0 would indicate that a subject attributed the prediction error either entirely internally or, respectively, entirely externally. The relative visual weight was significant for all amounts of manipulation (one-sample one-tailed t-tests), but also quantitatively modulated by the absolute amount of manipulation: increasing error sizes resulted in decreasing shares of the internally attributed error component (paired one-tailed t-tests). *(C) Perceived pointing direction in perceptual probe trials.* The recalibration of subjects' internal sensory predictions was reflected by the PPD in perceptual probe trials (blue curve), which is here plotted versus the feedback manipulation applied in the immediately preceding feedback trial. Recalibration was not proportional to the preceding prediction error, i.e. the preceding feedback manipulation, but instead resembled the error component which subjects had attributed internally, i.e. their PPD in the preceding feedback trial (compare A). By way of illustration, the green line shows the assumption that prediction errors would not induce any recalibration. Likewise, the red line corresponds to the assumption that subjects adjusted the perceived pointing direction to the entire amount of the preceding feedback manipulation. *(D) Relative recalibration of internal sensory predictions.* We defined the relative recalibration to compare the recalibration induced by prediction errors of variable size. The relative recalibration was the quotient of the offset-corrected PPD in a given perceptual probe trial (compare C) and the manipulation applied in the preceding feedback trial. The relative recalibration was significant for amounts of manipulation as large as 10°, 20° and 40° (one-sample one-tailed t-tests), which means that manipulations induced recalibration if exceeding a minimum threshold. Moreover, the amount of manipulation modulated the relative recalibration quantitatively: increasing amounts of manipulation resulted in decreasing values of relative recalibration (paired one-tailed t-tests). Diagrams show mean values ± standard errors calculated across subjects. All reported P-values are Bonferroni-corrected for multiple comparisons within each measure (*** $P<.001$, ** $P<.01$, n.s. $P\geq.10$). Positive angles denote counterclockwise rotations.
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pointing movements (MPD). When estimating their pointing direction (EPD), subjects consequently needed to rely entirely on internal action-related information. Thus, we assumed that, in perceptual probe trials, the estimated pointing direction and, hence, also the *perceived pointing direction* (PPD = EPD – MPD) reflected an *internal sensory prediction*.

We expected subjects' internal sensory predictions to recalibrate in response to the prediction errors which we generated in feedback trials. Specifically, this recalibration should be de-

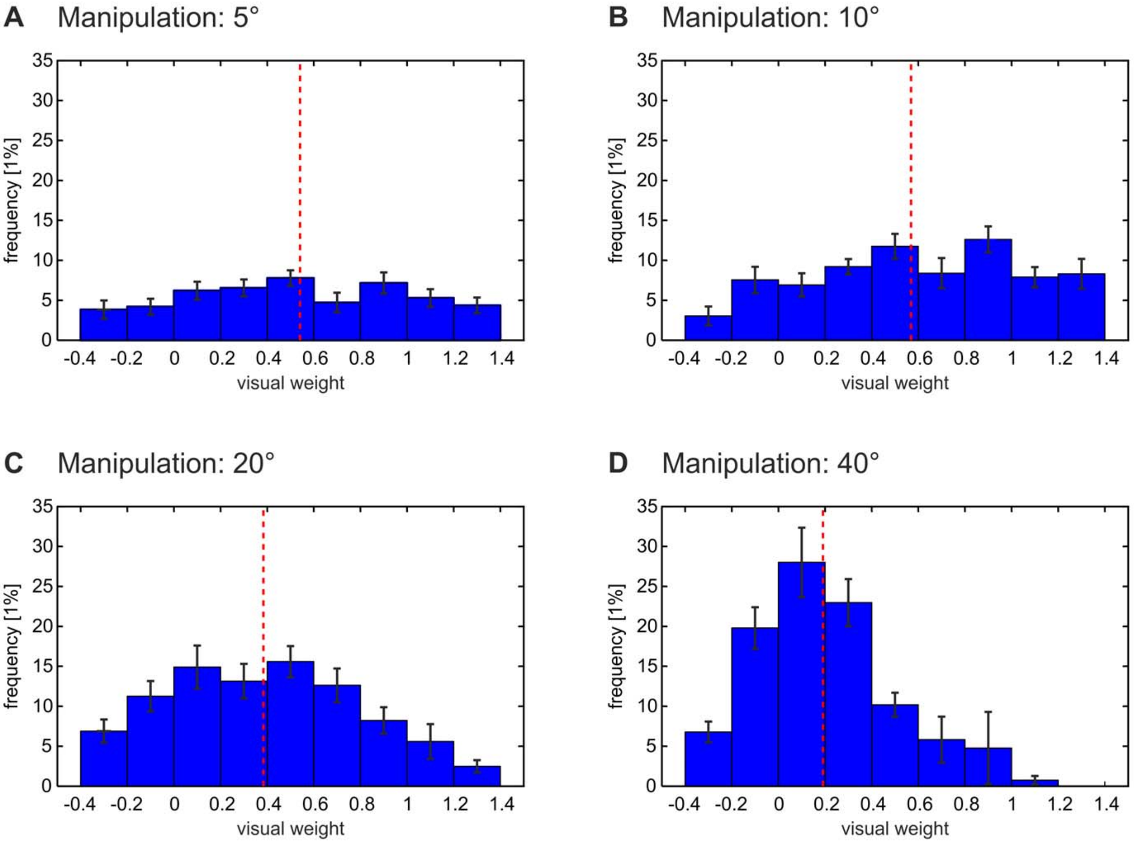

Figure 4. Distribution of the relative weight of visual information. These histograms (mean ± standard error) display the density distribution of the relative weight of visual information across feedback trials. The relative weight of visual information was defined as the quotient of subjects' offset-corrected perceived pointing direction and the feedback manipulation applied in the same trial (compare Figure 3B). For all amounts of feedback manipulation (5° in A, 10° in B, 20° in C, 40° in D), the histogram exhibits one single peak, indicating a *unimodal* density distribution. This peak corresponds to the mean relative weight of visual information (broken red line). This finding shows that subjects *integrated* the internally predicted and the actual sensory consequences of their actions on the level of *individual* trials when estimating their pointing direction. Alternatively, subjects could have based their estimates solely on internal signals in one trial (corresponding to a relative visual weight of 0) while relying entirely on visual information in another (corresponding to a relative visual weight of 1). This would have resulted in bimodal density distributions, which are not supported by our data. To further support this notion, we statistically examined the distribution of the relative visual weight in feedback trials separately for each subject ($n = 11$) and for each amount of feedback manipulation (5°, 10°, 20°, 40°). We applied the *Shapiro-Wilk test* to each of these 44 distributions, testing the null hypothesis that the sample came from a normally distributed population. We found that the null hypothesis was tenable in 41 of the 44 samples ($P \geq .05$, uncorrected). This indicates that, indeed, the relative visual weight was normally and therefore unimodally distributed, both across subjects and feedback manipulations.
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termined by the component of the prediction error which subjects attributed to internal causes. Accordingly, the perceived pointing direction in perceptual probe trials should shift in the orientation of the feedback manipulation applied in the preceding feedback trial. Moreover, the perceived pointing direction in perceptual probe trials should quantitatively mirror the internally attributed component of this feedback manipulation, i.e. the perceived pointing direction in the preceding feedback trial.

When plotting the perceived pointing direction in perceptual probe trials versus the visual manipulation applied in the respective preceding feedback trials (Figure 3C), we obtained another s-shaped curve: counterclockwise manipulations shifted subjects' estimates of their pointing direction in a counterclockwise fashion and, vice versa, clockwise manipulations induced a clockwise shift – if the manipulations were larger than 5°. This suggests that prediction errors resulted in a recalibration of subjects' internal sensory predictions, even if these prediction errors were externally caused. The shape of the plot also suggests that the recalibration of subjects' internal sensory predictions related to the absolute error in a less than proportional manner – thus resembling the internally attributed component of the prediction error (compare Figure 3C to Figure 3A).

To quantitatively compare how visual prediction errors of different size recalibrated subjects' internal sensory predictions, we defined the *relative recalibration* by dividing the offset-corrected perceived pointing direction in perceptual probe trials by the manipulation applied in the preceding feedback trial (Figure 3D, compare Methods and Figure S1B). This quotient equals 1 if and only if a subject's perceived pointing direction in a perceptual probe trial matches the visual feedback rotation in the preceding feedback trial (red line in Figure 3C). The quotient equals 0 if and only if the estimated pointing direction and the motor pointing direction are identical (green line in Figure 3C).

If the recalibration of internal sensory predictions was proportional to the absolute prediction error, the relative recalibration would be constant across feedback manipulations. In contrast, if the recalibration of internal sensory predictions reflected the attribution of prediction errors to internal causes, then the relative recalibration should – along with the relative weight of visual information – decrease for increasing amounts of feedback manipulation. Indeed, the relative recalibration showed a maximum of 0.20 at rotations of ±10° and decreased via 0.14 at ±20° to 0.07 at ±40° of rotation (Figure 3D).

To investigate the relative recalibration statistically, we performed a repeated-measures ANOVA with the factors *orientation* (counterclockwise, clockwise) and *amount* of manipulation (5°, 10°, 20°, 40°). We found a significant main effect of amount of manipulation (F(1.77, 17.65) = 4.81, P = .025). There were no significant main effect of orientation (F(1, 10) = 1.29, P = .283) and no significant interaction (F(1.47, 14.69) = 1.18, P = .319). We therefore pooled the data across counterclockwise and clockwise manipulations of the same amount (see Figure 3D).

The relative recalibration differed significantly from 0 for all amounts of manipulation except for those of 5° (one-sample one-tailed t-tests, Bonferroni-corrected for multiple comparisons, Figure 3D). Apparently, prediction errors needed to exceed a certain *threshold* to recalibrate subjects' internal sensory predictions. However, when exceeding this threshold, one *single* error was sufficient to induce recalibration. The significant main effect of amount of manipulation was explained by post-hoc tests which showed that the relative recalibration decreased significantly if the visual manipulation increased from 10° via 20° to 40° (P = .041, r = 0.18 and P = .015, r = 0.41 respectively, planned paired one-tailed t-tests to verify the assumption that recalibration(5°)>recalibration(10°)>recalibration(20°)>recalibration(40°), Bonferroni-corrected for multiple comparisons, Figure 3D). These findings show that – in quantitative terms – the recalibration of internal sensory predictions could not be explained by the absolute size of the prediction error alone.

Instead, the recalibration of internal sensory predictions in a given trial should – according to our hypothesis – be explained by the internally attributed component of the prediction error in the preceding trial. To test this idea directly, we ran a linear regression analysis using the perceived pointing direction in individual feedback trials to predict the perceived pointing direction in the consecutive perceptual probe trials (for details, see Table S1). For ten of our eleven subjects, this linear model was significant. On average, the correlation coefficient within each subject was 0.252±0.039 (mean ± standard error), indicating a positive correlation of moderate effect size (Figure 5). The average regression coefficient was 0.219±0.037, i.e. an increase of the perceived pointing direction in a feedback trial by 10° would, on average, have resulted in an increase of the perceived pointing direction in the following perceptual probe trial by approximately 2°. To minimise the effect of noise inherent to the estimation of the perceived pointing direction, we tested the correlation not only on the level of individual trials, but also across average perceived pointing directions (feedback trials versus perceptual probe trials, matched by visual manipulation). In the latter case, we found a correlation coefficient of 0.56±0.09 (mean ± standard error) within each subject, which emphasised the importance of causal error attribution in recalibration.

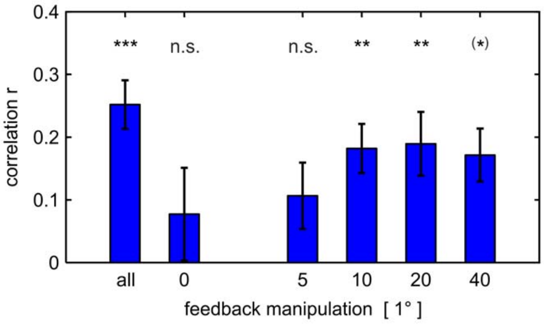

Figure 5. Trial-by-trial recalibration of internal sensory predictions. To investigate the recalibration of internal sensory predictions on a trial-by-trial basis, we performed a linear regression analysis using the perceived pointing direction in feedback trials (Figure 3A) to predict the perceived pointing direction in the consecutive perceptual probe trials (Figure 3C). This analysis was applied to *single* manipulation values as well as to *all* manipulation values. When analysing the correlation coefficients obtained for single manipulation values by a repeated-measures ANOVA, we found no significant main effect of orientation of manipulation (F(1, 10) = 0.66, P = .435), no significant main effect of amount of manipulation (F(3, 30) = 0.70, P = .557) and no significant interaction (F(3, 30) = 2.35, P = .092). We therefore pooled the correlation coefficients across counterclockwise and clockwise manipulations of the same amount. The figure displays the correlation coefficient *r* for *all* manipulation values, for *veridical* feedback (i.e. manipulations of 0°) and for *single* amounts of manipulation of 5°, 10°, 20° and 40° (mean ± standard error across subjects, compare Table S1 for details). If the amount of visual feedback manipulation was larger than 5°, the internally attributed component of the visual prediction error in a given feedback trial explained the recalibration of subjects' internal sensory predictions. All reported P-values are Bonferroni-corrected for multiple comparisons (one-sample one-tailed t-tests, *** $P<.001$, ** $P<.01$, (*) $P<.10$, n.s. $P\geq.10$).
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The correlation between the error component which subjects attributed to internal causes and the consecutive recalibration of the perceived pointing direction – which we calculated across errors of *varying* size – could have possibly been confounded by the absolute *size* of the errors. Specifically, the correlation might have resulted from a decrease of the relative recalibration for increasing absolute error size which was independent of any causal attribution of feedback errors. For instance, such decrease could have been caused by reduced sensitivity of recalibration to large errors [13].

Therefore, we repeated the trial-by-trial regression analysis separately for each manipulation angle (Figure 5, calculated on the level of individual trials). These analyses again revealed positive correlations irrespective of whether the analysed perceptual probe trials were preceded by visual manipulations of either 10° or 20° or 40°, respectively. These correlations suggest that the causal attribution of the prediction error explains the recalibration of subjects' internal sensory predictions independently of a given absolute error size. In contrast, for both those trials following on veridical feedback (manipulations of 0°) and those trials following on manipulations of 5°, the average correlation coefficient was not significantly different from 0 (one-sample one-tailed t-tests, Bonferroni-corrected for multiple comparisons, compare Figure 5). This finding suggests that, for small visual manipulations, the perceived pointing direction in feedback trials and the perceived pointing direction in the consecutive perceptual probe trials were independent. This is consistent with the fact that small prediction errors resulted in a strong weighting of visual information in subjects' perceptual estimates (Figure 3B) but did not significantly recalibrate their internal sensory predictions (Figure 3D).

To assess the evidence our data provide in favour of the hypothesis that the causal attribution of error signals guides the recalibration of sensory predictions, we calculated Bayes factors. A Bayes factor quantifies the evidence for a hypothesis relative to the evidence for an alternative hypothesis. In our case, the alternative hypothesis assumed that recalibration is independent of any causal attribution of error signals. We expected the correlation between the error component attributed to internal causes and the consecutive recalibration to be positive (i.e. within the range from 0 to 1), with small correlation coefficients being more likely than large correlation coefficients. Hence, we modelled the prediction of our hypothesis as a half-normal distribution with a mode of 0 and a standard deviation of 0.5, as suggested by Dienes, 2011 [21]. For each absolute feedback manipulation, we calculated a Bayes factor B according to the procedure described by Dienes [21]. Bayes factors of more than 1 provide evidence for the hypothesis over the alternative hypothesis whereas factors of less than 1, vice versa, favour the alternative. Bayes factors above 3 and below 1/3, respectively, can be considered as substantial evidence [22]. Specifically, our Bayes factors allowed us to evaluate the empirical support for the notion that the causal attribution of error signals guides the recalibration of sensory predictions versus the alternative hypothesis that recalibration is independent of any causal attribution of error signals. We found the following Bayes factors: $B(10^\circ) = 151.81$, $B(20^\circ) = 74.57$ and $B(40^\circ) = 4.62$. This is substantial support for the correlation of error attribution and recalibration. For errors of 5°, the Bayes factor was $B(5^\circ) = 0.89$ and thus did not allow to decide for any of the two hypotheses with certainty. Importantly, the Bayes factor for the correlation between the perceived pointing direction in veridical feedback trials and the perceived pointing direction in the consecutive perceptual probe trials was $B(0^\circ) = 0.42$. This yielded further evidence in favour of the assumption that, for veridical feedback trials and their consecutive perceptual probe trials, subjects' perceived pointing directions were independent. The absence of correlation for those trials following on veridical feedback suggests that the overall correlation between error attribution and recalibration, which we found for absolute amounts of error of 10°, 20° and 40°, was unlikely mediated by an unspecific transfer from feedback trials to the consecutive perceptual probe trials, e.g. due to a drift of the perceived pointing direction during the course of the experiment.

Given the independence of both subjects' *motor* pointing directions (one-sample two-tailed t-test, $t(10) = -0.80$, $P = .444$) and subjects' *estimated* pointing directions (one-sample two-tailed t-test, $t(10) = -0.42$, $P = .685$) across feedback trials and consecutive perceptual probe trials, respectively, the systematic change of the *perceived* pointing direction in perceptual probe trials was unlikely mediated by some unspecific behavioural or perceptual bias unrelated to subjects' actual movements. For detailed analyses and assessments of these biases, please also refer to Discussion S1. Finally, we asked whether any systematic *direction-dependent* differences in subjects' perceived pointing direction could have interfered with the recalibration of subjects' internal sensory predictions. In this case, the *motor* pointing direction *per se* should (partially) explain the *perceived* pointing direction (i.e. the difference between the estimated direction and the motor pointing direction). However, in the perceptual probe trials following on veridical feedback trials, the perceived pointing direction did not covary significantly with the motor pointing direction. Within subjects, a correlation coefficient of 0.038 ± 0.0681 (mean ± standard error) was found (one-sample two-tailed t-test, $t(10) = 0.56$, $P = .590$). Hence, systematic direction-dependent differences in subjects' perceived pointing direction which might have possibly interfered with the recalibration of subjects' internal sensory predictions by the feedback manipulation could not be detected. For the density distribution of the motor pointing direction in space, compare Figure S2. In summary, these findings support – though indirectly – the notion that subjects' perceived pointing direction in perceptual probe trials indeed captured adaptive changes of internal *movement-related* reference signals, i.e. a recalibration of internal sensory predictions.

Generalisation of Learning to Motor Behaviour

Based on subjects' perceived pointing direction in perceptual probe trials, our findings suggest that the manipulation of the visual feedback about subjects' actions in the preceding feedback trials resulted in a recalibration of subjects' internal sensory predictions. In addition to the change in subjects' action perception, one would expect this recalibration of internal sensory predictions to translate into a modification of subjects' motor performance [9,23,24,25]. Specifically, in perceptual probe trials, subjects should change their motor pointing directions in a manner which compensates for the altered visual consequences of their pointing movements. We provide evidence for this notion by analysing the average *motor* pointing direction in perceptual probe trials as a function of the manipulation applied in the *preceding* feedback trials (Figure 6B).

In comparison to those perceptual probe trials which followed on feedback trials with veridical feedback (0° manipulation), subjects performed movements which on average exhibited a more clockwise direction if the visual feedback had been rotated counterclockwise in the preceding feedback trial. Analogously, if the visual feedback had been rotated in a clockwise fashion, the next movement on average showed a more counterclockwise direction than the movements in the perceptual probe trials which were preceded by veridical feedback. Indeed, feedback manipulation significantly modulated the direction of the movement in the immediately following perceptual probe trial (repeated-measures ANOVA, $F(8, 80) = 3.79$, $P = .001$). Moreover, the average *motor* pointing direction in perceptual probe trials (compare Figure 6B) correlated negatively with the average *perceived* pointing direction (compare Figure 3C) in the perceptual probe trials preceded by the same manipulation: analysed on the population level, this correlation exhibited a strong effect size and was highly significant ($r(7) = -0.88$, $P = .002$). Subjects thus adjusted their motor performance to the altered visual consequences of the preceding movement. In feedback trials themselves, however, we found no systematic online correction of subjects' movement trajectories in response to deviating feedback. Here, subjects' motor pointing direction did not differ significantly across manipulations (repeated-measures ANOVA, $F(3.84, 38.42) = 0.94$, $P = .448$, compare Figure 6A).

