It wasn't me: External error attribution dampens efferent-based predictions but not proprioceptive changes in hand localization

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Abstract

Knowing one's limb location is crucial in order to produce efficient movements. When a movement error is experienced, people account for whether the source of the error is external or internal in nature. When the error is clearly not caused by oneself, it is intuitive to correct for these errors without updating internal models for movement or estimating the position of the effector. That is, there should be reduced or no reliance on implicit learning. However, merely inducing explicit adaptation does not affect measures of implicit learning. Here, we use different visual manipulations that make the external nature of the error clear, and test how these manipulations affect both motor behaviour and hand location estimates.

We manipulate the extent of external error attribution in four ways, while participants learn to perform a 30-degree visuomotor rotation task: a Non-instructed control group that receives neither instructions nor different visual stimuli, an Instructed group that receives a counter strategy for dealing with the rotation, a Cursor Jump group that sees the cursor misalignment mid-reach on every training trial, and a Hand View group that sees both the misaligned cursor and their actual hand on every trial. Although an initial advantage in learning is seen for the Instructed group, performance across all groups are not different by the end of training, suggesting that any effects observed for changes in motor behaviour and hand localization are due to the manipulations.

During reaches without visual feedback about the cursor location, participants are instructed to perform reaching movements, while either including or excluding any strategy they may have developed during adaptation training to counter for the visuomotor rotation. All groups show awareness of the nature of the perturbation except for the Non-instructed group. Implicit changes in motor behaviour, measured with reach aftereffects, persist for all groups but are

greatly reduced for the Hand View group. For hand localization, participants either generate their own movement (allowing for hand localization with both afferent-based proprioceptive information and efferent-based predictions of sensory consequences) or a robot moves their hand (allowing for only proprioceptive information). We find that afferent-based changes in hand localization persists across all groups, but efferent-based changes are reduced for only the Hand View group. These results show that the brain incorporates source attribution for estimating the position of the effector during motor learning, and that proprioceptive recalibration during hand localization is an implicit process impervious to external error attribution.

Acknowledgements

I would like to express my gratitude for Dr. Denise Henriques and Dr. Marius 't Hart, as their mentorship have been a tremendous help for the creation of this thesis. I would also like to thank Dr. Peter Kohler, for his contributions as a committee member. Thank you to my amazing lab mates for their continuing support and advice. Finally, thank you to my partner for helping me get through this journey for the past two years.

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Chapter 1: General Introduction and Literature Review

It is crucial for people to continuously know the location of their limbs, in order to move efficiently within constantly changing environments. Given that changing circumstances may lead to movement errors, motor adaptation is our ability to modify our known motor skills, such that performance is restored to an ideal level (Martin et al., 1996; Krakauer et al., 2000; Bastian, 2008; Shadmehr et al., 2010; Krakauer et al., 2019). However, appropriately adapting our movements depends on whether the cause of the error is external or internal in nature (Berniker and Kording, 2008; 2011; Wei and Kording, 2009; Wilke et al., 2013; Kong et al., 2017; Maurer et al., 2019). Consider, for example, a person who is throwing a ball towards a target. For such a task, a movement error may be produced if a strong gust of wind pushes the ball's trajectory to another direction (externally caused), or if the throwing arm of the person becomes fatigued (internally caused). The identification of what causes the error is known as source attribution, and the person must take this into account when adjusting their movements accordingly. While motor adaptation has been shown to lead to changes in internal estimates of limb position (Cressman and Henriques, 2009; 2015; Cameron et al., 2012; Ostry and Gribble, 2016; Leech et al., 2018; Modchalingam et al., 2019; Sombric et al., 2019), these changes should be reduced or not occur when the cause of the error experienced during adaptation is obviously external in nature. The goal of this thesis is to investigate how experiencing externally caused errors during motor adaptation, affects changes in estimating the limb position.

Motor adaptation

People perform multiple reaching movements with their hand on a daily basis, and investigating adaptation involves perturbing this well-known movement. Traditionally, motor

adaptation studies have been conducted using wedge prisms attached to spectacles that shifted

the visual field of the participant towards either the left or right direction (Martin et al., 1996; see

Shadmehr et al., 2010 for review). However, the whole visual field is shifted in this paradigm.