Discussion

This study shows that the recalibration of internal predictions about the visual consequences of one's actions depends on the attribution of visual prediction errors to internal causes. In a virtual-reality setup, we dissociated subjects' pointing movements and their visual consequences by online rotation of the visual feedback. We thus generated unpredictable discrepancies between the actual and the internally predicted visual consequences of subjects' actions, i.e. visual prediction errors. Subjects' visual estimate of their pointing direction allowed us to indirectly

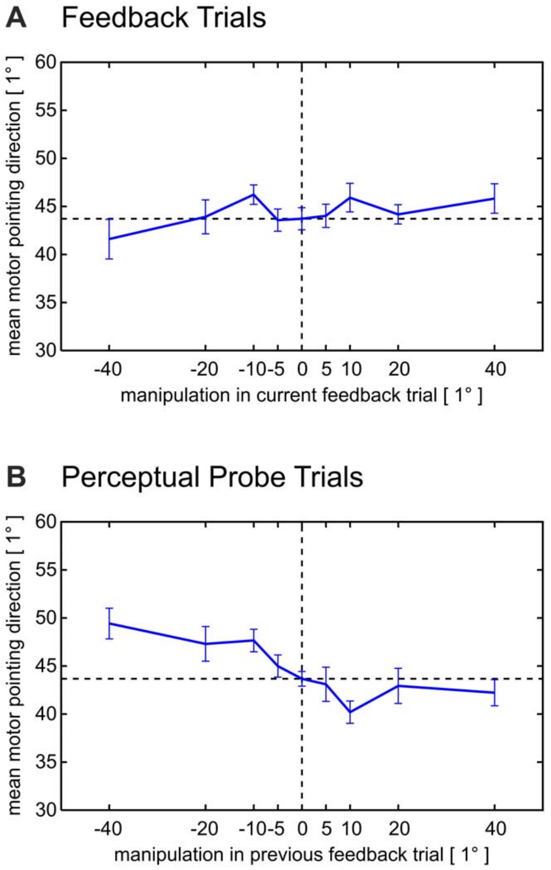

Figure 6. Motor pointing direction as a function of feedback manipulation. *(A) Feedback trials.* The mean *motor* pointing direction in feedback trials (mean ± standard error) is plotted as a function of the visual manipulation, with 0° representing the rightward direction and 90° representing the anterior direction. Subjects showed no systematic online correction of their movement trajectories when presented with deviating visual feedback. *(B) Perceptual probe trials.* The mean *motor* pointing direction in perceptual probe trials (mean ± standard error) is plotted as a function of the visual manipulation applied in the *preceding* feedback trials. Subjects adjusted their motor performance in a manner which compensated for the recalibrated visual movement consequences (compare Figure 3C). Positive angles denote counterclockwise rotations. For the density distribution of the motor pointing direction in space, compare Figure S2.
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quantify the component of the prediction errors which they attributed to internal causes. This internally attributed error component explained the recalibration of subjects' internal sensory predictions on a trial-by-trial basis: recalibration was not proportional to absolute error size, but instead correlated with the internally attributed error component. We also revealed adaptation in subjects' motor performance which reflected their recalibrated sensory predictions. More generally, our findings suggest that sensorimotor recalibration depends on a causal interpretation of error information.

Causal Attribution of Sensory Prediction Errors

We used feedback trials to generate visual prediction errors and to estimate the component of these errors which subjects attributed to internal causes (compare Figure 2B). We generated the prediction errors by rotating the visual feedback about subjects' movements by various, randomly chosen angles. Subjects were thus faced with an unpredictable discrepancy between the actual and the internally predicted visual consequences of their actions. When estimating their pointing direction, subjects could have attributed this discrepancy – i.e. the prediction error – either to internal causes, or to external causes, or to both internal and external causes. Subjects' perceived pointing direction reflected both the visual feedback and the motor pointing direction, indicating that subjects attributed the prediction error to internal *and* external causes.

Moreover, the relative weight of visual information [18], which captured the internally attributed error share, showed a unimodal distribution across trials (for details, compare Figure 4), i.e. the values of the relative visual weight scattered around their mean for each amount of manipulation. This distribution does not support a dichotomous error attribution [14,15] to either internal or, alternatively, external causes, but rather suggests a continuous attribution mechanism on the level of *single* trials. Such partial attribution of prediction errors to internal causes would be consistent with the notion that the perception of one's actions builds on the *integration* of internal and external action-related cues [26,27,28,29].

Quantitatively, we manipulated the relative weight of visual information in this integration – and thus the internally attributed *share* of the prediction error – by varying the size of the prediction errors: the relative visual weight decreased significantly with increasing amounts of feedback manipulation (see Figure 3B), hereby reflecting the decrease in the probability that the prediction error resulted from internal causes [13,14,15,16,17]. If the discrepancy between the actual and the internally predicted visual feedback was small, the perceived pointing direction strongly reflected the feedback manipulation (red line in Figure 3A), which indicated that subjects attributed the prediction error mainly to internal causes. In contrast, if the prediction error was large, subjects' estimated pointing direction rather resembled the motor pointing direction (green line in Figure 3A), which indicated that they attributed the prediction error mainly to external causes. This decrease of the internally attributed error share with increasing error size is consistent with the detection thresholds for visuomotor rotations which were found in comparable tasks [30,31,32]: feedback rotations of approximately 13° are commonly detected as externally caused in every second trial. In our study, the internally attributed share was more than 0.5 for prediction errors below this detection threshold and decreased to less than 0.5 for prediction errors above the detection threshold.

Recalibration of Internal Sensory Predictions through Causal Error Attribution

We analysed the effect of feedback manipulations on subjects' internal predictions about the visual consequences of their actions on the basis of subjects' perceived pointing directions in perceptual probe trials (compare Figure 2C). Since, in these trials, subjects received no visual feedback about their pointing movements and since these movements were internally guided, i.e. not directed by any external visual goal, subjects' perceptual estimate of their pointing direction needed to rely entirely on internal cues related to the actual movement. Such cues could be efference copies of motor commands [4,33], corollary discharge [5,34] and/or proprioception [35], as discussed in detail elsewhere [8]. Since subjects needed to base the perceptual estimate of their movements entirely on internal information, we assumed that the perceived pointing direction in perceptual probe trials captured a prediction of the visual action consequences which is based on internal information – i.e. it captured an *internal* sensory prediction [6,36].

Subjects' internal sensory predictions recalibrated in response to the prediction errors [12] which we generated in feedback trials. Recalibration occurred although these prediction errors were unpredictable. Thus, no consistent discrepancy between the actual and the internally predicted visual action consequences [8,37] was necessary to induce recalibration. Remarkably, large prediction errors, i.e. amounts of feedback manipulation of 20° and 40°, resulted in a less than proportional recalibration of subjects' internal sensory predictions in comparison to the recalibration induced by small errors, i.e. amounts of manipulation of 10°. Correspondingly, the relative recalibration, i.e. the quotient of recalibration and preceding feedback manipulation, decreased significantly with increasing error size (Figure 3D). A model which assumes that the recalibration of subjects' internal sensory predictions increases proportionally with the prediction error thus cannot account for our results because one would then expect the relative recalibration to be constant across feedback manipulations [38,39]. Instead, the recalibration of subjects' internal sensory predictions correlated significantly with the internally attributed component of the prediction error, i.e. the perceived pointing direction in the preceding feedback trial (Figure 5 and Table S1). We thus characterised the recalibration of internal sensory predictions employing an indirect measure of each subject's causal attribution of single prediction errors and following a *trial-by-trial* approach [19,20]: our results suggest that the recalibration of internal sensory predictions depends on the *attribution* of prediction errors to internal causes. Notably, the correlation between subjects' perceived pointing direction in feedback trials and their perceived pointing direction in the consecutive perceptual probe trials could also be found *within* errors of equal size (Figure 5). This means that also those differences in the recalibration of subjects' internal sensory predictions which resulted from errors of the *same* size could be predicted by the component of the prediction error which subjects attributed to their sensorimotor system. In other words, if recalibration occurred, then the causal attribution of the error was decisive for recalibration independently of the given error size.

We found significant recalibration only for those errors which exceeded 5° of amount. The observation that feedback manipulations of 5° failed to induce any recalibration (Figure 3D) despite obtaining significant weight in subjects' perceived pointing direction (Figure 3B) is suggestive of an *error deadzone*, i.e. errors need to surpass some minimum threshold to recalibrate one's internal sensory predictions [40,41]. This absence of adaptation was supported by an absence of correlation between the perceived pointing direction in feedback trials and the perceived pointing direction in the consecutive perceptual probe trials for errors of 5° (Figure 5). The putative error deadzone could reflect an ecologically valuable means to take into account the noise which is inherent to any nervous system, namely by limiting the recalibration of sensory predictions to those errors that exceed the noise level. Actually, the absence of recalibration for errors of 5° parallels the fact that these errors were well below the detection thresholds for visuomotor rotations which were found in comparable paradigms (approximately 13°) [30,31,32]. Still, we cannot exclude that our experiment might have failed to capture subjects' recalibration to small errors due to the limited sensitivity of our methods.

Possible Constraints of Measuring Recalibration

The systematic change of the perceived pointing direction in perceptual probe trials – which we interpreted as recalibration of subjects' sensory predictions in response to the experimentally generated prediction errors – could have possibly been mediated by unspecific biases in subjects' behaviour unrelated to any recalibration of subjects' sensory predictions, which we address here. With regard to such biases, it is notable that the influence of the feedback manipulation in feedback trials on subjects' perceived pointing direction in the consecutive perceptual probe trials was unlikely due to an unspecific transfer from feedback trials to perceptual probe trials since, in perceptual probe trials, subjects were not required to reproduce the motor pointing direction of the preceding feedback trial, but were instructed – as for feedback trials – to freely choose any directions in the sector between the subjective directions of anterior and rightwards for their movements. Indeed, subjects did not systematically reproduce the motor pointing direction of feedback trials in the consecutive perceptual probe trials (compare Discussion S1). Analogously, subjects did not systematically reproduce the perceptual estimate of their pointing direction in feedback trials in the consecutive perceptual probe trials (as quantified by the estimated pointing direction, not the perceived pointing direction, compare Discussion S1). Furthermore, the perceived pointing direction, which is a relative measure of subjects' perception of their actions, was unbiased by the motor pointing direction (compare Results: Recalibration of internal sensory predictions). Likewise, there were no significant differences in gaze direction across feedback manipulations (Figure S3), neither in feedback nor in perceptual probe trials, which could have possibly confounded the influence of the feedback manipulation on subjects' perception of their pointing direction [42]. Moreover, the change of subjects' perceived pointing direction in perceptual probe trials was unlikely caused by subjects' visual reference system being modified by the preceding feedback rotations. In a comparable task, perceptual and motor adaptation to a constant visuomotor rotation were not accompanied by any bias in subjects' visual estimates of the rightward or the anterior direction [8]. In summary, it thus seems likely that the systematic change of subjects' perceived pointing direction in perceptual probe trials truly captured a recalibration of subjects' internal sensory predictions in response to the experimentally generated prediction errors.

Plastic Distinction of Self- and Externally Caused Sensory Afference

To distinguish between *externally* and *internally caused* sensory afference, sensory predictions about one's own movements remain to appear suitable internal reference signals [1,2,3]. As our findings suggest, these sensory predictions are no absolute references, but rather represent plastic and relative quantities: sensory predictions are internal reference signals which allow a causal attribution of sensory afference *and* in turn are recalibrated themselves based on the causal attribution of the sensory afference. However, given that sensory predictions were thought to capture the part of sensory afference which is *internally* caused [2,3], how can the prediction error – which supposedly reflects the *externally* caused component of the sensory afference – then be (partially) attributed to *internal* causes? We propose that this inference builds on additional information associated with the prediction errors. Such disambiguating information could result from sensorimotor processes directly [43,44], for instance in the form of error size [13,16], error systematics [45] and accompanying sensory events in other modalities [27]. The causal attribution of error signals could also be informed by one's prior assumptions about the world and oneself [46,47], by one's goals [48] and by the reward [49] or the affective outcomes [50] connected with one's actions. The role of *implicit* and *explicit* processes in this attribution thereby remains a question for future research [51,52]. In contrast to the aforementioned sources of information, the particular ecological value of internal sensory predictions consists – despite the continuous need for recalibration – in their rapid and reliable availability [27,53].

Generalisation of Learning to Motor Behaviour

Internal sensory predictions have been shown to subserve both *perception* [11,54] and *control* of one's actions [8,9,23]. Indeed, subjects' average motor pointing direction in perceptual probe trials changed in a manner which compensated for the predicted change in the visual consequences of the pointing movements (compare Figure 6B, also see [24,25]). Specifically, in perceptual probe trials, subjects' average *motor* pointing direction and their average *perceived* pointing direction correlated significantly in a negative manner (compare Results: Generalisation to motor behaviour). This finding provides, to our knowledge, first evidence for previous assumptions made in research of the *motor* domain which suggested that causal inferences about motor errors determine the degree of motor adaptation [16]: Wei and colleagues [16] proposed that the *relevance* of motor errors, i.e. the probability that a motor error results from intrinsic causes, would explain the subproportional relation between the size of movement errors and adaptive changes in motor behaviour. This relation has been frequently observed, e.g. in the adaptation of goal-directed reaching to visual movement errors [16], in saccadic adaptation to visual saccade errors [55] or in the adaptation of straight movements in disturbing force fields [56]. Our findings specify this notion by demonstrating that the relevant errors are those errors which are attributed to internal causes. Our study thus provides evidence for a general role of causal inferences about error information in sensorimotor learning: Sensorimotor recalibration occurs in response to those errors which – from the perspective of the nervous system – likely originate from internal causes. Moreover, our findings suggest that both the recalibration of motor performance and the recalibration of internal sensory predictions build on adaptive changes in a shared internal forward model [9,23].

The notion of a shared internal sensory prediction is supported by previous visuomotor adaptation experiments [8,30,31]. However, motor and sensory recalibration could still be processes which occur simultaneously [24,25,57], yet dissociate from each other [49,58,59]. Such dissociation might thereby be grounded in the differential objectives of motor and sensory learning: Unlike the recalibration of sensory predictions about one's movements, motor learning does not primarily aim at establishing congruence between the actual and the internally predicted sensory consequences of one's movements. Instead, motor learning can be understood as optimising the achievement of external goals [12,60]. The degree to which prediction errors are relevant to motor learning thus not only depends on the causal attribution of these errors to internal versus external causes [16,43], but also on (reward) prediction errors related to the achievement of one's goals [49].

Causality and Systematics of Errors in Learning

The relevance which error signals receive in sensorimotor learning could also reflect the *systematics* in the occurrence of errors [59]: While our findings emphasise the role of error causality for *unsystematic* errors, the causal attribution of errors to external versus internal sources might be equally important for learning from *systematic* errors [45]. This might be surprising at first glance since – in contrast to the case of unsystematic errors – it seems plausible to compensate for any systematic error irrespective of whether this error is internally or externally caused. Yet, the way *how* one compensates for internally versus externally caused systematic errors might be different: First, the causal attribution of *systematic* errors to an *external* cause could be understood as a change of context. The causal attribution of errors to a specific external context is essential to allow *context-dependent* learning. Only thus can we learn to reliably and efficiently predict the sensory consequences of our movements in specific external contexts (e.g. with versus without wearing glasses). Second, the causal attribution of *systematic* errors to *internal* causes is decisive if internal changes within the sensorimotor system are to induce learning which is independent of external contexts (e.g. transfer of rehabilitation training to everyday tasks). Thus, the causality of errors appears relevant to sensorimotor learning also in view of error systematics.

In summary, the causal attribution of error signals may provide a general framework for understanding the plasticity of both perception and control of one's actions.

Materials and Methods

Subjects

Eleven right-handed healthy subjects (4 women, 7 men, mean age ± standard error: 28.09 ± 1.77 years) with normal or corrected-to-normal visual acuity participated in the study. All subjects gave written informed consent according to the Declaration of Helsinki. The study was approved by the ethics committee of the University of Tübingen, Germany.

Experimental Setup

Subjects performed pointing movements in a *virtual-reality setup* [8,30,31] in which the visual consequences of their movements could be manipulated in real time (compare Figure 2A). They were seated in front of a horizontal board with their heads stabilised in a head-and-chin rest. Via a horizontal mirror, subjects viewed a computer screen which was positioned horizontally and upside-down above the mirror. Since the mirror was located halfway between the board and the screen, this screen – on which visual feedback about subjects' movements was provided – appeared to be in the plane of the horizontal board. Subjects were instructed to place both hands on the board and therefore could not see their hands. To reduce spatial information for orientation, we conducted the experiment in darkness.

We instructed subjects to perform their pointing movements with their right index finger on the board surface. We recorded the position of the fingertip online using a three-dimensional ultrasound-based motion-tracking system (*Zebris CMS 70 P*, Isny, Germany). Via the mirror-screen setup, we could provide subjects with visual feedback about the position of their right index fingertip in real time (60 Hz).

The experiment was realised using *Cogent Graphics* developed by John Romaya at the Laboratory of Neurobiology at the Wellcome Department of Imaging Neuroscience (London, UK) and the *Psychophysics Toolbox* [61,62].

Experimental Procedure

Subjects performed centre-outward-and-back *pointing movements* with their right index finger on the board surface (see Figure 2A). A haptic marker on the board defined the starting and end point of these movements. On the screen, this marker was veridically represented by a white disc (0.25° radius). Subjects were instructed to move out and back as straight and fast as possible. In each trial, the pointing amplitude was indicated by a briefly flashed circle (300 ms duration, 9.0° radius) whose centre corresponded to the starting point. Subjects did not receive specific visual targets for their pointing movements, but were instructed to freely choose any directions in the upper right quarter of the initially flashed circle, i.e. the sector between the subjective directions of anterior and rightwards.

The two *experimental conditions*, feedback trials and perceptual probe trials, were presented alternately. In *feedback trials* (Figure 2B), subjects received online visual feedback about their movement. Specifically, subjects' fingertip was represented by a white disc (radius: 0.20°) which moved in an experimentally controlled relation to the fingertip. This *visual feedback* was either veridical or, alternatively, rotated around the starting point by various angles. In each trial, the rotation angle was randomly drawn from a discrete uniform distribution over the values 5°, 10°, 20°, 40° (counterclockwise rotation), −5°, −10°, −20°, −40° (clockwise rotation) and 0° (veridical feedback). To prevent online correction of subjects' movements, we provided visual feedback only for the peripheral part of the movements (amplitude >4.5°) and limited feedback presentation to 1000 ms after movement onset. In *perceptual probe trials* (Figure 2C), subjects did not receive any visual feedback about their movement. Here, we only presented the central white disc and the circle which indicated pointing amplitude.

After each pointing movement, subjects visually estimated the direction of their actual movement by placing – with their left hand – a trackball-guided cursor in the respective direction. The procedure by which subjects estimated their pointing direction was identical in feedback and perceptual probe trials. Note that subjects were not required to reproduce their movement. Instead, rotation of the trackball was transformed into circular movement (4.5° radius) of another white disc (0.15° radius) around the starting position (0.25° radius). When having placed this disc relative to the starting position in the *estimated direction* of their movement, subjects confirmed their estimate by pressing the right trackball button. Note that subjects were instructed to fixate their gaze on the starting point during movement execution, but that fixation was not required during the subsequent estimation of the movement direction.

During the measurement, trials were declared invalid if the amplitude of the executed movement was less than half of the instructed amplitude or if subjects provided no perceptual estimate of the pointing direction. Altogether, each subject needed to complete 180 valid feedback trials and 180 valid perceptual probe trials. To ensure that subjects could execute the task correctly, we had them perform 20 practice trials in advance (first a block of 10 veridical feedback trials, then a block of 10 perceptual probe trials).

Data Analysis

We recorded each movement trajectory for offline analysis. The direction of the pointing movement was defined as the direction of a straight line which we fitted to the horizontal position samples acquired during the outward movement of the finger by means of a linear regression analysis (for details, compare [8]).

During offline analysis, we discarded those trials in which the curvature of the trajectory was particularly pronounced, thus ensuring to remove those trials in which subjects might have corrected their movement online. Specifically, if the maximum deviation of the outward movement from the straight line connecting the starting point and the end point of the outward movement exceeded 2.25° (i.e. one quarter of the instructed movement amplitude), this trial was excluded. Furthermore, to remove trials with sampling artefacts specific to our ultrasound-based motion-tracking method, we excluded those trials in which the absolute movement velocity exceeded 120°/s. As we evaluated perceptual probe trials in terms of the manipulation applied in the respective preceding feedback trials, we further discarded all perceptual probe trials which immediately followed on invalid or discarded feedback trials.

On average, subjects performed 185.55±3.64 feedback trials and 183.82±3.32 perceptual probe trials (mean ± standard error). After applying the above exclusion criteria, we evaluated 171.09±3.60 feedback trials and 163.45±6.68 perceptual probe trials. The number of evaluated trials did not differ significantly across manipulation angles, neither for feedback trials (repeated-measures ANOVA, F(3.55, 35.47) = 1.32, P = .282) nor for perceptual probe trials (repeated-measures ANOVA, F(3.52, 35.22) = 1.59, P = .205). In all analysed feedback trials, pointing amplitude was more than 4.5°, which confirms that subjects indeed received visual feedback in these trials.

To account for our *within-subject design*, we analysed subjects' performance using two-way repeated-measures ANOVAs with the factors orientation and amount of manipulation (see Results). We used Mauchly's test to check if the assumption of sphericity was tenable. Whenever sphericity was violated, we corrected the degrees of freedom according to Greenhouse and Geisser. We performed post-hoc analyses (paired one-tailed t-tests, Bonferroni-corrected for multiple comparisons) only if the according main effect was significant.

In all figures, we provide mean values and standard errors calculated across subjects. Figure 3A and 3C display subjects' *offset-corrected perceived pointing directions*. *Within subjects*, we offset-corrected the perceived pointing direction in feedback trials (see Figure 3A and Figure S1A) by subtracting the mean perceived pointing direction of feedback trials with veridical feedback. Analogously, we offset-corrected the perceived pointing direction in perceptual probe trials (see Figure 3C and Figure S1B) by subtracting the mean perceived pointing direction of those perceptual probe trials preceded by veridical feedback. We performed such offset-correction to account for systematic differences between the estimated and the motor pointing direction which are commonly revealed in comparable tasks [24,25,30,31].

To account for *between-subject* variance in our figures, further normalisation was performed as suggested by Masson and Loftus [63]: "Normalization is based on the deviation between a subject's [i] overall mean [m_i], computed across that subject's scores in each condition, and the grand mean [GM] for the entire sample of subjects […]. That deviation is subtracted from the subject's score [X] in each condition [j] (i.e., X_{ij} – (M_i – GM)) to yield a normalized score for that subject in each condition […]." Accordingly, across-subject averages remained unchanged by this normalisation while the measures of variability (specifically, the standard errors) excluded the between-subject variability and represented the *average within-subject variability* only.

Supporting Information

Figure S1 Perceived pointing direction before offset-correction. Panel (A) displays the perceived pointing direction (PPD, mean ± standard error) in *feedback trials* as a function of the manipulation applied to the visual feedback. Analogously, Panel (B) shows the PPD in *perceptual probe trials* as a function of the visual manipulation in the *preceding* feedback trial. Unlike in Figures 3A and 3C, the data displayed here are original data before offset-correction: the estimated direction of the pointing movement was

systematically shifted in relation to the motor pointing direction, which is a common finding in comparable tasks [8,24,25,30,31].
(TIF)

Figure S2 Spatial distribution of the motor pointing direction. Subjects did not receive specific visual targets for their pointing movements, but were instructed to freely choose any directions in the upper right quarter of the initially flashed circle, i.e. the sector between the subjective directions of anterior (90°) and rightwards (0°). In fact, subjects' motor pointing directions were mainly distributed between 10° and 70°, both in feedback (A) and perceptual probe trials (B), as the histograms illustrate (mean ± standard error across subjects).
(TIF)

Figure S3 Gaze direction during movement execution. Since gaze direction can modify the perception of one's hand position [42], systematic differences in gaze direction could have possibly confounded the influence of feedback manipulations on subjects' perceived pointing direction. We therefore required subjects to fixate on the starting point of their pointing movements during movement execution and, additionally, analysed subjects' gaze direction as a function of feedback manipulation. We recorded the position of subjects' left eye using a video-based dark-pupil tracking method (ViewPoint Eye Tracker, Arrington Research Inc., Scottsdale, USA). Eye position was sampled at 50 Hz and processed offline. After filtering the data (second-order 10 Hz Chebyshev digital low-pass filter Type II, $R = 3$), we removed artefacts owing to eye blinks by means of an eye position criterion. We analysed subjects' eye position during a period of 1000 ms starting at the moment that the finger-centre distance exceeded 4.5° visual angle. In other words, the epoch during which gaze was evaluated equalled the maximum possible period of feedback presentation during feedback trials (see Methods, Experimental Procedure). For each trial, we determined the mean position of gaze on the movement plane. We then calculated the direction of this position from the starting point of the pointing movements and, finally, the direction of gaze *relative* to the direction of subjects' pointing movement. Eye movements were measured and evaluated for ten of our eleven subjects. Panel (A) shows subjects' *relative gaze direction* as a function of the visual manipulation in *feedback trials* (mean ± standard error). Panel (B) shows the relative gaze direction in *perceptual probe trials* as a function of the preceding feedback manipulation. Feedback manipulation did not modify the relative gaze direction significantly, neither in feedback trials (repeated-measures ANOVA, $F(8, 72) = 1.26$, $P = .279$) nor in perceptual probe trials (repeated-measures ANOVA, $F(8, 72) = 0.46$, $P = .882$). Thus, the differences in subjects' perceived pointing direction across feedback manipulations cannot be explained by systematic differences in gaze direction.
(TIF)

Table S1 Trial-by-trial recalibration of internal sensory predictions. A linear regression analysis revealed that subjects' internal predictions about the sensory consequences of their actions were recalibrated on a trial-by-trial basis. Specifically, we performed a linear regression analysis which used the perceived pointing direction in feedback trials to predict the perceived pointing direction in the consecutive perceptual probe trials. For each subject, the table reports the degrees of freedom (df), the correlation coefficient (r), the P-value (P) and the regression coefficient (m) obtained in this analysis.
(PDF)

Discussion S1 Possible constraints of sensorimotor recalibration.
(PDF)

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Author Contributions

Edited the manuscript: MS AL. Conceived and designed the experiments: AL CW. Performed the experiments: CW. Analyzed the data: CW. Wrote the paper: CW.

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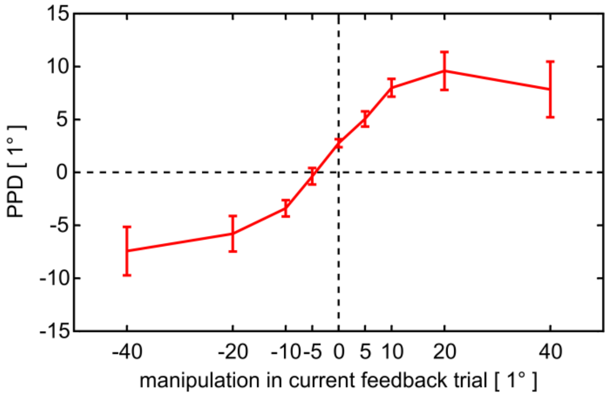
A Feedback Trials



B Perceptual Probe Trials

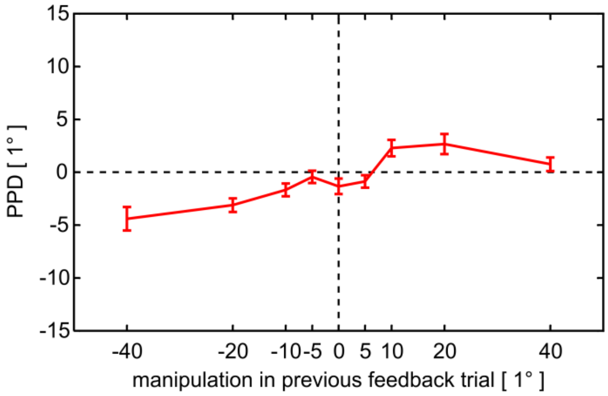


Figure S1. Perceived pointing direction before offset-correction.

Panel (A) displays the perceived pointing direction (PPD, mean ± standard error) in *feedback trials* as a function of the manipulation applied to the visual feedback. Analogously, Panel (B) shows the PPD in *perceptual probe trials* as a function of the visual manipulation in the *preceding* feedback trial. Unlike in Figures 3A and 3C, the data displayed here are original data before offset-correction: the estimated direction of the pointing movement was systematically shifted in relation to the motor pointing direction, which is a common finding in comparable tasks [8,24,25,30,31].

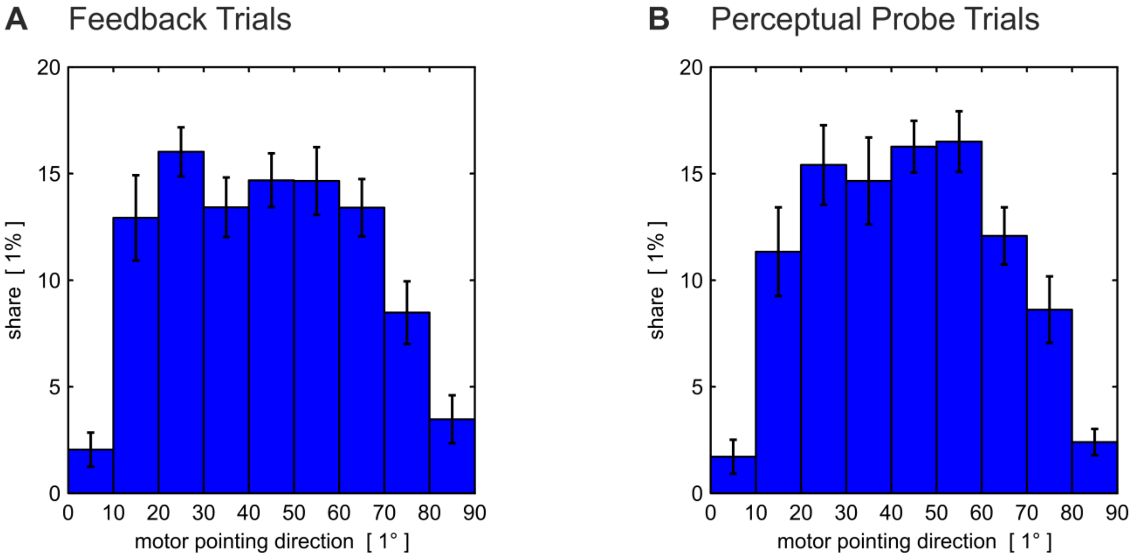
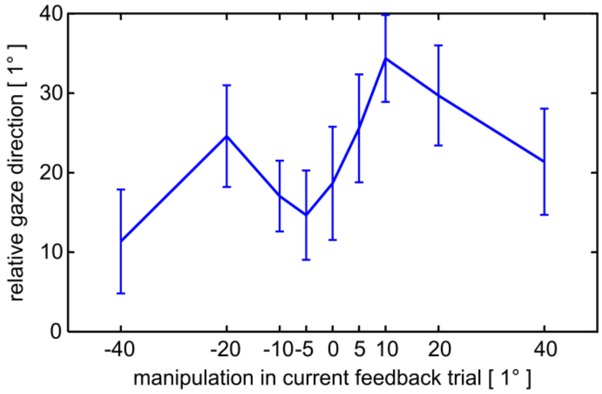


Figure S2. Spatial distribution of the motor pointing direction.

Subjects did not receive specific visual targets for their pointing movements, but were instructed to freely choose any directions in the upper right quarter of the initially flashed circle, i.e. the sector between the subjective directions of anterior (90°) and rightwards (0°). In fact, subjects' motor pointing directions were mainly distributed between 10° and 70°, both in feedback (A) and perceptual probe trials (B), as the histograms illustrate (mean ± standard error across subjects).

A Feedback Trials



B Perceptual Probe Trials

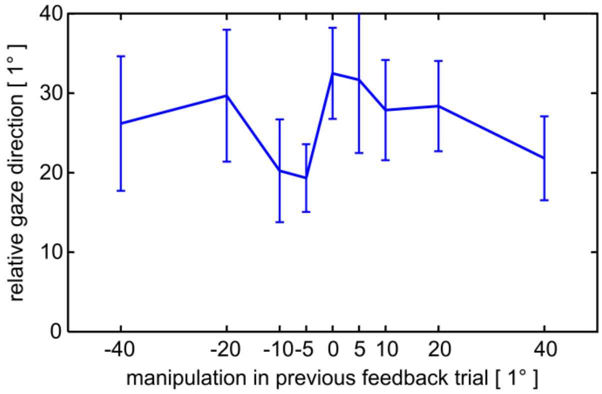


Figure S3. Gaze direction during movement execution.

Since gaze direction can modify the perception of one's hand position [42], systematic differences in gaze direction could have possibly confounded the influence of feedback manipulations on subjects' perceived pointing direction. We therefore required subjects to fixate on the starting point of their pointing movements during movement execution and, additionally, analysed subjects' gaze direction as a function of feedback manipulation.

We recorded the position of subjects' left eye using a video-based dark-pupil tracking method (ViewPoint Eye Tracker, Arrington Research Inc., Scottsdale, USA). Eye position was sampled at 50 Hz and processed offline. After filtering the data (second-order 10 Hz Chebyshev digital low-pass filter Type II, R = 3), we removed artefacts owing to eye blinks by means of an eye position criterion.

We analysed subjects' eye position during a period of 1000 ms starting at the moment that the finger-centre distance exceeded 4.5° visual angle. In other words, the epoch during which gaze was evaluated equalled the maximum possible period of feedback presentation during feedback trials (see Methods, Experimental Procedure). For each trial, we determined the mean position of gaze on the movement plane. We then calculated the direction of this position from the starting point of the pointing movements and, finally, the direction of gaze *relative* to the direction of subjects' pointing movement. Eye movements were measured and evaluated for ten of our eleven subjects.

Panel (A) shows subjects' *relative gaze direction* as a function of the visual manipulation in *feedback trials* (mean ± standard error). Panel (B) shows the relative gaze direction in *perceptual probe trials* as a function of the preceding feedback manipulation. Feedback manipulation did not modify the relative gaze direction significantly, neither in feedback trials (repeated-measures ANOVA, $F(8, 72) = 1.26$, $P = .279$) nor in perceptual probe trials (repeated-measures ANOVA, $F(8, 72) = 0.46$, $P = .882$). Thus, the differences in subjects' perceived pointing direction across feedback manipulations cannot be explained by systematic differences in gaze direction.

Table S1. Trial-by-trial recalibration of internal sensory predictions.

A linear regression analysis revealed that subjects' internal predictions about the sensory consequences of their actions were recalibrated on a trial-by-trial basis. Specifically, we performed a linear regression analysis which used the perceived pointing direction in feedback trials to predict the perceived pointing direction in the consecutive perceptual probe trials. For each subject, the table reports the degrees of freedom (df), the correlation coefficient (r), the P-value (P) and the regression coefficient (m) obtained in this analysis.

subject	df	r	P	m
1	166	0.176	0.022	0.134
2	176	0.331	< 0.001	0.303
3	106	0.065	0.505	0.056
4	158	0.211	0.008	0.228
5	177	0.175	0.019	0.152
6	134	0.292	< 0.001	0.165
7	174	0.221	0.003	0.184
8	173	0.236	0.002	0.216
9	169	0.538	< 0.001	0.508
10	167	0.374	< 0.001	0.330
11	176	0.151	0.045	0.133

Discussion S1. Possible constraints of sensorimotor recalibration.

The correlation between the component of the prediction error which subjects attributed to internal causes and the systematic change of subjects' sensory predictions which we observed in perceptual probe trials could have possibly been mediated by unspecific biases in subjects' motor behaviour or their perceptual reports. First, subjects could have reproduced the motor pointing direction of feedback trials in the following perceptual probe trials. Second, the manipulation of the visual feedback could have induced a common spatial bias of subjects' estimated pointing directions in both feedback trials and the consecutive perceptual probe trials. Each of these biases could have underlain the correlation between subjects' perceived pointing direction in feedback trials and the perceived pointing direction in the consecutive perceptual probe trials. Hence, each bias could challenge our interpretation that the causal attribution of prediction errors guided the recalibration of subjects' sensory predictions.

To exclude the possibility of reproduced motor pointing directions, we calculated the correlation of each subject's motor pointing directions in feedback and consecutive perceptual probe trials. Within subjects, this correlation was -0.071 ± 0.090 (mean ± standard error) and not significantly different from 0 (one-sample two-tailed t-test, t(10) = -0.80, P = .444). Additionally, we found no significant influence of feedback manipulation on this correlation (repeated-measures ANOVA, F(8, 80) = 0.45, P = .889). Hence, subjects did not systematically reproduce their motor pointing directions, but chose their motor pointing directions in feedback and consecutive perceptual probe trials independently.

To further exclude that the visual feedback had induced a spatial bias in the estimated pointing direction unrelated to the actual movement, we calculated the correlation of subjects' estimated pointing directions between feedback and consecutive perceptual probe trials. Within subjects, this correlation was -0.038 ± 0.091 (mean ± standard error) and not significantly different from 0 (one-sample two-tailed t-test, t(10) = -0.42, P = .685). Moreover, there was no significant influence of feedback manipulation on this correlation (repeated-measures ANOVA, F(8, 80) = 0.62, P = .763). We therefore assume that subjects did not systematically reproduce their estimated pointing directions in consecutive feedback and perceptual probe trials. In other words, a spatial bias in the estimation of the pointing directions which is unrelated to the actual motor pointing directions appears unlikely to explain the systematic change of subjects' perceived pointing directions in perceptual probe trials.

3.2. Modulation der Wahrnehmung eigener Bewegungen durch Handlungsergebnisse

Grundlage dieses Abschnitts ist die folgende Publikation: Wilke C*, Synofzik M*, Lindner A. (2012). The valence of action outcomes modulates the perception of one's actions. *Conscious Cogn* 21(1):18-29. (*These authors contributed equally.) Ergänzend finden sich in diesem Abschnitt auch die supplementären Informationen, welche online erschienen sind.

3.2.1. Zusammenfassung und Bezug zur Fragestellung

Die Wahrnehmung der eigenen Bewegungen und ihre Plastizität beruhen besonders auf dem Vergleich der tatsächlichen sensorischen Bewegungsfolgen mit der intern prädizierten Reafferenz. Jedoch müssen wir für unsere Interaktion mit der Umwelt oft weitere Informationen berücksichtigen, wie beispielsweise die Ergebnisse unserer Handlungen (*action outcomes*). Solche Handlungsergebnisse könnten insbesondere dann für die eigene Bewegungswahrnehmung bedeutsam sein, wenn Diskrepanzen zwischen den tatsächlichen sensorischen Bewegungsfolgen und der intern prädizierten Reafferenz bestehen – wenn also sensorische Prädiktionsfehler auftreten, welche eine kausale Attribution an interne oder externe Ursachen erfordern (Abschnitt 3.1.).

Das vorliegende Experiment testete, ob Handlungsergebnisse wirklich die kausale Attribution eines sensorischen Prädiktionsfehlers modulieren. Dazu wurde in einer virtuellen Umgebung das visuelle Feedback über Handbewegungen so manipuliert, dass unvorhersehbare visuelle Prädiktionsfehler entstanden. Zugleich wurden Handlungsergebnisse dadurch geschaffen, dass affektives Bildmaterial (International Affective Picture System, Lang et al. 2008) als Ergebnis der visuellen Handbewegung präsentiert wurde. Dabei wurde die affektive Valenz des Bildmaterials experimentell so manipuliert, dass affektiv positive Ergebnisse mit affektiv negativen Ergebnissen verglichen werden konnten (bei vergleichbarem Arousal).