To investigate reach adaptation more specifically, a view of the participant's hand is typically

replaced with a cursor, and the participant is instructed to perform reaching movements to move

the cursor to a target displayed on the screen (Fig. 1; Krakauer et al., 2000; Shadmehr et al.,

2010). Adaptation is then elicited with the introduction of visual or mechanical perturbations

(Fig. 1). Visual perturbations involve a mismatch between visual feedback of the cursor and
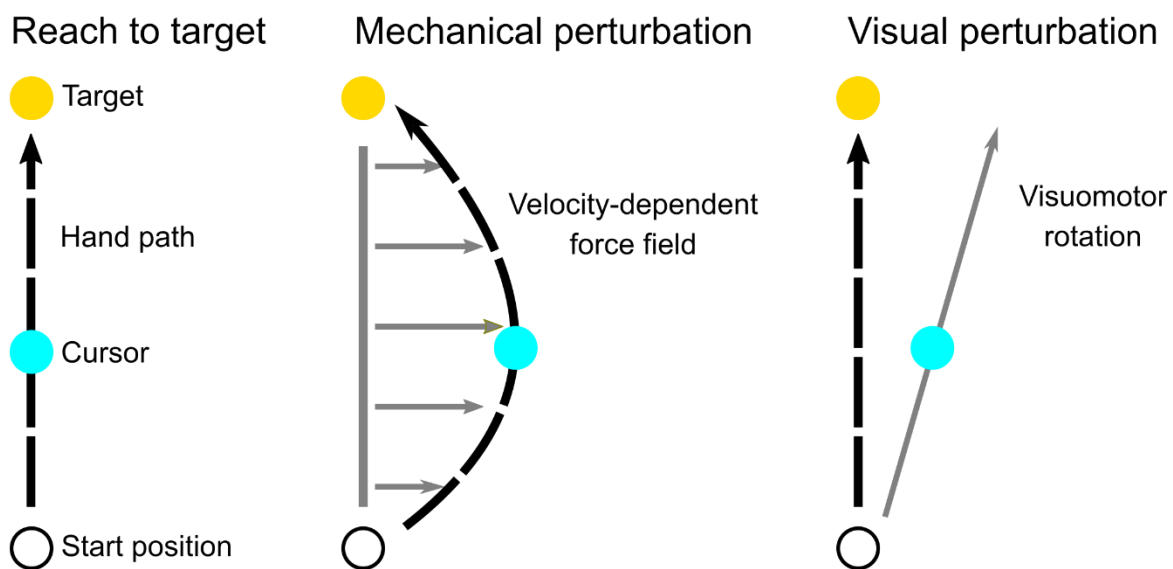
Reach to target   **Mechanical perturbation**   **Visual perturbation**

Target

Hand path

Cursor

Start position

Velocity-dependent
force field

Visuomotor
rotation

Fig. 1: Visuomotor adaptation paradigms. Reach adaptation is typically investigated by representing the unseen
hand location of a participant with a cursor (light blue circle). Participants are then instructed to hold an apparatus
(e.g. robot manipulandum) and to perform reaching movements that guide the cursor from a start position (hollow
black circle) towards a target (yellow circle, **left**). To induce adaptation, mechanical perturbations involve robot-
induced forces that push the hand of the participant, along with visual feedback of the cursor, towards a particular
direction. The magnitude of these forces depends on the velocity of the hand movement (**middle**). Visual perturbations
involve a mismatch between visual feedback of the cursor and the actual hand movement. One example is a visuomotor
rotation, where the cursor is rotated relative to the start position, making it deviate by a set magnitude from the hand
position (**right**).

actual hand movement direction (Krakauer et al., 1999; 2000; Cressman and Henriques, 2009; Cameron et al., 2012; Modchalingam et al., 2019), while mechanical perturbations typically involve robot-induced forces that push the hand of the participant towards a particular direction depending on their movement velocity (Shadmehr and Mussa-Ivaldi, 1994; Ostry et al., 2010; Mattar et al., 2011; Ostry and Gribble, 2016). The current study uses a visual perturbation called a visuomotor rotation, where the cursor position is rotated relative to a starting position, such that the cursor deviates by a set magnitude from the hand position (Fig. 1). Regardless of the paradigm used, adaptation proceeds in a generally similar manner, where initial errors in movement direction are gradually corrected with repeated trials.