Tatsächlich reflektierte die Wahrnehmung der eigenen Bewegungen nicht nur die sensorischen und die internen Bewegungsinformationen, sondern auch die experimentell generierten Handlungsergebnisse: Die wahrgenommene Richtung der Bewegungen entsprach eher den affektiv positiven Ergebnissen als den negativen. Die Probanden attribuierten visuelle Prädiktionsfehler also dann an das eigene sensomotorische System, wenn die tatsächlichen visuellen Bewegungsfolgen – bezogen auf die intern prädizierte Reafferenz – hin zu positiven Ergebnissen und weg von negativen Ergebnissen manipuliert waren. Derselbe Fehler wurde dagegen an externe Ursachen attribuiert, wenn die visuellen Bewegungsfolgen hin zu negativen und weg von positiven Ergebnissen manipuliert waren.

Damit zeigte das Experiment grundsätzlich, dass Handlungsergebnisse die kausale Attribution eines sensorischen Prädiktionsfehlers an interne versus externe Ursachen ändern können. Diese Attribution ist also nicht konstant für eine gegebene absolute Fehlergröße, sondern plastisch.

Darüber hinaus zeigte das Experiment, dass der Vergleich der tatsächlichen und der intern prädizierten sensorischen Bewegungsfolgen – anders als durch das Komparatormodell gefordert – keineswegs hinreichend für die Wahrnehmung der eigenen Bewegungen ist (Abschnitt 1.2.). Vielmehr können weitere Faktoren diese Wahrnehmung nachträglich – also postdiktiv – formen (Synofzik et al. 2013).

3.2.2. Originalpublikation

Die Reproduktion der Publikation im Rahmen der vorliegenden Dissertation erfolgte mit der freundlichen Genehmigung des Verlags Elsevier vom 11. August 2013.

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The valence of action outcomes modulates the perception of one's actions ☆

Carlo Wilke [a,1], Matthis Synofzik [b,c,*,1,2], Axel Lindner [a,*,2]

[a] *Department of Cognitive Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Hoppe-Seyler-Str. 3, 72076 Tübingen, Germany*
[b] *Department of Neurodegeneration, Hertie-Institute for Clinical Brain Research, University of Tübingen, Hoppe-Seyler-Str. 3, 72076 Tübingen, Germany*
[c] *German Centre for Neurodegenerative Diseases (DZNE), University of Tübingen, Germany*

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ABSTRACT

When interacting with the world, we need to distinguish whether sensory information results from external events or from our own actions. The nervous system most likely draws this distinction by comparing the actual sensory input with an internal prediction about the sensory consequences of one's actions. However, interacting with the world also requires an evaluation of the outcomes of self-action, e.g. in terms of their affective valence. Here we show that subjects' perceived pointing direction does not only depend on predictive and sensory signals related to the performed action itself, but also on the affective valence of the action outcome: subjects perceived their movements as directed towards positive and away from negative outcomes. Our findings suggest that the non-conceptual perception of the sensory consequences of self-action builds on both sensorimotor information related directly to self-action and a post hoc evaluation of the affective action outcome.

1. Introduction

To successfully interact with the world, we constantly need to assess whether afferent information results from the outside world or from our own actions. This distinction might be drawn by the nervous system through a simple computational mechanism (Frith, 1992; Frith, Blakemore, & Wolpert, 2000): in order to identify externally caused sensory input, the afference is compared with an internal prediction (Wolpert, Ghahramani, & Jordan, 1995; Wolpert, Miall, & Kawato, 1998) about the sensory consequences of one's actions which builds on internal action-related signals, such as efference copies (von Holst & Mittelstaedt, 1950) or corollary discharge (Sperry, 1950) of motor commands. In case of a match, the afference is interpreted as a result of self-action. In case of a mismatch, the difference is interpreted as a result of an externally caused event. This mechanism – often referred to as the comparator model – provides a parsimonious explanation for a basic constituent of a *sense of agency*, i.e. the registration that one is the initiator of one's sensory action consequences (Frith, 1992, 2005).

Recent approaches, however, have questioned whether the comparator model can indeed sufficiently explain a sense of agency, particularly on the level of self-agency judgements, i.e. when making the conceptual distinction "it was me" vs. "it was not me" (Synofzik, Vosgerau, & Newen, 2008a). Such judgements might rely much more on prior background beliefs and a post hoc processing of action outcomes – e.g. affective evaluation and ad hoc reasoning – than on signals derived from the motor commands which guide one's actions. In fact, these factors might be of particular importance for self-agency

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* Corresponding authors. Address: Department of Neurodegeneration, Hertie-Institute for Clinical Brain Research, University of Tübingen, Hoppe-Seyler-Str. 3, 72076 Tübingen, Germany (M. Synofzik).

E-mail addresses: matthis.synofzik@uni-tuebingen.de (M. Synofzik), a.lindner@medizin.uni-tuebingen.de (A. Lindner).

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judgements in everyday contexts. For example, when a gust of wind diverts the trajectory of a golf ball in such a way that the ball finally hits into the hole, a golf player might attribute this outcome to her own agency – even if the actual stroke (and thus the predicted flight trajectory) would have missed the hole clearly. In this example, the subject might be willing to accept agency for the respective outcome simply because she liked to see the event as a consequence of her action – even though there was no corresponding match between the predicted and the actual sensory action consequences at the sensorimotor level (Johansson, Hall, Sikstrom, & Olsson, 2005; Synofzik et al., 2008a; Wegner & Sparrow, 2004).

But is the same true not only for self-agency judgements, but also for the perception of the sensory consequences of one's actions? This basic perceptual faculty is closely linked to internal predictions (Bell, 2001; Haarmeier, Bunjes, Lindner, Berret, & Thier, 2001; Synofzik, Thier, & Lindner, 2006) and it remains to be ascertained whether it is fully determined by these signals or whether it can be influenced by post hoc cognitive processing.

Here we hypothesised that the perception of a very basic action feature – namely the direction of one's movements – builds not only on internal predictions about the sensory consequences of an action, but also on post hoc information resulting from the action outcome. In particular, the valence of an unpredictable action outcome might modify how we perceive the directions of our movements: we might perceive our actions as directed towards positive rather than towards negative action outcomes.

We tested this hypothesis in a virtual-reality setup which allowed us to modify the visual feedback about subjects' centre-outward-and-back pointing movements in real time as well as to present pictures with unpredictable affective content at the turning point of the visual movement trajectories. Due to the design of our experiment, these pictures can be considered an action outcome. Subjects' perceived pointing direction did not only depend on the performed action, but was additionally shifted by this affective action outcome, namely towards positive and away from negative action outcomes. As these action outcomes were unpredictable – and hence could not have consistently related to specific intentions preceding and guiding the actions – the perception of self-action appears to build on both (1) predictive signals related to self-action itself (and their comparison with the actual sensory consequences) and (2) a post hoc evaluation of the affective action outcome.

2. Methods

2.1. Participants

Seventeen right-handed healthy subjects (10 women, 7 men, mean age ± standard deviation: 26.0 ± 3.5 years) with normal or corrected-to-normal visual acuity participated in the study. All subjects gave written informed consent according to the Declaration of Helsinki.

2.2. General task design

Before detailing our methods, we briefly describe the general task design (Section 2.2) and report the way in which we instructed our subjects (Section 2.3).

We operationalised self-action by asking subjects to perform continuous centre-outward-and-back pointing movements in freely chosen directions but of precued amplitude. Pointing movements were performed in a virtual-reality setup in which the visual consequences of subjects' actions could be manipulated in real time (Fig. 1A, for further details: Synofzik et al., 2006). Specifically, the visual feedback about subjects' pointing movements was rotated around the starting point of the movements in either a clockwise (cw) or a counterclockwise (ccw) direction (Fig. 1B). Across trials, we varied both the amount and the direction of feedback rotation and asked subjects to report whether their true pointing direction was either clockwise or counterclockwise relative to the visual feedback. We thereby estimated subjects' detection threshold for feedback deviations as well as their point of subjective equivalence between the visual feedback direction and the perceived pointing direction (procedure described in further detail in Section 2.4).

In order to study the influence of affective action outcomes on subjects' perceived pointing direction, we associated pointing movements of certain amplitude with a pair of images of unpredictable affective content. Such an image pair appeared if and only if the amplitude of a movement approximately matched the precued amplitude. In this case, the image pair was centred on the point at which the visual trajectory of the centre-outward-and-back pointing movement reversed its direction, with one image being positioned counterclockwise and the other one clockwise. Thereby we could generate an *affective spatial gradient* along the same dimension in which the visual feedback was manipulated (compare Fig. 1B), namely by either placing a picture of positive valence on the counterclockwise side and another picture of negative valence on the clockwise side – or vice versa (Fig. 1C).

If indeed unpredictable affective outcomes of one's actions influenced the perception of self-action, then we would assume that the affective gradient should induce a measurable shift of subjects' perceived pointing direction towards positive and away from negative outcomes. Accordingly, a rotation of the visual feedback about one's actions should be less likely detected if this rotation is directed towards the positive than towards the negative content of the action outcome.

To test this prediction, we compared subjects' perceived pointing directions for three experimental conditions which determined the affective spatial gradient, i.e. the combination of the affective image contents in individual trials (Fig. 1C): with respect to the counterclockwise and the clockwise image position, subjects were either presented with $\text{positive}_{\text{ccw}}$–$\text{negative}_{\text{cw}}$

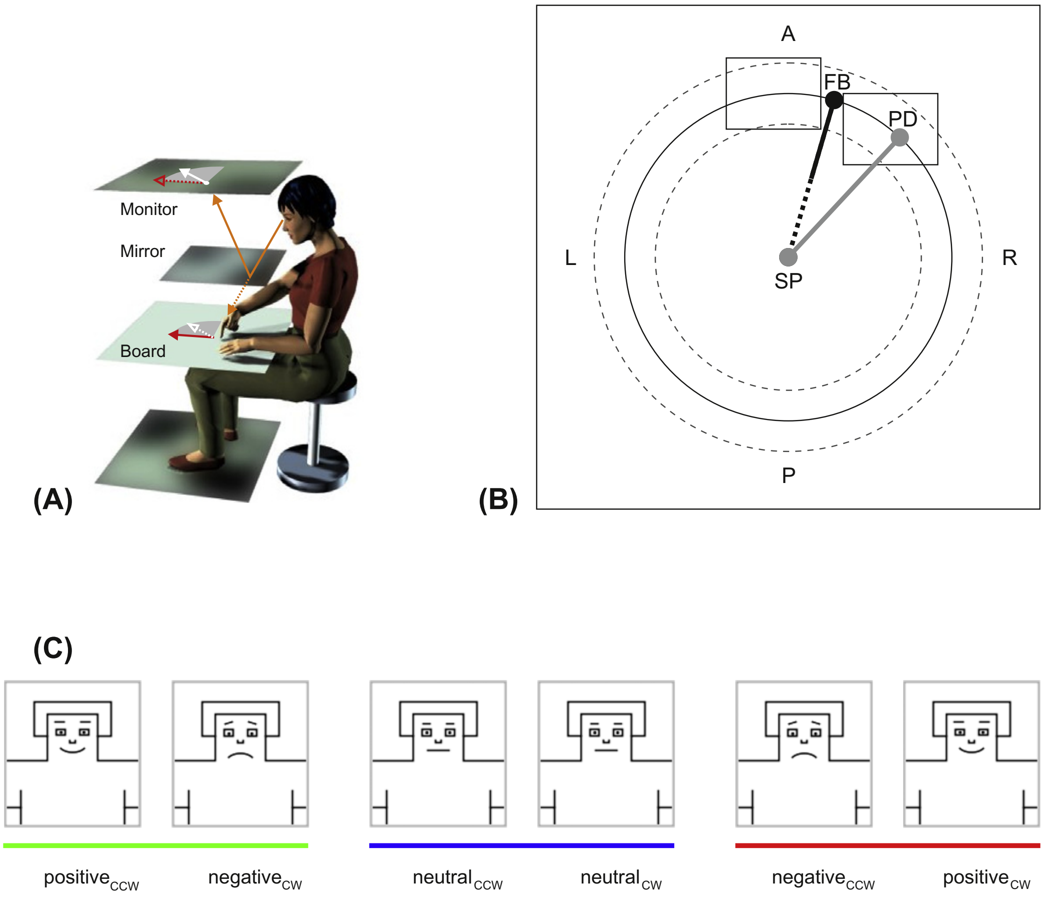

Fig. 1. Methods: (A) Setup. Subjects viewed a virtual image of their finger (white disc) on the feedback monitor via a mirror (solid orange arrow) while performing pointing movements. Due to geometric reasons, the virtual image appeared in the same plane as subjects' finger movements (dotted orange arrow). Visual feedback could be either veridical or manipulated online by rotation around the starting point of the movements (solid red arrow: actual movement vector, solid white arrow: rotated visual feedback vector, dotted arrows correspond to projections of these vectors into the monitor or the table plane, respectively). (B) Procedure. Subjects were instructed to freely choose varying pointing directions in the upper half of a circle (solid circle) which was flashed briefly at the beginning of each trial to instruct the movement amplitude. Visual feedback (FB) about the centre-outward-and-back pointing movement (PD) was provided in real time and only for the peripheral part of the movement trajectory (solid black line) in order to prevent any online correction of the movement. Subjects were informed that the visual feedback could be rotated either clockwise or counterclockwise (as in this example) around the starting point (SP) of the movements. When the finger reached the turning point of its trajectory (PD), two images (rectangles) were displayed in spatial alignment to the turning point of the visual feedback (FB). Importantly, the image pair appeared only if the pointing amplitude approximately matched the radius of the initially flashed circle (the two grey broken circles illustrate the respective range of adequate amplitudes; note that such lines were not shown to our subjects). In each trial, subjects finally reported the perceived direction of their actual movement relative to the visual feedback in a two-alternative forced-choice manner ("clockwise" vs. "counterclockwise"). In other words, subjects needed to decide whether they pointed rather towards the clockwise or the counterclockwise image. L, R, A and P denote left, right, anterior and posterior, respectively. (C) Experimental conditions. To create an affective gradient in space, two images taken from the Internal Affective Picture System, IAPS, were aligned to the turning point of the visual feedback. Three experimental conditions determined the combination of the affective contents in an image pair: positive$_{ccw}$–negative$_{cw}$ (green), neutral$_{ccw}$–neutral$_{cw}$ (blue) and negative$_{ccw}$–positive$_{cw}$ (red). To illustrate the average normative valence ratings in the three conditions, the portrait versions (Irtel, 2008) of the corresponding self-assessment manikins (Lang, 1980) are displayed.

or negative$_{ccw}$–positive$_{cw}$ image pairs or a baseline condition, i.e. neutral$_{ccw}$–neutral$_{cw}$ image pairs. Each subject had to complete 300 trials of adequate pointing amplitude, which were equally distributed across these three experimental conditions. The sequence of the experimental conditions was pseudo-randomised within each subject in a way which ensured that the trials of each condition were equally often preceded by trials of the other two conditions, respectively.

2.3. Task instructions

In the following, we provide a translated version of the key instructions issued verbally to the subjects by the experimenter. This information should help the reader to take a subject's perspective on our task.

"I would like you to perform pointing movements with your right index finger on the table surface. Please look at the mirror in front of you. There you will see a computer screen which is facing the mirror from above. For geometric reasons, this screen will appear in the same plane in which you will perform your movements. On this screen, you will see a white disc which moves in synchrony with your fingertip. The direction in which this disc moves, however, will deviate from the direction of your true movement. Specifically, the movement direction of the white disc will deviate from your true pointing direction to a variable extent, either being rotated in a clockwise or in a counterclockwise direction. Later, you will need to report whether your true pointing direction was either clockwise or counterclockwise relative to the movement direction of the white disc.

Start your movement when you see a white circle which shows briefly in the middle of the screen. For each pointing movement, freely choose any direction in the upper half of this circle, i.e. somewhere within the range of directions between nine and three o'clock. In the course of the experiment, choose various directions for your movements and try to distribute them equally between nine and three o'clock. Begin and end each movement with your right index fingertip on the nail head which you can feel on the table surface. Its location corresponds to the middle of the computer screen. When the circle appears, move your index finger in the chosen direction and move out as far as indicated by the flashed circle. Then immediately return with your finger to the nail head in the centre. Try to move out and back as straight and fast as you can.

If and only if the amplitude of your movement approximately matches the radius of the initially flashed circle, you will make a pair of images appear. Only if the image pair appears, you will be able to complete the trial. An image pair will appear at the very moment that you have completed the outward movement and start the backward movement. Movements too long and movements too short – in comparison to the circle line – will not result in the appearance of an image pair. If no image pair appears, wait until the circle shows up again and then start a new movement. The images will be spatially aligned to the turning point of the visual movement, i.e. the point where the white disc is furthest away from the centre. One image will appear at a counterclockwise position and another one at a clockwise position relative to this turning point.

After you completed your movement, I would like you to estimate your true pointing direction in comparison with the movement direction of the white disc: when having returned to the nail head, decide whether your true pointing movement was directed rather towards the counterclockwise or towards the clockwise positioned image. You need to decide in each trial – even if you are unsure. If you are unsure, select the direction of the image that more likely reflected your true pointing direction. When the images have disappeared, indicate your decision by pressing either of the two buttons of the button box with your left hand. Press "left" if you decided on "counterclockwise" and "right" if you decided on "clockwise".

In order to complete the experiment, you will have to make 300 image pairs appear and to decide in each case which of the two images rather represented your true pointing direction."

After receiving these instructions, subjects performed 30 practice trials in which – instead of an image pair – two grey rectangles were displayed if pointing movements of adequate amplitude were performed. These practice trials ensured that subjects could execute the task correctly. Before the actual experiment, task instructions were repeated to subjects in a shorter version.

2.4. Experimental procedures

2.4.1. Pointing movements

Pointing movements were realised in a virtual-reality setup (Fig. 1A, for further details: Synofzik et al., 2006). In short, pointing movements were recorded by a three-dimensional real-time motion-tracking system (Zebris CMS 70 P; Isny, Tübingen, Germany), which recorded the position of an ultrasound emitter mounted on top of subjects' right index finger. Positional information was transferred to a stimulus computer which visually fed back the position of the fingertip via a monitor-mirror system (Fig. 1A). Feedback consisted of a 0.4°-diameter white disc. For geometric reasons, the visual feedback about the unseen fingertip position appeared in the plane of the table surface, i.e. it was in spatiotemporal correspondence with subjects' index finger as long as the feedback was veridical. The position of the disc was updated online at 60 Hz.

Subjects were instructed to perform centre-outward-and-back movements as straight and fast as possible. A tactile cue located at the centre of the table served as the starting and end point of all outward-and-back movements. To prevent online correction of the pointing direction, we only provided visual feedback for the peripheral part of the movements (>2.4°) and limited the presentation time of the cursor to 1500 ms after movement onset. Moreover, trials with pronounced curvature of the pointing trajectory were excluded post hoc: if the maximum orthogonal distance of the outward movement from a straight line connecting the starting point and the turning point of a movement was greater than 2.25° (i.e. 1/4 of the instructed movement amplitude), the trial was discarded. We also excluded the trials in which absolute movement velocity exceeded 120°/s. The latter criterion served to remove trials with sampling artefacts specific to the acoustic tracking method used. The share of trials that was excluded post hoc according to these criteria was 3.5% and did not significantly differ across conditions (one-way repeated-measures ANOVA, $F(2, 32) = 1.13$, $p > .05$).

2.4.2. Self-action estimates

To measure the perception of self-action, we asked subjects to report the perceived direction of each movement in a two-alternative forced-choice manner after completing the outward-and-back pointing movement. We varied both the amount and the direction of feedback rotation according to subjects' previous decisions on whether their true pointing directions were clockwise or counterclockwise relative to the visual feedback. Within each experimental condition, the rotation angles of the visual feedback in individual trials were determined by three randomly interleaved staircase procedures (PEST, parameter estimation by sequential testing; Lieberman & Pentland, 1982). The three staircase procedures held equal shares of 33% of trials per condition. Two staircase procedures targeted the rotation angle at which subjects decided on "clockwise" with a probability of 75% and 25%, respectively (PEST parameters: start value = −40°/40°, initial step size = −24°/24°, WALD = 0.75 each, $n \sim 33$ trials each, respectively). These angles – referred to as detection thresholds – indicated subjects' ability to detect manipulations of the visual feedback. A third staircase procedure targeted the point of subjective equivalence between the perceived movement and the visual feedback, providing us with a measure of subjects' perceived pointing direction. At this rotation angle, subjects decided at chance level, i.e. they reported "clockwise" and "counterclockwise" decisions with a probability of 50% each (PEST parameters: start value = 10°, initial step size = −24°, WALD = 0.5, $n \sim 33$ trials).

By means of a probitanalysis (McKee, Klein, & Teller, 1985), all data collected by the three staircase procedures were used to estimate a psychometric function describing the probability of a "clockwise" decision as a function of feedback rotation within each experimental condition (Fig. 2). Based on this function, the point of subjective equivalence ("clockwise" decision in 50%) and the so called just noticeable difference were calculated for each experimental condition and each subject. The just noticeable difference was defined as the mean absolute difference between the two detection thresholds ("clockwise" decision in 25% and 75%) and the point of subjective equivalence.

2.4.3. Affective action outcomes

As the primary aim of our study was to investigate the influence of affective action outcomes on the aforementioned estimates of self-action perception, we associated these outcomes with movements of adequate amplitude. Towards this end, a pair of affective photographic images was presented if and only if the actual movement amplitude approximately matched (7.4° < accepted amplitude < 10.6°) the amplitude precued by the initially flashed circle (radius: 9°). Note that due to the short presentation time of the circle (300 ms), it was no longer visible by the time subjects reversed their movements. Thus, subjects could not correct movement amplitude online. Instead, they had to plan a movement of appropriate amplitude beforehand. Then, by performing such a pointing movement of adequate amplitude, subjects *caused* the appearance of the image pair. However, they could not influence the image contents as these were determined by the experimental conditions. The image pairs can hence be considered the outcomes of subjects' actions while at the same time conveying an unpredictable affective content.

In order to complete the overall number of 300 trials of adequate pointing amplitude, subjects on average performed 103 trials in each of our three experimental conditions, with the number of trials not differing significantly across conditions

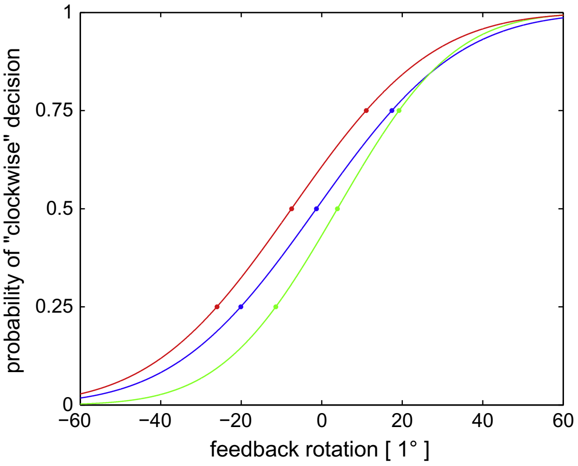

Fig. 2. Psychometric functions of an exemplary subject. Psychometric functions were calculated for each experimental condition (red: negative$_{ccw}$–positive$_{cw}$, blue: neutral$_{ccw}$–neutral$_{cw}$, green: positive$_{ccw}$–negative$_{cw}$): after each pointing movement, subjects needed to decide whether they pointed rather towards the clockwise image or, alternatively, towards the counterclockwise image, which were both spatially aligned to the visual feedback. In other words, subjects needed to report the perceived direction of their movements in comparison to the visual feedback. In each condition, a probit function was fitted to the data. This psychometric function described the probability of a "clockwise" decision as a function of the feedback rotation angle. Positive angles denote counterclockwise rotations. In this example, the points of subjective equivalence between the visual feedback and the perceived movement direction were 3.92° for the positive$_{ccw}$–negative$_{cw}$ and −7.47° for the negative$_{ccw}$–positive$_{cw}$ condition. This is in accordance with the hypothesis that subjects are more likely to perceive the trajectory of their movements as oriented towards a positive action outcome. For neutral$_{ccw}$–neutral$_{cw}$ image pairs, the point of subjective equivalence was −1.31° and thus located between the points of subjective equivalence of the non-neutral image pairs. In all conditions, the just noticeable differences – which represent how much the feedback needed to be rotated away from the point of subjective equivalence for the subject to decide on "clockwise" in 25% or 75% of trials – were of comparable size (18.77° in the neutral$_{ccw}$–neutral$_{cw}$ condition, 18.54° in the negative$_{ccw}$–positive$_{cw}$ condition and 15.31° in the positive$_{ccw}$–negative$_{cw}$ condition).

(one-way repeated-measures ANOVA, $F(2, 32) = 0.88$, $p > .05$). If subjects' movement amplitude was inadequate, no image pair was presented and the trial was declared invalid. The particular amount of feedback manipulation was then repeated by the adaptive procedure in the next trial. The average number of trials in which subjects both performed a movement of correct amplitude and provided a perceptual estimate was 98 in each condition and did not differ significantly across conditions (one-way repeated-measures ANOVA, $F(2, 32) = 0.81$, $p > .05$).

In case of pointing movements of adequate amplitude, the pair of images would appear when the finger reached the turning point of the centre-outward-and-back movement (Fig. 1B). The turning point of the movement trajectory was defined by the zero-crossing of the radial movement velocity (with positive and negative velocities reflecting outward and backward movements, respectively). Importantly, the two images were aligned to the turning point of the visual movement and not to the turning point of the actual movement. Images were 5.2° wide and 3.9° high. They were presented for 3500 ms and the absolute distance of each image centre from the visual turning point was 3.4°. One image was positioned counterclockwise with respect to the turning point while the other image was positioned clockwise. In other words, the image locations were in a constant relation to the visual feedback, but – due to the varying rotation of feedback – in a variable relation to the actual movement.

2.4.4. Experimental conditions

Three experimental conditions determined the combination of the individual image pair in a given trial. We selected 100 high-valence, 100 medium-valence and 100 low-valence colour images from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008), which will be referred to as positive, neutral and negative images, respectively.

The images were selected on the basis of the normative valence and arousal ratings provided in the IAPS manual. Valence ratings (1: unpleasant, 5: neutral, 9: pleasant) were 6.98 ± 0.56 for positive, 5.02 ± 0.29 for neutral and 3.05 ± 0.52 for negative images (mean ± standard deviation). Regarding valence, all three categories differed significantly from one another ($p < .05$, two-tailed independent *t*-tests, Bonferroni-corrected for multiple comparisons). Arousal ratings (1: calm, 5: neutral, 9: exciting) did not differ significantly for positive (5.19 ± 0.72) and negative images (5.27 ± 0.74). However, the arousal levels for these two image categories were significantly higher than for neutral images (3.15 ± 0.49), respectively ($p < .05$, two-tailed independent *t*-tests, Bonferroni-corrected for multiple comparisons).

By combining the images, we created 50 image pairs for each of the following three conditions (counterclockwise vs. clockwise positioned image): $\text{positive}_{\text{ccw}}$–$\text{negative}_{\text{cw}}$, $\text{neutral}_{\text{ccw}}$–$\text{neutral}_{\text{cw}}$, $\text{negative}_{\text{ccw}}$–$\text{positive}_{\text{cw}}$ (Fig. 1C). In all pairs, the images were matched for content category (human, animal, object, scene, environment) and arousal. A list of the IAPS serials of the image pairs can be found in Supplemental Table 1. All subjects viewed the same image pairs, but in an individually randomised sequence. Each image pair was presented twice to achieve a total of 300 trials.

Although all image pairs in themselves were matched for arousal, the mean arousal levels differed significantly between neutral and non-neutral image pairs. These differences in arousal (and thus in attention or in the weight attributed to the action outcomes) could possibly have introduced an experimental confound into our study (for empirical evidence see Press, Gherri, Heyes, & Eimer, 2010), which aimed at solely investigating the effect of valence on the perception of self-action. This confound must be considered when interpreting the results of our baseline condition, namely the $\text{neutral}_{\text{ccw}}$–$\text{neutral}_{\text{cw}}$ condition. Still, including the neutral image pairs in the experimental procedure was useful as the variable levels of arousal helped to maintain a high level of attention and interest throughout the experiment.

2.4.5. Eye movements

We did not restrict subjects' eye movements which were necessary to inspect the action outcomes under foveal vision. Still, we tested for possible differences in eye position across conditions which might have systematically biased subjects' self-action estimates. We therefore recorded the movements of subjects' left eye using a video-based dark-pupil tracking technique (ViewPoint Eye Tracker; Arrington Research Inc., Scottsdale, USA). Eye position was sampled at 50 Hz and processed offline using Matlab R2010b (The MathWorks, Natick, USA). After filtering the eye data (2nd-order 10 Hz Chebyshev digital low-pass filter Type II, $R = 3$), we removed artefacts due to eye blinks based on an eye position criterion. Then we calculated two-dimensional histograms of eye position for the time of image presentation (3500 ms). Specifically, we calculated the relative fixation time in which subjects' eyes remained at either of the two image positions. The size of each fixation window was slightly larger than the actual image (width 7.4°, height 5.5°). Yet, as in our setup subjects needed to direct their eyes downwards, with the upper lid often covering large parts of the pupil, eye movements could be reliably measured only in a subset of seven of our 17 subjects (see Supplemental Table 2).

3. Results

Our experiment tested whether the valence of action outcomes influences the perception of a basic feature of one's actions, namely the perception of one's pointing direction. Subjects performed centre-outward-and-back pointing movements of precued amplitude while the visual consequences of their movements were manipulated online. If the turning point of the visual movement approximated the precued amplitude, an image pair was presented at this turning point, producing an affective gradient in space. According to our hypothesis, the perceived pointing direction and, accordingly, the point of subjective equivalence between the visual feedback and the perceived movement should exhibit a relative shift along this affective gradient, namely towards the positive image and away from the negative image.

3.1. Points of subjective equivalence

Before detailing the results of those experimental conditions which actually conveyed an affective gradient in terms of valence, we focus on the point of subjective equivalence between the visual feedback and the perceived movement in our baseline condition, i.e. the neutral$_{ccw}$–neutral$_{cw}$ condition.

In this condition, we found an average point of subjective equivalence of −2.18 ± 1.52° (mean ± standard error). This means that, on average, visual feedback needed to be rotated clockwise by 2.18° with respect to the actual movement to be perceived as corresponding to subjects' performed pointing movements. Note that such a clockwise bias of the point of subjective equivalence has been consistently reported in our previous studies which used comparable experimental paradigms, but did not present images as affective action outcomes (Synofzik, Lindner, & Thier, 2008; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010; Synofzik et al., 2006). Other labs have reported a similar bias in proprioceptive estimates of hand position (Cressman & Henriques, 2009, 2010; Cressman, Salomonczyk, & Henriques, 2010; Jones, Cressman, & Henriques, 2010). Obviously, the clockwise bias of the point of subjective equivalence observed in the neutral condition is unlikely to be caused by the presentation of the image pairs, but rather reflected a general directional bias in perceiving one's hand movements, as we will discuss in detail below (compare Section 4). Importantly, however, the same bias should underlie all experimental conditions of this experiment. Thus, any directional changes in subjects' self-action estimates should not be interpreted in absolute (clockwise vs. counterclockwise) but in relative terms (more clockwise vs. more counterclockwise).

In fact, a clockwise bias was also observed in the positive$_{ccw}$–negative$_{cw}$ and the negative$_{ccw}$–positive$_{cw}$ condition while, across conditions, the point of subjective equivalence differed significantly (one-way repeated-measures ANOVA, $F(2, 32) = 4.32$, $p = .022$): for negative$_{ccw}$–positive$_{cw}$ image pairs, a clockwise rotation of the visual feedback by 5.10° (point of subjective equivalence: −5.10 ± 1.56°) was necessary to establish a correspondence with subjects' perceived movements (Fig. 3). In contrast, if positive$_{ccw}$–negative$_{cw}$ image pairs were presented, the visual feedback matched subjects' perceived movements if rotated only by a clockwise angle of 2.04° (point of subjective equivalence: −2.04 ± 1.58°). In other words, if the positive image was on the clockwise side and the negative image on the counterclockwise side, subjects perceived one and the same pointing direction geared more strongly towards the clockwise side than if the positive image was presented on the counterclockwise side and the negative image on the clockwise side. This difference regarding the point of subjective equivalence was significant (one-tailed pairwise t-test, Bonferroni-corrected for multiple comparisons, $t(16) = 2.49$, $p = .012$).

If the aforementioned differences in subjects' self-action estimates reflected an influence of an affective gradient in action outcomes, one might further expect that the point of subjective equivalence in the neutral$_{ccw}$–neutral$_{cw}$ condition should fall in between the points of subjective equivalence of the other two conditions. While we certainly agree with this notion, we again want to stress that the specific results for the neutral condition need to be interpreted with care since it significantly differed from all other experimental conditions in terms of arousal (refer to Section 2.4.4 for further details). For this reason, we draw our main conclusions solely from the comparison of the negative$_{ccw}$–positive$_{cw}$ and the positive$_{ccw}$–negative$_{cw}$ condition. Yet, irrespective of this putative experimental confound, our results are at least compatible with the aforementioned expectation. There was a trend for a statistical difference in the points of subjective equivalence between the neutral$_{ccw}$–neutral$_{cw}$ (−2.18 ± 1.52°) and the negative$_{ccw}$–positive$_{cw}$ (−5.10 ± 1.56°) condition ($t(16) = 2.24$, $p = .060$, one-tailed pairwise t-test, Bonferroni-corrected for multiple comparisons): compared to the neutral condition, subjects' perceived movement directions shifted clockwise if the positive image was presented at the clockwise position. Moreover, the point of subjective equivalence in the positive$_{ccw}$–negative$_{cw}$ condition (−2.04 ± 1.58°) was shifted counterclockwise with respect to the neutral condition. However, this difference was not significant ($t(16) = 0.15$, $p > .05$, one-tailed pairwise t-test, Bonferroni-corrected for multiple comparisons).

The same principle pattern of results can be exemplified by the psychometric functions of a single subject (Fig. 2). In the neutral$_{ccw}$–neutral$_{cw}$ condition (blue), the visual feedback needed to be rotated clockwise by 1.31° to establish a subjective equivalence between the visual feedback and the perceived movement (point of subjective equivalence: −1.31°). In other words, if the visual feedback was rotated clockwise by 1.31°, the subject would have made "clockwise" and "counterclockwise" decisions in 50% of trials each. In contrast, in the negative$_{ccw}$–positive$_{cw}$ condition (red), the same feedback rotation led to an increase in the probability of "clockwise" decisions to more than 50%, corresponding to a clockwise shift of the point of subjective equivalence (relative to the neutral$_{ccw}$–neutral$_{cw}$ condition), here to an angle of −7.47°. Vice versa, in the positive$_{ccw}$–negative$_{cw}$ condition (green), there was a counterclockwise shift of the point of subjective equivalence, namely to 3.92°.

In summary, subjects' perception of self-action was significantly modulated by the affective outcomes of their actions: the point of subjective equivalence exhibited a relative shift towards the image which conveyed a high valence and away from the image which conveyed a low valence.

3.2. Just noticeable differences

The just noticeable difference corresponds to the slope of a subject's psychometric curve and provides a measure of the sensitivity to detect rotations of the visual feedback. In the single subject example (Fig. 2), all psychometric curves exhibited similar

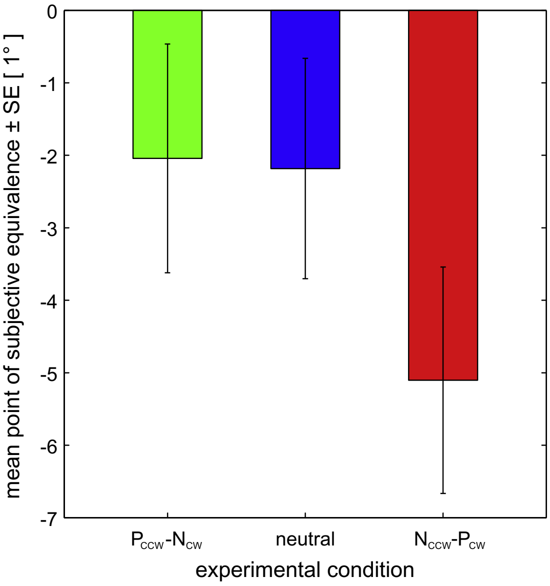

Fig. 3. Average points of subjective equivalence. This figure depicts the average point of subjective equivalence between the visual feedback and the perceived movement direction (mean ± standard error) in each of the three experimental conditions. In comparison to the $neutral_{ccw}$–$neutral_{cw}$ condition (neutral, blue), the point of subjective equivalence shifted clockwise in the $negative_{ccw}$–$positive_{cw}$ condition (N_{ccw}–P_{cw}, red). However, there was no comparable counterclockwise shift if $positive_{ccw}$–$negative_{cw}$ image pairs were presented (P_{ccw}–N_{cw}, green). Still, we found a significant difference between the $positive_{ccw}$–$negative_{cw}$ and the $negative_{ccw}$–$positive_{cw}$ condition, which indicated a relative shift of the perceived pointing direction towards positive and away from negative action outcomes. Positive angles denote counterclockwise rotations.

slopes, indicating that the subject was equally sensitive to detect rotations of the visual feedback across conditions. Accordingly, in this subject, the just noticeable difference was of comparable size for all three conditions: 18.77° in the $neutral_{ccw}$–$neutral_{cw}$ condition, 18.54° in the $negative_{ccw}$–$positive_{cw}$ condition and 15.31° in the $positive_{ccw}$–$negative_{cw}$ condition.

Similar to the single subject example, the just noticeable difference of feedback rotation did not differ across the three experimental conditions on the group level (one-way repeated-measures ANOVA, $F(2, 32) = 1.68$, $p > .05$). Specifically, the just noticeable difference was 9.93 ± 1.60° in the $neutral_{ccw}$–$neutral_{cw}$ condition, 11.16 ± 1.36° in the $positive_{ccw}$–$negative_{cw}$ condition and 8.73 ± 1.42° in the $negative_{ccw}$–$positive_{cw}$ condition. This finding indicates that the different experimental conditions did not influence subjects' sensitivity in detecting visual feedback manipulations. Therefore, the relation between the affective action outcomes and the perception of self-action – as measured by subjects' points of subjective equivalence – could not be explained by unspecific changes in perceiving one's actions.

3.3. Separating the role of positive vs. negative valence

In an additional analysis of specific subsets of trials, we tried to disentangle whether the modulation of self-action perception by the affective gradients was primarily due to an *attraction effect* by the positive image, a *repulsion effect* by the negative image or a combination of both effects (for details, see Supplemental Table 3). This additional analysis built on the assumption that – in case of an attraction effect – subjects' point of subjective equivalence between the visual feedback and the perceived movement might covary with differences in the valence of the positive image if the valence of the negative image is kept constant on average. Analogously, in case of a repulsion effect, the point of subjective equivalence might covary with differences in the valence of the negative image if the valence of the positive image is kept constant. Yet, in this analysis, we could not reveal any covariation between valence and subjects' self-action estimates: highly positive images did not attract the point of subjective equivalence significantly stronger than did moderately positive images (dependent two-tailed *t*-tests, Bonferroni-corrected for multiple comparisons: $t(16) = 0.01$, $p > .05$ in the $positive_{ccw}$–$negative_{cw}$ condition and $t(16) = -0.33$, $p > .05$ in the $negative_{ccw}$–$positive_{cw}$ condition). Comparably, highly negative images did not lead to a significantly stronger repulsion than did moderately negative images (dependent two-tailed *t*-tests, Bonferroni-corrected for multiple comparisons: $t(16) = 0.43$, $p > .05$ in the $positive_{ccw}$–$negative_{cw}$ condition and $t(16) = -1.65$, $p > .05$ in the $negative_{ccw}$–$positive_{cw}$ condition; for a detailed comparison, refer to Supplemental Table 3). However, one has to keep in mind that our experiment was not designed to discriminate such attraction and repulsion effects. Accordingly, the number of trials within the analysed subsets might have been simply too small to allow a distinction of any effect mediated by the comparatively small differences in valence between highly positive and moderately positive images and between highly negative and moderately negative images, respectively. Hence, future experiments which address this question directly might be able to unveil a differential influence of both attraction and repulsion effects on the perception of one's actions.