Once individuals are in an adapted state, removing the perturbation leads to participants persistently making erroneous deviations in hand movements towards the opposite direction of the perturbation. These are known as reach aftereffects and suggest that there has been an internal remapping of representations in the brain (Krakauer, 2006; Bastian, 2008; Krakauer, 2009; Krakauer et al., 2019). Such a remapping has been shown to depend on the cerebellum, as patients with cerebellar lesions show less improvement during adaptation and smaller reach aftereffects compared to healthy controls (Martin et al., 1996; Tseng et al., 2007; Bastian, 2008). The theoretical framework, referred to as the internal model, captures the remapping that occurs during adaptation and its consequent manifestation as reach aftereffects (Fig. 2). An internal inverse model determines the motor commands necessary to get the hand from its starting position to the target, based on incoming sensory information such as vision and proprioception. However, the processing of these afferent signals takes time. Hence, the internal model also consists of a forward model component, where the brain uses a copy of the outgoing motor command, known as an efference copy, and the current hand position to predict the sensory
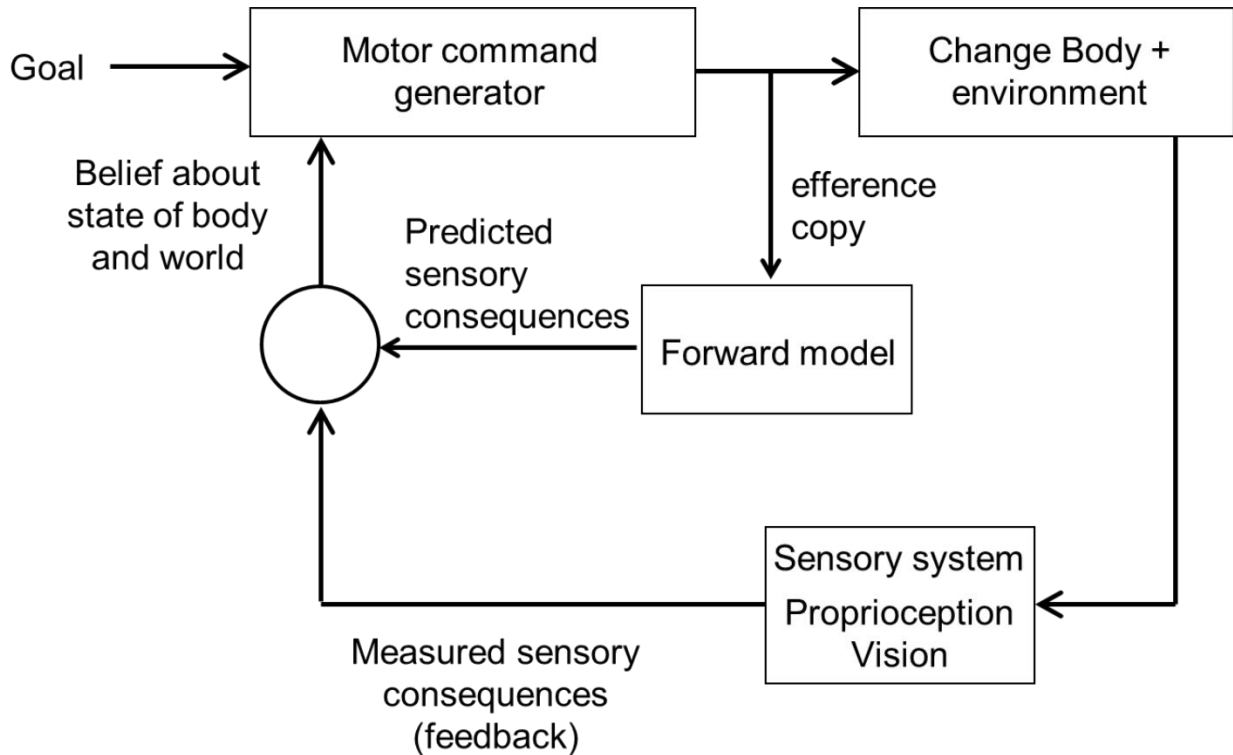
Fig. 2: Internal model. The internal model consists of forward and inverse model components. This simplified diagram starts with a movement goal. The inverse model is involved in determining the necessary motor commands in order to accomplish the movement, based on incoming sensory information such as vision and proprioception. However, sensory feedback is not the only source of information about the movement. An efference copy of the outgoing motor command is incorporated into forward model computations to get a predicted estimate of the movement. Both sensory feedback and the predicted sensory consequences of the movement are then combined to update our estimate of the state of the body.