3.4. Possible influences of gaze and pointing direction

Since gaze direction can affect the perception of one's hand position, at least for proprioception-based estimates (compare Fiehler, Rosler, & Henriques, 2010), gaze direction could have affected the dependent variable in the current experiment, namely the point of subjective equivalence. In the context of our experiment, it is particularly important to control for such a possible influence because the duration of fixation could have differed between pictures of high and low valence (Isaacowitz, Allard, Murphy, & Schlangel, 2009; Nummenmaa, Hyona, & Calvo, 2006). Consequently, a systematic difference in gaze direction across conditions might explain the observed differences in subjects' perceived pointing directions. An analysis of the relative fixation time during which subjects' eyes remained at either of the two image locations, however, did not reveal any significant differences – neither across conditions ($F(1.10, 6.60) = 0.37$, $p > .05$) nor for image side ($F(1, 6) = 0.04$, $p > .05$). Therefore, gaze direction is unlikely to explain the observed differences in the points of subjective equivalence (see Supplemental Fig. 2 and Table 2 for further details). We cannot exclude the possibility, however, that any minor changes of gaze direction could still have an influence. Such minor changes might have not been detectable due to the small subset of subjects available for this analysis and due to the rather poor quality of the video-based eye position data owing to downward gaze (compare Section 2.4.5).

Likewise, self-action estimates can differ for varying pointing directions (Synofzik et al., 2006; van Beers, Wolpert, & Haggard, 2002). Accordingly, systematic differences in pointing direction across conditions might have possibly confounded our results. This can be ruled out, however, since the median pointing direction did not differ significantly from 90° (i.e. the direction of twelve o'clock) in all conditions (two-tailed one-sample t-tests, Bonferroni-corrected for multiple comparisons, $p > .05$) and did not differ significantly across conditions (one-way repeated-measures ANOVA, $F(2, 32) = 2.26$, $p > .05$; see Supplemental Fig. 1).

4. Discussion

This study indicates that the perception of one's actions does not only depend on internal predictions building on efferent information and proprioception (Bays & Wolpert, 2007; Bell, 2001; Blakemore, Frith, & Wolpert, 1999; Haarmeier et al., 2001; Shergill, Bays, Frith, & Wolpert, 2003; Synofzik et al., 2006; Voss, Ingram, Haggard, & Wolpert, 2006), but is also influenced by post hoc information about the actions. Specifically, our findings suggest that the valence of an action outcome can modulate the perception of the sensory consequences of one's actions. This is evidenced by the fact that subjects' perception of the sensory consequences of their actions shifted alongside the affective gradient created by the action outcomes: subjects were more likely to accept and "internalise" deviations of the visual consequences of their movements if these visual consequences deviated towards positive action outcomes and – at the same time – away from negative action outcomes.

Importantly, this effect was not mediated by manipulation of a *predictive* representation of the action outcomes, as already observed e.g. in effect-priming studies. Such studies have demonstrated consistently that showing the effect of an action as a prime before the action itself can modulate the sense of agency – even if primes and effects are unrelated to the action itself (Aarts, Custers, & Wegner, 2005; Linser & Goschke, 2007; Sato, 2009; also see Moore, Wegner, & Haggard, 2009; but Synofzik, Vosgerau, & Lindner, 2009 for a comment). In contrast, in our study, no information about the action outcome was available before the action. At movement onset, the action outcome was unpredictable. Thus, the action outcome could not have consistently related to any specific prediction or intention preceding and guiding the action. Thus, any consistent influence of the action outcome on the perception of this action would need to be integrated *post hoc*.

Moreover, what was modulated by the affective content of the action outcomes was not the perception of *external events in the context of self-action*, but the perception of the sensory consequences of one's actions: subjects were not required to report, for example, on causation or content of the *appearing images*, but needed to estimate the *perceived visual consequences of their actions*. This distinction is important as – at first glance – the affective content of action outcomes may appear more likely to modulate the perception of external events related to self-action than to modify the perception of sensory action consequences. Whereas the former draws more strongly on prior expectations, goal representations, context information and post hoc evaluations (Johansson et al., 2005; Synofzik et al., 2008a; Wegner & Sparrow, 2004), the latter is commonly seen as tied more closely to efferent and afferent signals linked to an action per se, in particular, the comparison of the actual sensory afference with internal predictions based on efferent information as well as on proprioception (Frith, 2005; Synofzik et al., 2009, 2008a; Wohlschläger, Engbert, & Haggard, 2003).

Correspondingly, the comparison of internal predictions with visual feedback could be expected to determine entirely the perception of self-action in those situations in which subjects need to report how they perceive their sensory action consequences. Our results suggest, however, that even this basic perceptual faculty is not entirely determined by this comparator mechanism: even though subjects only needed to indicate the perceived direction of their movements relative to the visual feedback, but not any features of the appearing image pairs, the points of subjective equivalence between the perceived and the visual movement differed significantly between the experimental conditions. As mentioned before, subjects' perception of the pointing direction was found to shift towards positive and away from negative action outcomes.

Yet, we could not provide any evidence in favour of the assumption that this effect would be primarily due to an *attraction effect* by the positive image or, alternatively, primarily due to a *repulsion effect* by the negative image. However, there is a broad range of evidence that negative events mobilise physiological, affective and cognitive resources more strongly than do positive or neutral events (for reviews, see Peeters & Czapinski, 1990; Taylor, 1991). Such positive–negative asymmetries have been shown to apply to judgements on valence-encoding information, to causal attributions and to attention (Peeters & Czapinski, 1990; Taylor, 1991). An analogous positive–negative asymmetry might also affect the perception of the sensory consequences of one's actions, with negative outcomes (i.e. repulsion effects) receiving greater weight. Further studies are therefore needed to investigate whether different affective valences contribute differently to the modulation of self-action perception.

Furthermore, the question remains what specific features of an individual explain whether and how her/his perception of self-action is modified by the affective content of action outcomes. Future studies will therefore also need to explore how interindividual differences in, for example, preferences, attitudes, moods and affect dispositions (Scherer, 2005) influence the modulatory effect of affective action outcomes on self-action perception. The fact, however, that in the majority of subjects the perceived pointing direction was attracted by the positive image and/or a repelled by the negative image is consistent with earlier findings on categorical self-agency judgements (Johansson et al., 2005; Wegner & Sparrow, 2004) and with the phenomenon of a *self-serving bias*, according to which individuals tend to attribute success internally and failure externally (Beckman, 1970; Johnson, Feigenbaum, & Weiby, 1964; Wolosin, Sherman, & Till, 1973; for reviews, see Miller & Ross, 1975; Tetlock & Levi, 1982). Note that, however, in contrast to the aforementioned studies, which mainly investigated conceptual judgements, our study focused on the modulatory effect of affective action outcomes on the non-conceptual perception of one's actions – probably operating on much lower levels of integration (Synofzik, Vosgerau, & Newen, 2008b).

Though being highly significant on the group level, the absolute size of the modulatory effect of the action outcome was comparatively small: between the positive$_{ccw}$–negative$_{cw}$ condition and the negative$_{ccw}$–positive$_{cw}$ conditions the points of subjective equivalence differed by approximately 3°, amounting to roughly 31% of the just noticeable difference, which was about 10° on average. The small size of the observed effect could possibly be explained by the aforementioned interindividual differences. Moreover, the small effect might more directly result from the fact that, in the present study, subjects only needed to compare the directions of the visual feedback and the perceived movement while the affective content of the action outcomes was present only after the outward pointing movement was completed and, moreover, completely irrelevant to completing the task. Thus, if the available cues related to self-action were integrated according to their relevance in a given situation (as suggested for sensorimotor integration [Körding & Wolpert, 2004] as well as for the perception of agency [Synofzik et al., 2009, 2010]), one would expect the modulatory effect – and thus the weight – of action outcomes to be rather small compared to the weight of internal sensory predictions.

Our study cannot prove such integration of sensorimotor and affective information in individual trials due to methodological limitations (because we employed a two-alternative forced-choice paradigm). Nor can we, for the same reasons, quantify the respective weights that subjects attributed to these signals. This is important as we cannot rule out that subjects based their decision on the affective gradient in one trial and, alternatively, on the congruency between internal predictions and sensory feedback in another, which on average could also lead to the observed pattern of results. Nevertheless, our results are at least compatible with the notion of Bayesian cue integration and, moreover, an elaboration of our findings within this framework might have interesting implications: for instance, schizophrenia patients suffering from delusions of influence seem to rely more strongly on visual information since their internal sensory predictions are rather unreliable (Synofzik et al., 2010). It is tempting to speculate whether these patients would also weight any visually encoded affective outcomes of their actions in a pathologically exaggerated fashion. Even in healthy subjects, some individuals seem to rely more heavily on visual feedback than others (Fourneret & Jeannerod, 1998). It would thus also be interesting to see whether the impact of affective action outcomes on self-action estimates in healthy subjects would scale accordingly.

Moreover, the clockwise bias in subjects' visual estimates of pointing direction could be also interpreted within this Bayesian framework: it might be that action perception is biased by the statistics of the workspace in which an effector is operating. Specifically, the frequency distribution of the effector being engaged in the various regions of the workspace could act as a prior on self-action estimates. In other words, we might be inclined to perceive movements of our right hand as directed towards the right side (Cressman & Henriques, 2009, 2010; Cressman et al., 2010; Jones et al., 2010; Synofzik et al., 2006; Synofzik, Linder, et al., 2008; Synofzik et al., 2010, 2006) and movements of our left hand as directed towards the left side (Jones et al., 2010) because our effectors usually operate in the respective space. Such an *effector bias* might also explain why there was no pronounced difference in the points of subjective equivalence between the neutral$_{ccw}$–neutral$_{cw}$ condition and positive$_{ccw}$–negative$_{cw}$ image pairs, but between the neutral$_{ccw}$–neutral$_{cw}$ condition and the negative$_{ccw}$–positive$_{cw}$ image pairs: the effector bias might render the affective gradient working against this bias less effective (i.e. for positive$_{ccw}$–negative$_{cw}$ image pairs), while enhancing an affective gradient working in the same direction (i.e. for negative$_{ccw}$–positive$_{cw}$ image pairs).

Finally, we would like to stress that the post hoc modulation of self-action perception by affective action outcomes might be limited to the *particular response* which we measured, namely the visual perceptual estimate of one's pointing direction. It would be interesting, however, to test whether affective action outcomes would also modify motor performance or, alternatively, if the impact of these outcomes on action and self-action perception would be distinct (Goodale & Milner, 1992; Schenk, Franz, & Bruno, 2011; Smeets, Brenner, de Grave, & Cuijpers, 2002). This could be tested, for instance, by probing for directional pointing biases in double-step pointing tasks in which the perception of the initial pointing step depends on an integration of the affective movement outcomes: if the modulatory effects which we observed for the perceptual domain also translated into a modification of motor behaviour, then the direction of pointing towards the second target should account for this modulation of self-action perception (for a similar experimental approach using eye movements, compare Sommer & Wurtz, 2002). We already probed for the generalisation of perceptual self-action estimates to motor behaviour in earlier experiments which also modified subjects' self-action estimates but by means of adaptation. Interestingly, motor behaviour always changed in step with the adaptation of self-action estimates and in a way that would account for this adaptation (Synofzik et al., 2006). Similarly, a pathologically diminished ability to modify self-action estimates in cerebellar patients was also accompanied by a lack of motor adaptation (Synofzik, Linder, et al., 2008). Note, however, while there was an obvious relation of self-action perception and motor performance in these subject groups, so far we were not able to prove the same relation at the level of individual subjects (Synofzik et al., 2006).

In conclusion, our study provides a proof of principle that the perception of the sensory consequences of self-action does not only depend on signals related directly to self-action (e.g. internal predictions, actual sensory consequences, proprioception), but also on a post hoc evaluation of unpredictable action outcomes. In our study, affective action outcomes were capable of modulating the perception of one's actions even though they were not reflected by the intentions or any other prospective representation preceding or guiding one's actions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.concog.2011.06.004.

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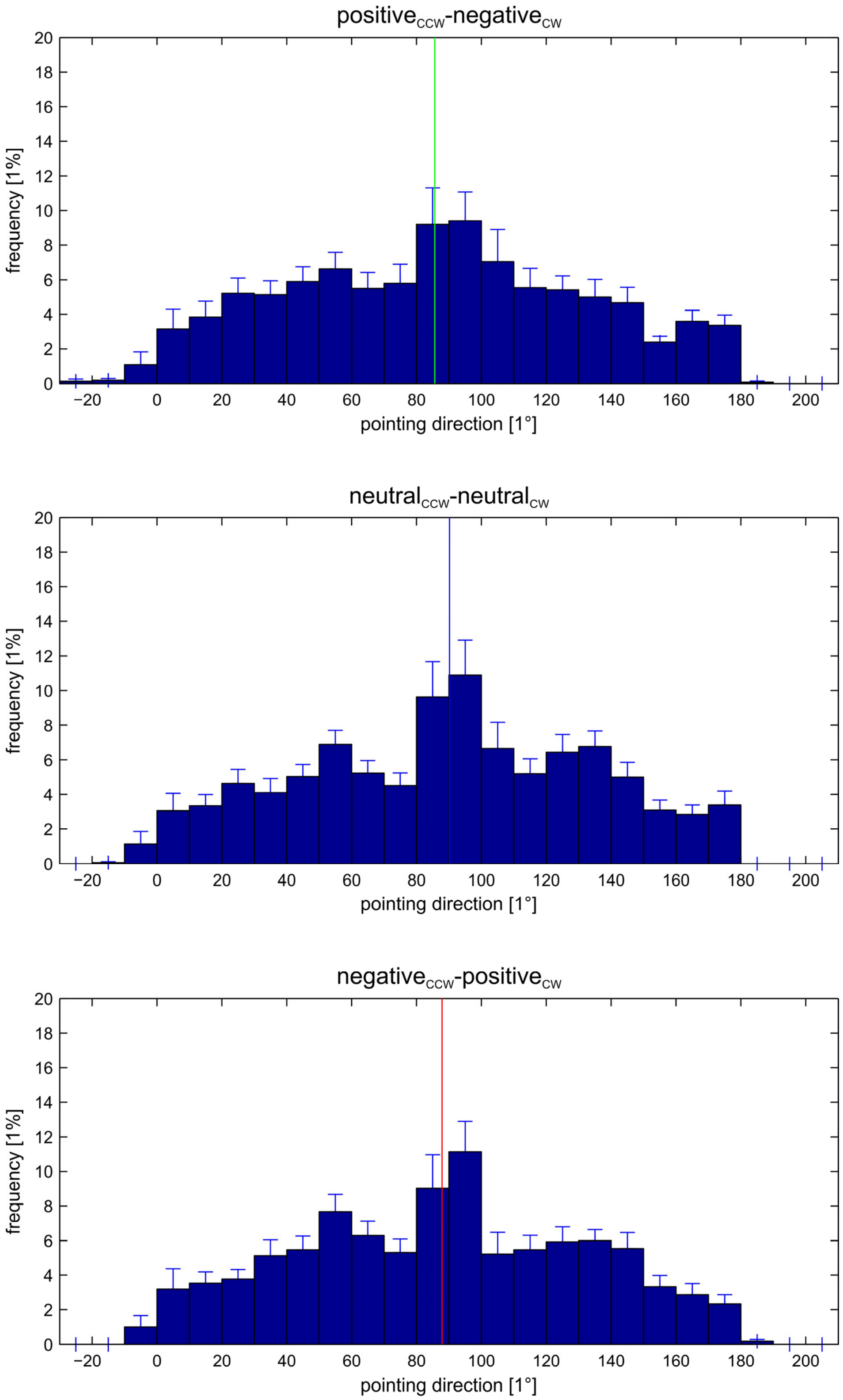
The valence of action outcomes modulates the perception of one’s actions

Supplemental Table 1. IAPS image pairs.

The following images were selected from the International Affective Picture System (Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International affective picture system (IAPS): Affective ratings of pictures and instruction manual.* Gainesville, Florida: University of Florida). For each experimental condition, the serials of the displayed image pairs are provided. Serials on the left of each column correspond to images presented in the counterclockwise (ccw) position. Serials on the right correspond to images in the clockwise (cw) position.

neutral$_{ccw}$-neutral$_{cw}$		positive$_{ccw}$-negative$_{cw}$		negative$_{ccw}$-positive$_{cw}$	
2840	2190	1920	1270	9561	1460
2397	2411	1630	1111	1275	1810
2890	2393	1540	1274	9181	1721
2102	2870	1440	1090	1220	1660
2221	9210	1720	1304	1202	1722
2104	2980	1710	1052	1300	1560
2200	2513	5982	9280	9469	5300
8312	2357	5994	5973	9295	1731
2396	2493	7570	9941	5961	5660
2020	2002	5700	9623	9630	5260
2383	2215	5836	2590	6010	2650
2101	9260	2092	9220	2312	2311
2512	2214	2030	2715	2455	2165
2377	7513	2362	2278	9440	2391
2191	2441	4572	29001	2301	1999
2595	9070	4575	9041	9417	8120
2749	2446	4624	20551	2457	2340
7010	7175	4625	2115	9584	8280
7004	7031	8467	3181	6561	4542

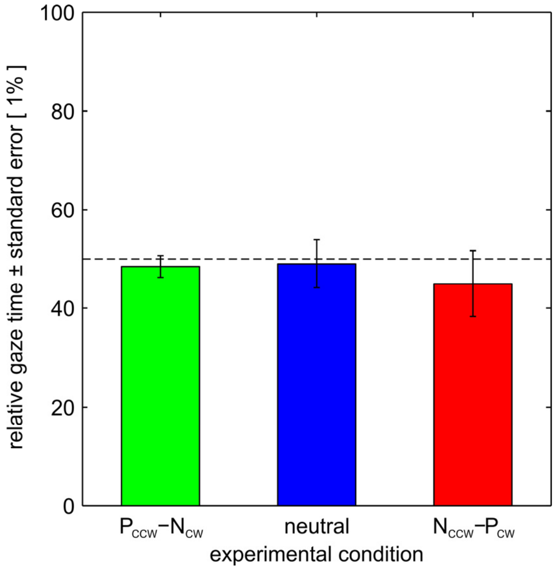
neutral$_{ccw}$-neutral$_{cw}$		positive$_{ccw}$-negative$_{cw}$		negative$_{ccw}$-positive$_{cw}$	
7950	7020	62502	7361	9596	4250
7006	7080	8540	2751	2120	2160
7090	7150	8117	9270	9592	2075
7026	7185	5622	8231	6240	4641
7035	7040	8041	3230	9332	2045
7050	7059	8031	9590	9520	4505
7233	5510	8040	3185	2710	8001
7205	7179	4007	9043	3051	8021
7053	5520	4599	9424	9420	4645
7161	7234	8380	9042	6220	8260
7030	7012	8116	3550	6211	4597
5500	7038	8251	9800	6840	5470
7052	7009	8161	2683	65701	8499
7003	7055	8034	8480	6821	8200
7160	7056	8490	6370	6312	8080
5534	7032	8370	9250	9810	8179
6150	7001	7530	9110	7078	5202
7300	7014	7286	9395	9390	7238
7045	7255	7320	9290	9832	7280
7057	7019	7410	7079	6241	7480
7016	7062	7390	9831	9830	7352
7207	7043	7482	9320	9373	7200
5532	5531	7450	6610	9301	7260
9401	7058	8503	2692	9302	7230
7182	7487	5635	9000	9001	2598
5535	7830	4600	9926	2694	8371
5471	7547	7499	9495	9403	7660
7500	27451	7501	9491	9911	5833
7036	7130	5450	9920	9621	8210
2514	7493	5626	9905	9909	8190
7037	7595	8163	9622	9600	5629



Supplemental Figure 1. Distributions of pointing directions.

Supplemental Figure 1. Distributions of pointing directions.