consequences of the movement (Blakemore et al., 1998). If the predictions do not match the

actual sensory consequences (termed sensory prediction error; Bastian, 2008), the forward model

is updated in order to match the current state more closely. As a result, the motor command is

updated, in order to perform the reaching movement correctly (Haith & Krakauer, 2013). In this

framework, adaptation is thus guided by sensory prediction error-based learning, and reach

aftereffects show that the internal model has been updated.

For small or gradually introduced visual or mechanical perturbations, the resulting

adaptive changes are traditionally considered to be implicit in nature (Krakauer et al., 2000;

Krakauer, 2009). This is because the sensory prediction errors used by the brain to update the internal forward model occur without conscious awareness (Taylor et al., 2014). However, reach aftereffects also occur with larger and abruptly introduced perturbations that increase conscious awareness of the nature of the perturbation. This suggests that explicit processes may account for a part of the resulting adaptive change (Mazzoni and Krakauer, 2006; Taylor et al., 2010; Benson et al., 2011; Taylor and Ivry, 2011; 2012; Taylor et al., 2014; Bond and Taylor, 2015; Werner et al., 2015; Neville and Cressman, 2018; Modchalingam et al., 2019). Aside from using large and abruptly introduced perturbations, explicit awareness of the perturbation can also be elicited through instruction about the nature of the perturbation and by providing a strategy that can be used to compensate for it (Mazzoni and Krakauer, 2006; Taylor et al., 2010; Benson et al., 2011; Modchalingam et al., 2019). For example, participants may be instructed to reach towards a neighbouring target that reflects the magnitude of the imposed visuomotor rotation (Mazzoni and Krakauer, 2006). That is, if a 45° clockwise (CW) rotation is imposed, then the participant must reach to the neighbouring target that is in the counterclockwise (CCW) direction of the current trial's target location. Alternatively, participants may be shown an image of a clock face that uses the numbers on the clock to illustrate appropriate reach directions to counter for the rotation (Benson et al., 2011). In these cases, if the target is at the 12 o'clock position and a 30° CW rotation is imposed, reaching directly towards the 12 position would bring the cursor to the 1 position. To counter the rotation, the participant must then reach towards the 11 position. Although explicit knowledge of the perturbation leads to an initial advantage in learning, asymptotic learning and measures of aftereffects are not different from conditions that rely on mainly implicit learning (Mazzoni and Krakauer, 2006; Benson et al., 2011; Werner et al., 2015; Neville and Cressman, 2018; Modchalingam et al., 2019). Adaptation-induced changes in motor

behaviour (i.e., aftereffects) should then reflect the relative contributions of explicit and implicit processes.

There are different methods for measuring the relative contributions of explicit and implicit processes to adaptation. First, questionnaires may be implemented at the end of the experiment (Benson et al., 2011; Werner et al., 2015; Modchalingam et al., 2019), where participants are assigned a score depending on their responses to a series of questions. Their overall score would then determine their explicit awareness (or lack thereof) about the nature of the perturbation. Another method instructs participants to verbally report which landmark they intend to reach towards on every trial, in order to get the cursor to the target (Taylor et al., 2014; Bond and Taylor, 2015). This method uses the difference between the participant's reported location and the location of the actual hand movement to determine explicit contributions, while the location of the actual hand reflects implicit contributions. A third method uses a process dissociation procedure (PDP; Werner et al., 2015) where participants perform reaches towards a target without visual feedback from the hand-cursor (see also Neville and Cressman, 2018; Modchalingam et al., 2019). While making the reaches, participants are instructed to either include any strategy they may have developed during adaptation training or to deliberately exclude such a strategy. Thus, including a strategy in no-cursor reaches measures both explicit and implicit contributions, while excluding a strategy would measure only implicit contributions. The inability to switch between using and not using such a strategy would suggest a lack of explicit awareness about the nature of the perturbation. In the current study, we adapt the PDP to quantify implicit and explicit contributions to learning across different visual manipulations, that are intended to vary the extent to which the experienced error is attributed externally.