Subjects were instructed to choose their pointing directions freely between the subjective directions of nine and three o'clock, that is in the top half of the circle flashed at the beginning of each trial. To assess whether subjects' selection of pointing directions could have confounded our results, we analysed the distribution of the directions in which subjects actually made their movements. For each experimental condition, the histogram depicts the mean frequency (± standard error) of subjects pointing into a given sector of directions (bin width: 10°). The direction of three o'clock corresponds to 0° while the directions of twelve and nine o'clock correspond to 90° and 180°, respectively. Subjects exhibited no tendency to prefer a particular directional quadrant. Particularly, subjects' median pointing directions (represented by solid vertical lines) did not differ significantly from 90°, i.e. the direction of twelve o'clock (two-tailed one-sample t-tests, Bonferroni-corrected for multiple comparisons, $p > .05$). Moreover, subjects' median pointing directions did not differ significantly across conditions (one-way repeated measures ANOVA, $F(2,32) = 2.26$, $p > .05$) and, thus, could not explain the differences in subjects' perception of their pointing directions.



Supplemental Figure 2. Relative fixation time of counterclockwise image.

This diagram shows the average time (mean ± standard error) during which subjects' gaze was directed at the counterclockwise positioned image as a quotient of the entire duration during which gaze was directed at either the counterclockwise or the clockwise positioned image. The quotient is depicted for all three experimental conditions (green: positive_{ccw}-negative_{cw}, blue: neutral_{ccw}-neutral_{cw}, red: negative_{ccw}-positive_{cw}).

Across conditions, systematic differences in gaze direction could have possibly modified subjects' perception of their pointing directions. To exclude gaze as a possible confound, we analysed the average time during which gaze remained at each image location (relative to the complete image presentation time) using a 3x2 repeated measures ANOVA with the factors *condition* (positive_{ccw}-negative_{cw}, neutral_{ccw}-neutral_{cw} and negative_{ccw}-positive_{cw}) and *image side* (counterclockwise, clockwise). There were no significant main effects, neither for condition ($F(1.10,6.60) = 0.37$, $p > .05$) nor for image side ($F(1,6) = 0.04$, $p > .05$), and no significant interaction ($F(2,12) = 0.12$, $p > .05$). These findings suggest that the differences in subjects' perceived pointing direction across conditions cannot be explained by systematic differences in gaze direction.

Note that the eyetracking results reported here were obtained in a subset of seven of our 17 subjects. In these subjects, however, the pattern of results regarding the point of subjective equivalence – as well as the just noticeable difference – resembled the pattern in the overall population. Due to the configuration of the experimental setup, it was only in this subset that vertical eye movements could be measured reliably as subjects needed to direct their eyes downwards, with the upper lid covering much of the eye in this position (compare Supplemental Table 2).

Supplemental Table 2. Subpopulation of subjects with eyetracking.

Eye movements could only be recorded in a subset of seven subjects. Importantly, both the point of subjective equivalence and the just noticeable difference in these subjects resembled the results obtained in the overall population of 17 subjects. The respective measures (means ± standard errors) for both groups of subjects and for all three experimental conditions are provided in the table below.

subject group	point of subjective equivalence [1°]			just noticeable difference [1°]		
	positive$_{ccw}$-negative$_{cw}$	neutral$_{ccw}$-neutral$_{cw}$	negative$_{ccw}$-positive$_{cw}$	positive$_{ccw}$-negative$_{cw}$	neutral$_{ccw}$-neutral$_{cw}$	negative$_{ccw}$-positive$_{cw}$
subset of 7 subjects with eyetracking	-2.80 ± 2.38	-2.79 ± 1.54	-4.39 ± 2.96	10.27 ± 2.42	10.38 ± 3.08	10.62 ± 1.89
overall population of 17 subjects	-2.04 ± 1.58	-2.18 ± 1.52	-5.10 ± 1.56	11.16 ± 1.36	9.93 ± 1.60	8.73 ± 1.42

Supplemental Table 3. Separating the role of positive vs. negative valence.

Wondering whether the differences in subjects' perceived pointing direction between the non-neutral conditions might primarily reflect an *attraction effect* by the positive image, a *repulsion effect* by the negative image or a combination of both, we further investigated whether different affective valences contributed differently to the modulation of self-action perception.

We hence analysed the non-neutral conditions (positive$_{ccw}$-negative$_{cw}$ and negative$_{ccw}$-positive$_{cw}$ image pairs) by asking whether the strength of the affective gradient influenced the extent to which the affective gradient would shift subjects' perceived pointing direction. To this end, we performed median splits on all image pairs within the non-neutral conditions by splitting the image pairs with regard to the valence of one image within the pair (referred to as independent). Such median splits were performed both for the counterclockwise (ccw) and the clockwise (cw) positioned images. Within the pairs, the second image will be referred to as the dependent image.

Specifically, we formed subsets of positive$_{ccw}$-negative$_{cw}$ image pairs with [A] highly positive ccw-images vs. [B] moderately positive ccw-images as well as [C] highly negative cw-images vs. [D] moderately negative cw-images. Analogously, we divided the negative$_{ccw}$-positive$_{cw}$ image pairs into four additional subsets, namely [E] highly positive cw-images vs. [F] moderately positive cw-images and [G] highly negative ccw-images vs. [H] moderately negative ccw-images. Thus, we obtained a total of eight image pair subsets. Importantly, the independent images – whose saliency in terms of valence defined the image pair subsets – did not differ significantly regarding their arousal. Note that, for each splitting, there were no significant differences in valence for the dependent images. However, in two of four cases, the dependent images differed significantly in arousal.

We proceeded by calculating the point of subjective equivalence for each of the eight subsets and then comparing the obtained points in a pairwise fashion within subjects ([A] vs. [B], [C] vs. [D], [E] vs. [F], [G] vs. [H]). In case of a graded attraction effect towards positive images, we would have expected [A] > [B] and [E] < [F]. In case of a graded repulsion away from negative images, we would have expected [C] > [D] and [G] < [H]. Note that, within the same experimental condition, attraction and repulsion *per se* should shift the point of subjective equivalence in the same direction while one would expect, for both attraction and repulsion, the $\text{positive}_{\text{ccw}}$-$\text{negative}_{\text{cw}}$ and $\text{negative}_{\text{ccw}}$-$\text{positive}_{\text{cw}}$ condition to induce opposite shifts of the point of subjective equivalence, respectively. We accounted for the orientation of the affective gradient in the statistical analysis by comparing – for both conditions and both effects, respectively – the point of subjective equivalence in the subset of high saliency to the point of subjective equivalence in the subset of moderate saliency.

In this way, disentangling attraction and repulsion effects could have been possible. Yet, our analyses revealed no differences in the point of subjective equivalence for subsets of high and moderate saliency, irrespective of whether the strength of the gradient was modulated via the negative or the positive image. One needs to acknowledge, however, that the number of observations was halved due to the median split and, thus, could be insufficient to obtain reliable results. Therefore, the source of the observed shifts in subjects' perceived pointing direction induced by the affective gradients in our experiment will remain elusive. Our additional analyses also do not allow deciding whether the perceived pointing direction depends on the affective gradient in a gradual or in a categorical fashion.

experimental condition	positive$_{ccw}$-negative$_{cw}$				negative$_{ccw}$-positive$_{cw}$			
independent image								
subset	positive		negative		negative		positive	
position	ccw		cw		ccw		cw	
saliency	high	moderate	high	moderate	high	moderate	high	moderate
code letter	A	B	C	D	E	F	G	H
valence	7.26	6.45	2.64	3.46	2.55	3.50	7.55	6.68
arousal	5.31	5.07	5.35	5.20	5.47	5.07	5.22	5.16
difference in arousal (independent two-tailed t-test, Bonferroni-corr.)	t(48) = 1.26, p > .05		t(48) = 0.72, p > .05		t(48) = 1.94, p > .05		t(48) = 0.31, p > .05	
dependent image								
subset	negative		positive		positive		negative	
position	cw		ccw		cw		ccw	
valence	3.12	2.98	6.78	6.92	7.22	7.02	2.98	3.11
difference in valence (independent two-tailed t-test, Bonferroni-corr.)	t(48) = 1.02, p > .05		t(48) = -0.53, p > .05		t(48) = 1.26, p > .05		t(48) = -0.82, p > .05	
arousal	5.56	4.99	5.39	4.99	5.43	4.97	5.25	5.27
difference in arousal (independent two-tailed t-test, Bonferroni-corr.)	t(48) = 2.94, p = .020		t(48) = 2.12, p = .016		t(48) = 2.24, p > .05		t(48) = -0.08, p > .05	
behavioural data								
point of subjective equivalence – mean [1°]	-2.34	-2.35	-1.67	-1.92	-4.54	-5.23	-3.62	-6.20
point of subjective equivalence – SE [1°]	1.80	1.67	2.02	1.45	1.94	1.80	2.03	1.45
difference in point of subjective equivalence (dependent two-tailed t-test, Bonferroni-corr.)	attraction? t(16) = 0.01, p > .05		repulsion? t(16) = 0.43, p > .05		repulsion? t(16) = -1.65, p > .05		attraction? t(16) = -0.33, p > .05	

4. Diskussion

Die vorliegende Dissertation untersuchte die Wahrnehmung der eigenen Bewegungen anhand der visuellen Wahrnehmung der eigenen Handbewegungen. Um die Plastizität dieser Wahrnehmung zu studieren, wurde in einer virtuellen Umgebung das tatsächliche visuelle Bewegungsfeedback von den prädizierten visuellen Bewegungsfolgen dissoziiert, sodass visuelle Prädiktionsfehler entstanden. Diese Prädiktionsfehler bewirkten eine Aktualisierung der prädizierten Bewegungsfolgen. Es gelang, die kausale Attribution der Prädiktionsfehler an interne versus externe Ursachen zu quantifizieren und anhand dieser kausalen Attribution die Aktualisierung der Bewegungswahrnehmung zu charakterisieren: Die Wahrnehmung der eigenen Bewegungen wurde durch diejenige Komponente der Fehler aktualisiert, welche die Probanden an Ursachen innerhalb des eigenen sensomotorischen Systems attribuierten. Zudem wurden experimentell Faktoren identifiziert, welche die kausale Attribution der Fehler an interne versus externe Ursachen modulieren: Sowohl die Größe des Prädiktionsfehlers als auch die Handlungsergebnisse mit ihrer affektiven Valenz änderten die Fehlerkomponente, welche die Probanden an interne Ursachen attribuierten. Damit wird die Wahrnehmung der eigenen Bewegungen nicht vollständig durch sensomotorische Signale bestimmt: Sensorisches Feedback und sensorische Prädiktionen – sowie ihr Vergleich – sind für die Wahrnehmung der eigenen Bewegungen nicht hinreichend. Vielmehr haben auch kausale Annahmen und post hoc verfügbare Informationen über die eigenen Bewegungen einen Einfluss auf deren Wahrnehmung und auf die Plastizität dieser Wahrnehmung.

4.1. Kausale Attribution der sensorischen Prädiktionsfehler

Um visuelle Prädiktionsfehler zu erzeugen, rotierten wir das visuelle Feedback über die Handbewegungen der Probanden um verschiedene, zufällig gewählte Winkel. Auf diese Weise konfrontierten wir die Probanden mit unvorhersehbaren Diskrepanzen zwischen den tatsächlichen und den intern prädizierten visuellen Folgen ihrer Bewegungen. Die Probanden hätten diese Diskrepanzen, die Prädiktionsfehler, entweder internen Ursachen oder externen Ursachen oder sowohl internen und externen Ursachen zuschreiben können. Um diejenige Komponente der Fehler zu quantifizieren, welche die Probanden an interne Ursachen attribuierten, instruierten wir die Probanden, ihre wahrgenommene Zeigerichtung visuell zu schätzen (Abschnitt 3.1.2., Figure 2B). Tatsächlich reflektierte die wahrgenommene Zeigerichtung der Probanden sowohl das rotierte visuelle Feedback als auch die tatsächliche motorische Zeigerichtung (Abschnitt 3.1.2., Figure 3A). Dies deutete darauf hin, dass die Probanden den Prädiktionsfehler an interne und externe Ursachen attribuierten.

Dabei zeigte die relative Gewichtung der visuellen Information (van Beers et al. 2002), welche hier den an interne Ursachen attribuierten Fehleranteil erfasste, eine unimodale Häufigkeitsverteilung (Abschnitt 3.1.2., Figure 4): Die Werte der relativen visuellen Gewichtung streuten um ihren Mittelwert für jeden Manipulationsbetrag. Diese Verteilung unterstützt keine *dichotome* Fehlerattribution (Franck et al. 2001, Farrer et al. 2003) an entweder interne oder externe Ursachen, sondern legt vielmehr eine *kontinuierliche* Attribution auf der Ebene der einzelnen Prädiktionsfehler nahe. Eine derartige teilweise Attribution von Prädiktionsfehlern an interne Ursachen würde mit der These übereinstimmen, dass die Wahrnehmung der eigenen Bewegungen auf der Integration interner und externer bewegungsbezogener Signale beruht (Ernst und Banks 2002, Synofzik et al. 2008b, Synofzik et al. 2009, Reuschel et al. 2010, Reuschel et al. 2011, Moore und Fletcher 2012).

Quantitativ manipulierten wir die relative Gewichtung der visuellen Information in dieser Integration, und damit den intern attribuierten Anteil des Prädiktionsfehlers, indem wir die Größe der Prädiktionsfehler variierten: Die relative visuelle Gewichtung nahm für zunehmende Feedback-Manipulationen ab (Abschnitt 3.1.2., Figure 3B). Dies entsprach der für zunehmende Fehlergrößen abnehmenden Wahrscheinlichkeit, dass der Prädiktionsfehler einer internen Ursache entstammt (Franck et al. 2001, Farrer et al. 2003, Stetson et al. 2006, Wei und Körding 2009, Marko et al. 2012). Wenn die Diskrepanz zwischen dem tatsächlichen und dem intern prädizierten visuellen Feedback klein war, dann reflektierte die wahrgenommene Zeigerichtung überwiegend die Feedback-Manipulation (Abschnitt 3.1.2., Figure 3A: rote Linie). Die Probanden attribuierten kleine Prädiktionsfehler also überwiegend an interne Ursachen. Wenn im Gegensatz dazu der Prädiktionsfehler groß war, ähnelte die von den Probanden geschätzte Zeigerichtung eher ihrer motorischen Zeigerichtung (Abschnitt 3.1.2., Figure 3A: grüne Linie). Das bedeutet, dass die Probanden große Prädiktionsfehler überwiegend an externe Ursachen attribuierten. Die absolute Fehlergröße gehört somit zu den Faktoren, welche einen Einfluss auf die kausale Attribution von Fehlern haben (Abschnitt 4.5.).

4.2. Aktualisierung der internen Prädiktionen durch kausale Fehlerattribution

Um die Auswirkung der Prädiktionsfehler auf die internen Prädiktionen der visuellen Bewegungsfolgen zu messen, untersuchten wir Zeigebewegungen ohne visuelles Feedback (Abschnitt 3.1.2., Figure 2C). Da die Probanden bei diesen Bewegungen kein visuelles Feedback über ihre Zeigebewegung erhielten und da die Zeigebewegungen intern gesteuert wurden (d. h. kein externes visuelles Ziel vorgegeben war), musste die perzeptuelle Schätzung der wahrgenommenen Zeigerichtung vollständig auf internen Signalen beruhen, welche die tatsächliche Bewegung abbilden. Solche Signale könnten Efferenzkopien motorischer Befehle (von Holst und Mittelstaedt 1950, Bell 1981), *corollary discharge* (Sperry 1950, Poulet und Hedwig 2002, Sommer und Wurtz 2002) und/oder Propriozeption sein (Bell 2001, für eine ausführliche Darstellung: Synofzik et al. 2006). Da die Probanden ihre perzeptuelle Schätzung der Bewegung vollständig anhand von internen Informationen vornehmen mussten, nahmen wir an, dass die wahrgenommene Zeigerichtung bei Bewegungen ohne visuelles Feedback eine Prädiktion der visuellen Bewegungskonsequenzen abbilden würde, die auf internen Informationen beruht, also eine interne sensorische Prädiktion (Wolpert et al. 1995, Tsakiris et al. 2005, Synofzik et al. 2006).

Die internen sensorischen Prädiktionen der Probanden wurden tatsächlich durch die experimentell generierten Prädiktionsfehler (Shadmehr et al. 2010) aktualisiert. Eine Aktualisierung fand statt, obwohl diese Prädiktionsfehler unvorhersehbar waren (Abschnitt 3.1.2., Figure 3C). Somit war keine konstante Diskrepanz zwischen den tatsächlichen und den prädizierten visuellen Bewegungskonsequenzen notwendig, um eine Aktualisierung der internen Prädiktionen zu induzieren (Shadmehr und Mussa-Ivaldi 1994, Synofzik et al. 2006).

Dabei bewirkten große Fehler (Manipulationen von 20° und 40°) eine *unterproportionale* Aktualisierung im Vergleich zu derjenigen Aktualisierung, welche durch kleine Fehler induziert wurde (Manipulationen von 10°). Entsprechend nahm die relative Rekalibrierung (definiert als Quotient aus Aktualisierung und vorangegangener Feedback-Manipulation, vergleiche Abschnitt 3.1.2., Figure 3D) mit zunehmender Fehlergröße ab. Ein Modell, das annimmt, dass die Aktualisierung der internen sensorischen Prädiktionen proportional zum Prädiktionsfehler zunimmt (Wolpert und Kawato 1998, Scheidt et al. 2001), kann daher die Ergebnisse nicht erklären, da sonst zu erwarten wäre, dass die relative Rekalibrierung über die verschiedenen Feedback-Manipulationen hinweg konstant bleiben würde.

Stattdessen korrelierte die Aktualisierung der internen sensorischen Prädiktionen mit derjenigen Komponente des Prädiktionsfehlers, welche die Probanden an interne Ursachen attribuierten (Abschnitt 3.1.2., Figure 5). Somit charakterisierten wir die Aktualisierung der internen sensorischen Prädiktionen, indem wir ein indirektes Maß der kausalen Attribution der Prädiktionsfehler verwendeten – und zwar auf der Ebene der *einzelnen* Fehler (Lutz et al. 2002, Bland et al. 2011): Unsere Ergebnisse legen nahe, dass die Aktualisierung der internen sensorischen Prädiktionen auf der Attribution des Prädiktionsfehlers an interne Ursachen beruhte. Dieser Zusammenhang wurde sogar für Fehler einer und derselben Größe gefunden (Abschnitt 3.1.2., Figure 5). Das bedeutet, dass auch diejenigen Differenzen in der Aktualisierung der sensorischen Prädiktionen, welche bei gleich großen Fehlern auftraten, durch diejenige Komponente des Prädiktionsfehlers erklärt werden konnten, welche die Probanden ihrem eigenen sensomotorischen System zuschrieben. Die kausale Attribution des Fehlers war also wesentlich für die Aktualisierung unabhängig von der gegebenen Fehlergröße.

4.3. Kausale Fehlerattribution als Prinzip sensomotorischen Lernens

Die gefundene Korrelation zwischen der Fehlerkomponente, welche die Probanden an interne Ursachen attribuierten, und dem durch den Prädiktionsfehler induzierten Lernen (Abschnitt 3.1.2.) unterstützt den Gedanken, dass kausale Annahmen über Fehlersignale das quantitative Ausmaß sensomotorischer Adaptation erklären. So nahmen Wei und Körding (2009) an, dass die *Relevanz* motorischer Fehler – im Sinne der Wahrscheinlichkeit, dass ein motorischer Fehler das Ergebnis interner Ursachen ist – die *subproportionale* Beziehung zwischen der Größe der motorischen Fehler und den zugehörigen adaptiven Änderungen des motorischen Verhaltens erklären würde. Diese Beziehung (Marko et al. 2012) wurde häufig beobachtet, zum Beispiel in der Adaptation von zielgerichteten Handbewegungen durch visuelle Fehler (Wei und Körding 2009), in der Adaptation von Sakkaden durch Endpunktfehler (Robinson et al. 2003) oder in der Adaptation von geradlinigen Bewegungen durch Kraftfelder (Fine und Thoroughman 2007). Die gefundene Korrelation (Abschnitt 3.1.2.) der an interne Ursachen attribuierten Fehlerkomponente mit dem nachfolgenden Lernen spezifiziert diesen Gedanken: Die Korrelation zeigt, dass die relevanten Fehler tatsächlich diejenigen Fehler sind, die an interne Ursachen attribuiert werden. Die vorliegende Arbeit erbringt damit Belege für eine allgemeine Rolle kausaler Annahmen über Fehlerinformation beim sensomotorischen Lernen:

Sensomotorische Anpassungen geschehen in Antwort auf jene Fehler, die – aus der Perspektive des Nervensystems – wahrscheinlich von internen Ursachen herrühren (Körding und Wolpert 2004, Berniker und Körding 2008).