Proprioceptive recalibration

The adaptation of reach movements to visual or mechanical perturbations leads not only to changes in motor behaviour, but to changes in estimating the hand position as well (Cressman and Henriques, 2009; 2015; Ostry and Gribble, 2016). In a visuomotor rotation task (Fig. 1), particularly, the individual perceives a mismatch between the visual feedback representing the hand position (cursor) and the actual felt location of the hand (proprioception). Adapting to such conditions leads to changes in proprioceptive estimates of hand location, known as proprioceptive recalibration. For example, when participants are instructed to complete a two-alternative forced choice (2AFC) task to indicate the location of their unseen and adapted hand relative to a reference marker, hand position estimates are shifted towards the direction of the altered visual feedback experienced during adaptation training (Cressman and Henriques, 2009). Moreover, these shifts emerge quickly (Ruttle et al., 2016) and account for about 20% of the visual misalignment of the hand (Cressman and Henriques, 2009; 2015). Recalibrated proprioception is not only observed in 2AFC tasks, but also when the visible and untrained hand is used to indicate the location of the unseen and adapted hand ('t Hart and Henriques, 2016). It has been shown to emerge within different types of perturbations other than visuomotor rotations, such as translations (Cressman and Henriques, 2009), force fields (Ostry et al., 2010), visuomotor gains (Cameron et al., 2012), and locomotion (Leech et al., 2018; Sombric et al., 2019). This recalibration is also preserved as people age (Cressman et al., 2010; Vachon et al., 2019). Thus, proprioceptive recalibration seems to be a robust form of sensory plasticity.

Estimates of hand position are not only based on afferent proprioceptive information, but on efferent-based predicted sensory consequences of the hand movement as well. Given that efferent-based predictions are updated due to sensory prediction errors (Mazzoni and Krakauer,

2006; Bastian, 2008; Synofzik et al., 2008; Shadmehr et al., 2010; Izawa et al., 2012; Haith and Krakauer, 2013; Wong et al., 2019), hand position estimates are also changed based on these updated predictions. To measure these estimates, previous research had participants perform self-generated movements towards an arc with their unseen and adapted right hand (Synofzik et al., 2008; Izawa et al., 2012). Importantly, self-generated movements produce a motor command, allowing for efferent-based predictions of sensory consequences. Participants then indicated where they perceived their unseen right hand had crossed the arc by either using their left hand to move a mouse-guided cursor towards the location of their adapted hand (Synofzik et al., 2008), or by using their visible left hand to point where they believed the right hand intersected the arc (Izawa et al., 2012). Following adaptation training, estimates of hand location after self-generated hand movements are shifted in the direction of the altered visual feedback. These shifts in hand location estimates were observed for both healthy participants and patients with cerebellar damage, although shifts were smaller for the patients (Synofzik et al., 2008; Izawa et al., 2012). These reduced changes in hand position estimates may be explained by an impairment in sensory prediction error-based learning for patients with cerebellar damage. However, shifts in hand position estimates are still observed, and could suggest that a separate signal is contributing to these shifts.

Given that all movements, whether self-generated or not, involve proprioceptive information, the afferent-based recalibration of proprioception should contribute to shifts in hand location estimates. The measurement of afferent-based contributions requires inhibiting the generation of a motor command, such that no efference copy is used to predict the sensory consequences of the movement and only proprioceptive information is available. One way to accomplish this is to have the apparatus passively move the participant's hand towards a