4.4. Plastische Unterscheidung von Selbst und Nicht-Selbst

Um zwischen extern und intern verursachten sensorischen Afferenzen zu unterscheiden, wurden bisher sensorische Prädiktionen über die eigenen Bewegungen als geeignete interne Referenzsignale gesehen (von Helmholtz 1867, von Holst und Mittelstaedt 1950, Frith 1992, Frith et al. 2000b). Wie jedoch die Ergebnisse der vorliegenden Arbeit zeigen, sind diese sensorischen Prädiktionen keine absoluten Referenzen, sondern vielmehr plastische und relative Größen: Sensorische Prädiktionen sind interne Referenzsignale, die einerseits eine kausale Attribution der sensorischen Afferenz erlauben (Abschnitt 1.2.) und andererseits selbst durch eine kausale Attribution anhand der sensorischen Afferenz aktualisiert werden (Abschnitt 3.1.2.). Sensorische Prädiktionen als solche sind also nicht hinreichend, um extern und intern verursachte sensorische Afferenzen zu unterscheiden. Angesichts der bisherigen Vorstellung, dass die sensorischen Prädiktionen diejenige Komponente der sensorischen Afferenz abbilden würden, welche interne Ursachen hat (Frith 1992, Frith et al. 2000b, Abschnitt 1.2.), ist es insbesondere überraschend, dass der Prädiktionsfehler – der angeblich die extern verursachte Komponente der sensorischen Afferenz erfassen würde – (zumindest teilweise) an interne Ursachen attribuiert werden kann. Diese Beobachtung wird erklärbar, wenn man annimmt, dass die Attribution des Prädiktionsfehlers zusätzliche Faktoren berücksichtigen kann, welche Rückschlüsse auf die Ursache des Prädiktionsfehlers erlauben. Solche Faktoren, welche die kausale Attribution von Fehlersignalen an interne versus externe Ursachen disambiguieren oder modulieren, werden im folgenden Abschnitt 4.5. besprochen. Jedoch ist dann zu fragen, ob sensorische Prädiktionen noch notwendig sind, um zwischen Exafferenz und Reafferenz zu unterscheiden. Auch in einem multifaktoriellen Modell der Unterscheidung von Selbst und Nicht-Selbst sind sensorische Prädiktionen weiterhin wichtig. Denn der besondere ökologische Nutzen der internen sensorischen Prädiktionen besteht – trotz der Notwendigkeit ihrer kontinuierlichen Aktualisierung durch zusätzliche Informationen – in ihrer schnellen und zuverlässigen Verfügbarkeit (Wolpert und Flanagan 2001, Synofzik 2008, Synofzik et al. 2009, Abschnitt 1.2.).

4.5. Modulation der kausalen Fehlerattribution

Informationen, welche die kausale Attribution eines Fehlersignals an interne versus externe Ursachen disambiguieren, können sich unmittelbar aus *sensomotorischen* Prozessen ergeben (Körding und Wolpert 2004, Berniker und Körding 2008). Zum Beispiel haben Fehlergröße (Wei und Körding 2009, Marko et al. 2012, siehe auch Abschnitt 3.1.2.), Fehlersystematik (Berniker und Körding 2011, siehe auch Abschnitt 4.7.) und begleitende sensorische Ereignisse in anderen Modalitäten (Synofzik et al. 2009, Moore und Fletcher 2012) einen Einfluss auf die Attribution eines Fehlersignals.

Neben sensomotorischen Informationen könnte die Fehlerattribution auch Faktoren berücksichtigen, welche den eigenen Bewegungen vorausgehen oder diesen nachfolgen: Insbesondere könnten die eigenen Ziele (Preston und Newport 2010) bzw. die Ergebnisse der eigenen Bewegungen (Johansson et al. 2005, Izawa und Shadmehr 2011) die Attribution der mit den Bewegungen verbundenen Fehlersignale modulieren. Jedoch wurden die Ergebnisse der eigenen Bewegungen in Hinblick auf die Fehlerattribution bisher nicht unabhängig von vorbestehenden Zielen oder Erwartungen untersucht.

Wie die Ergebnisse in Abschnitt 3.2.2. nahelegen, wird die kausale Attribution der visuellen Prädiktionsfehler nicht vollständig durch sensomotorische Faktoren bestimmt. Vielmehr lässt sich diese Attribution postdiktiv verändern: Insbesondere können Handlungsergebnisse mit ihrer affektiven Valenz (*action outcomes*, siehe Abschnitt 3.2.2.) die Wahrnehmung der sensorischen Bewegungsfolgen modulieren. So attribuierten die Probanden eine Abweichung der tatsächlichen Bewegungsfolgen von den prädizierten eher an ihr eigenes sensomotorisches System, wenn diese Abweichung mehr mit positiven Handlungsergebnissen als mit negativen verbunden war (Abschnitt 3.2.2., Fig. 3).

Diese Modulation der kausalen Fehlerattribution wurde nicht durch die Manipulation einer *prädiktiven* Repräsentation der Handlungsergebnisse vermittelt. Eine derartige Manipulation hatten Effekt-Priming-Studien nachgewiesen. Diese Studien zeigten, dass die Attribution der Urheberschaft für sensorische Bewegungsfolgen dadurch moduliert wird, dass man das Ergebnis einer Bewegung vor der Bewegung selbst zeigt (Aarts et al. 2005, Linser und Goschke 2007, Moore et al. 2009, Sato 2009, Synofzik et al. 2009). Im Unterschied dazu war in der hier berichteten Studie keine Information über das Ergebnis der Bewegung vor der Bewegung selbst verfügbar. Zum Zeitpunkt des Bewegungsbeginns war das Ergebnis der Bewegung also unvorhersehbar. Deshalb konnte das Handlungsergebnis keinen konsistenten Bezug zu spezifischen Prädiktionen oder Intentionen haben, die der Bewegung vorausgehen würden. Deshalb musste jeglicher Einfluss des Handlungsergebnisses auf die Fehlerattribution nachträglich integriert werden. Handlungsergebnisse können also die kausale Attribution von Fehlersignalen *postdiktiv* modulieren.

Dass Handlungsergebnisse die Wahrnehmung unserer eigenen Bewegungen postdiktiv modulieren, haben andere Studien zwischenzeitlich bestätigt: Auch Experimente unter Verwendung des Intentional-Binding-Paradigmas (Haggard et al. 2002) fanden, dass die Selbstzuschreibung der sensorischen Bewegungsfolgen postdiktiv modulierbar ist: Eine Modulation wurde dabei für die affektive Valenz der Handlungsergebnisse (Takahata et al. 2012) und für die quantitativen Eigenschaften der Handlungsergebnisse (Kawabe 2013) nachgewiesen.

Eine offene Frage bleibt jedoch, welche Eigenschaften eines *Individuums* erklären, ob und wie seine Wahrnehmung der eigenen Bewegungen durch die affektiven Inhalte der Handlungsergebnisse moduliert wird (Berninger und Döring 2012). Insbesondere ist zu untersuchen, welche interindividuellen Unterschiede bei Präferenzen, Überzeugungen, Stimmungen oder Affektneigungen den modulatorischen Effekt der affektiven Handlungsergebnisse auf die Wahrnehmung der eigenen Bewegungen beeinflussen (Scherer 2005). Von Bedeutung könnten dabei u. a. vorbestehende Annahmen über die Welt und das Selbst sein (Ramachandran und Hirstein 1998, Lenggenhager et al. 2007, Obhi et al. 2012).

Die Tatsache, dass die meisten Probanden die visuellen Prädiktionsfehler eher an interne Ursachen attribuierten, wenn die Prädiktionsfehler mehr mit positiven als mit negativen Handlungsergebnissen verbunden waren, ist mit früheren Beobachtungen zur Urheberschaftsattribution (Wegner und Sparrow 2004, Johansson et al. 2005) und mit dem Phänomen der *selbstwertdienlichen Verzerrung* vereinbar. Dieses Phänomen besteht darin, dass Individuen dazu neigen, Erfolg an interne Ursachen und Misserfolg an externe Ursachen zu attribuieren (Johnson et al. 1964, Beckman 1970, Wolosin et al. 1973, Miller und Ross 1975, Tetlock und Levi 1982).

Zusammenfassend ist deutlich geworden, dass verschiedene Faktoren die kausale Attribution von Fehlersignalen in der Wahrnehmung der eigenen Bewegungen modulieren: Dazu gehören sensomotorische Informationen, prädiktive Repräsentationen der Bewegungen und postdiktive Informationen, wie die Handlungsergebnisse (Synofzik et al. 2013). Auch scheinen situationsübergreifende Faktoren in Form der Eigenschaften des Individuums in die perzeptuelle Fehlerattribution einzufließen. Offen ist dabei jedoch, welche Rolle konzeptionelle und nicht-konzeptionelle Prozesse bei der Fehlerattribution spielen, also auf welchen kognitiven Ebenen die genannten Faktoren die Fehlerattribution jeweils beeinflussen (Frith et al. 2000b, Mazzoni und Krakauer 2006, Synofzik et al. 2008b, Berninger und Döring 2012).

4.6. Generalisation des perzeptuellen Lernens auf die Motorik

Interne sensorische Prädiktionen liegen, wie frühere Studien zeigten, sowohl der *Wahrnehmung* (Lindner et al. 2005, Synofzik et al. 2006, Cameron et al. 2012) als auch der *Kontrolle* (Haruno et al. 2001, Flanagan et al. 2003, Synofzik et al. 2006) der eigenen Bewegungen zu Grunde. Entsprechend bewirkten die visuellen Prädiktionsfehler auch eine Änderung der motorischen Zeigerichtung, welche die Änderung der prädizierten visuellen Bewegungsfolgen kompensierte (Abschnitt 3.1.2., Figure 6B). Wie angenommen, erfolgte dabei die Anpassung der motorischen Zeigerichtung entgegen der Anpassung der sensorischen Prädiktionen. Insbesondere korrelierten die angepasste motorische Zeigerichtung und die angepasste wahrgenommene Zeigerichtung negativ. Diese Beobachtung könnte bedeuten, dass sowohl die Anpassung des motorischen Verhaltens als auch die Anpassung der internen sensorischen Prädiktionen auf adaptiven Veränderungen eines gemeinsamen Vorwärtsmodells beruhen (Haruno et al. 2001, Flanagan et al. 2003, Synofzik et al. 2006).

Die Idee, dass interne sensorische Prädiktionen gemeinsam von motorischer Kontrolle und Wahrnehmung der eigenen Bewegungen genutzt werden, wird durch frühere visuomotorische Adaptationsexperimente unterstützt (Synofzik et al. 2006, Synofzik et al. 2008a, Synofzik et al. 2010). Jedoch könnten motorische und sensorische Adaptation auch Prozesse sein, welche gleichzeitig stattfinden (Haith et al. 2008, Cressman und Henriques 2009, 2010), aber möglicherweise voneinander dissoziieren (Goodale et al. 1991, Goodale und Milner 1992, Smeets et al. 2002, Cressman und Henriques 2011, Izawa und Shadmehr 2011, Salomonczyk et al. 2011). Eine derartige Dissoziation könnte dabei ihre theoretische Grundlage in den verschiedenen Zielen des motorischen und des perzeptuellen Lernens haben: Anders als die Aktualisierung der sensorischen Prädiktionen über die eigenen Bewegungen zielt motorisches Lernen nicht primär darauf, eine Kongruenz zwischen den tatsächlichen und den intern prädizierten sensorischen Konsequenzen der eigenen Bewegungen herzustellen. Stattdessen kann motorisches Lernen als Optimierung der Erreichung externer Ziele verstanden werden (Shadmehr et al. 2010, Wolpert et al. 2011). Das Ausmaß, in dem Prädiktionsfehler für motorisches Lernen relevant sind, beruht damit nicht nur auf der kausalen Attribution dieser Fehler an interne Ursachen versus externe Ursachen (Berniker und Körding 2008, Wei und Körding 2009), sondern auch auf Prädiktionsfehlern in Hinblick auf die Erreichung der eigenen Ziele (*reward prediction error*, Izawa und Shadmehr 2011, siehe auch Abb. 4).

4.7. Kausalität und Systematik von Fehlern beim Lernen

Die Relevanz, welche Fehlersignale beim sensomotorischen Lernen erhalten, könnte auch die Systematik des Auftretens der Fehlersignale innerhalb eines Zeitintervalls reflektieren (Salomonczyk et al. 2011): Während die vorliegenden Studien die Rolle der Fehlerkausalität für *unsystematische* Fehler untersuchten, könnte die kausale Attribution von Fehlern an interne versus externe Ursachen auch bedeutsam für das Lernen bei *systematischen* Fehlern sein (Berniker und Körding 2011): Auf den ersten Blick mag das überraschend sein, da es – anders als im Fall der unsystematischen Fehler – plausibel erscheinen könnte, jeden systematischen Fehler zu kompensieren, unabhängig davon, ob dieser Fehler interne oder externe Ursachen hat. Doch könnte die Weise, *wie* intern versus extern verursachte systematische Fehler kompensiert werden, verschieden sein: (1) Die kausale Attribution systematischer Fehler an eine externe Ursache kann als Änderung des Kontexts verstanden werden. Die kausale Attribution von Fehlern an einen spezifischen externen Kontext ist essentiell, um kontextabhängiges Lernen zu erlauben (Wolpert et al. 2011). Nur dadurch können wir lernen, zuverlässig und effizient die sensorischen Konsequenzen unserer Bewegungen in spezifischen externen Kontexten vorherzusagen (Beispiel: visuelle Reafferenz bei Augenbewegungen mit und ohne Brille). (2) Die kausale Attribution systematischer Fehler an interne Ursachen ist entscheidend, wenn interne Veränderungen innerhalb des sensomotorischen Systems solches

Lernen induzieren sollen, das von externen Kontexten unabhängig ist (Beispiel: Transfer aus dem Rehabilitationstraining in alltägliche Aufgaben). Damit könnte die Kausalität von Fehlern auch angesichts der Systematik von Fehlern eine Bedeutung für sensomotorisches Lernen haben.

4.8. Schlussfolgerung

Zusammenfassend wurde die plastische Wahrnehmung unserer eigenen Bewegungen in Hinblick auf sensorische Prädiktionsfehler untersucht. Hierbei gelang es, die kausale Attribution der Prädiktionsfehler (an interne versus externe Ursachen) zu quantifizieren und (für dieselben Prädiktionsfehler) zur Vorhersage der nachfolgenden Aktualisierung der Prädiktionen über die eigenen Bewegungen zu verwenden: Diese Aktualisierung war nicht proportional zum extern erzeugten Prädiktionsfehler, sondern wurde durch die Komponente des Fehlers erklärt, welche die Probanden kausal an ihr eigenes sensomotorisches System attribuierten. Die gemessene Attribution war jedoch keine Konstante für alle Fehler der gleichen Größe, sondern ließ sich experimentell modulieren (durch Fehlergröße und Handlungsergebnisse). Damit könnte die kausale Attribution von Fehlersignalen ein allgemeines Prinzip bieten, um die Wahrnehmung der eigenen Bewegungen in Hinblick auf ihre Plastizität zu verstehen. Trotz der diskutierten Einschränkungen legen die Ergebnisse zudem nahe, dass eine kausale Attribution von Fehlersignalen auch für die motorische Kontrolle der eigenen Bewegungen von Bedeutung ist, also für sensomotorisches Lernen im weiteren Sinne.

5. Zusammenfassung

Unsere Wahrnehmung der eigenen Bewegungen basiert auf dem Vergleich der tatsächlichen sensorischen Bewegungsfolgen mit internen Prädiktionen über unsere Bewegungen. Da sich die Eigenschaften unseres sensomotorischen Systems kontinuierlich ändern, werden diese Prädiktionen anhand von sensorischen Prädiktionsfehlern aktualisiert. Jedoch haben Prädiktionsfehler nicht nur interne Ursachen, die aus dem eigenen sensomotorischen System resultieren, sondern auch externe Ursachen, die aus externen Störungen resultieren. Um eine zuverlässige Wahrnehmung der eigenen Bewegungen zu gewährleisten, sollte die Aktualisierung der internen Prädiktionen zwischen intern und extern verursachten Fehlersignalen differenzieren.

Deshalb testete die vorliegende Dissertation die Hypothese, dass die Aktualisierung der Wahrnehmung der eigenen Bewegungen auf einer kausalen Attribution der sensorischen Prädiktionsfehler (an interne versus externe Ursachen) basiert, und untersuchte, welche Faktoren diese Attribution modulieren. Dazu wurde die Wahrnehmung der eigenen Handbewegungen psychophysisch gemessen. Um visuelle Prädiktionsfehler zu generieren, wurde das visuelle Bewegungsfeedback von den tatsächlichen Bewegungen unvorhersehbar dissoziiert.

Wenn die Probanden mit experimentellen Prädiktionsfehlern konfrontiert wurden, aktualisierten sie ihre internen Prädiktionen über die sensorischen Bewegungsfolgen. Diese Aktualisierung war jedoch nicht proportional zu den extern generierten Prädiktionsfehlern, sondern korrelierte stattdessen mit derjenigen Fehlerkomponente, welche die Probanden an interne Ursachen attribuierten. Die Aktualisierung der eigenen Bewegungswahrnehmung reflektierte also tatsächlich die Ursache, an welche die Probanden den Prädiktionsfehler attribuierten. Die kausale Fehlerattribution war dabei jedoch keine Konstante, sondern ließ sich experimentell modulieren: Die Fehlerattribution reflektierte insbesondere die absolute Fehlergröße und die affektiven Handlungsergebnisse, die experimentell mit den Handbewegungen assoziiert wurden.

Die Ergebnisse zeigen, dass für unsere Wahrnehmung der eigenen Bewegungen der Vergleich zwischen sensorischen Bewegungsfolgen und internen Prädiktionen (den Komparatormodell und Reafferenzprinzip fordern) nicht hinreichend ist, sondern mit weiteren modulierenden Faktoren zu ergänzen ist (wie z. B. Handlungsergebnissen). Auch können die Differenzen, welche aus dem Vergleich resultieren, als Fehlersignale für die Aktualisierung der internen Prädiktionen dienen – und zwar dann, wenn sie an interne Ursachen attribuiert werden. Damit könnte die kausale Attribution von Fehlersignalen ein allgemeines Prinzip bieten, um die Wahrnehmung der eigenen Bewegungen in Hinblick auf ihre Plastizität zu verstehen.

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7. Eigenanteil

7.1. Publikation in Abschnitt 3.1.2.

Die Durchführung des Experiments (einschließlich der Programmierung), die Analyse der Daten und die Erstellung des Artikels habe ich allein vorgenommen. Die Entwicklung der Fragestellung und das Design des Experiments habe ich zusammen mit Dr. Axel Lindner vorgenommen. Dr. Axel Lindner und Dr. Matthis Synofzik halfen durch die kritische Durchsicht des Manuskripts. Die Beiträge der einzelnen Autoren sind zudem in der Veröffentlichung im Abschnitt Author Contributions dokumentiert.

7.2. Publikation in Abschnitt 3.2.2.

Die Durchführung des Experiments (einschließlich der Programmierung) und die Analyse der Daten habe ich allein vorgenommen. Die Erstellung des Artikels habe ich zusammen mit Dr. Matthis Synofzik vorgenommen. Die Entwicklung der Fragestellung und das Design des Experiments habe ich mit Dr. Matthis Synofzik und Dr. Axel Lindner vorgenommen. Dr. Axel Lindner und Dr. Matthis Synofzik halfen außerdem durch die kritische Durchsicht des Manuskripts.

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