particular location ('t Hart and Henriques, 2016). In this set-up, the movement of the participant could either be self-generated (active) or robot-generated (passive), and they are then instructed to estimate the location of their unseen hand with their visible left hand (see Fig. 3e in Chapter 2; 't Hart and Henriques, 2016; Ruttle et al., 2018; Modchalingam et al., 2019; Mostafa et al., 2019). When comparing shifts in hand location estimates between these two movement types, active movements show a larger magnitude of shifts than in passive movements ('t Hart and Henriques, 2016), which is expected because active movements contain information from both afferent and efferent-based contributions. However, the difference in the magnitude of shifts between the two movement types are not drastic, suggesting that shifts in hand position estimates are mainly accounted for by proprioceptive recalibration. The difference between the two movement types would then be likely due to efferent-based contributions. Thus, it seems that afferent and efferent-based estimates have distinct contributions to hand localization, where updates in efferent-based predictions are due to sensory prediction error-based learning and proprioceptive recalibration is due to a separate signal from the visuo-proprioceptive discrepancy experienced ('t Hart and Henriques, 2016; Ruttle et al., 2018; Mostafa et al., 2019). Evidence for this comes from intact proprioceptive recalibration in people with mild cerebellar ataxia (Henriques et al., 2014). Instead, the recalibration of proprioception seems to be processed within the posterior parietal cortex (PPC), as disrupting this region has been shown to affect visuo-proprioceptive realignment (Block et al., 2013). Moreover, paradigms that prevent updates to the internal forward model, but still allow for proprioceptive recalibration, have been shown to lead to reach aftereffects (Cressman and Henriques 2010; Cameron et al., 2012; Salomonczyk et al., 2013; Henriques et al., 2014; Mostafa et al., 2019). This shows that in addition to afferent

and efferent-based estimates contributing to hand localization separately, these two implicit processes may also be contributing to changes in motor behaviour independently.

External error attribution

The attribution of errors to an external source should make it clear to an individual that the perturbation being experienced is not due to their own internal motor system, and decreases in performance are likely transient (Berniker and Kording, 2008; 2011; Wei and Kording, 2009; Wilke et al., 2013; Kong et al., 2017; Maurer et al., 2019). That is, throwing a ball outdoors where a strong gust of wind is blowing should be different from throwing a ball indoors. In such cases, it would be advantageous for the individual to correct for errors in an equally transient way. Because implicit learning will have longer lasting effects, it should be engaged in less or not at all in response to external perturbations. However, it has been shown that merely increasing explicit knowledge about the nature of the perturbation, through instructions and larger perturbation sizes, does not reduce implicit aftereffects and changes in afferent and efferent-based estimates of hand location (Modchalingam et al., 2019). This suggests that explicit learning does not necessarily correspond to external error attribution. Therefore, in the current experiment, we specifically test how external error attribution affects implicit changes in motor behaviour and hand location estimates.

Research Question

The research question we investigate is how the absence of ambiguity, about the nature and source of error during motor adaptation, affects implicit aftereffects as well as afferent and efferent-based estimates of hand position. In addition to having groups where participants are either instructed about the nature of the perturbation and given a strategy to counter for it or not

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(Instructed and Non-instructed groups), we further manipulate the extent of external error attribution in two other groups. Specifically, we either have visual feedback of the hand-cursor jump to the imposed visuomotor rotation mid-reach on every training trial (Cursor Jump group), or cursor feedback is shown along with a view of the actual hand of the participant (Hand View group). These manipulations should make it clear to the participants that the error experienced is not due to their own internal motor system. We then use reaches without visual feedback of the cursor to measure corresponding reach aftereffects across all four groups. We also adapt the PDP (Werner et al., 2015; Neville and Cressman, 2018; Modchalingam et al., 2019) during these no-cursor reaches, to quantify explicit and implicit learning for each group. For hand location estimates, we implement a localization task with active and passive movements ('t Hart and Henriques, 2016; Modchalingam et al., 2019). Given that the two movement types include either afferent and efferent-based estimates or afferent-based estimates only, we are able to measure the relative contribution of each estimate to shifts in hand localization following adaptation.

We hypothesize that increased external error attribution, particularly for the Cursor Jump and Hand View groups, will lead to reduced changes in motor behaviour and hand location estimates following adaptation. First, we expect that our manipulations will increase explicit knowledge about the external nature of the perturbation, such that a difference would be observed between reaches that use any strategy learned during adaptation, from reaches that do not use such a strategy. Furthermore, given that implicit learning should be engaged in less, we also expect external error attribution to lead to reduced reach aftereffects. Second, both afferent and efferent-based estimates of hand location should be considered implicit processes. As such, we expect that shifts in both estimates of hand location should be reduced, especially for the Hand View group, as it is the clearest demonstration that the source of the error is external in

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nature. Taken together, these findings will provide insights into how source attribution plays a

role in hand localization and how these affect corresponding motor behaviour.

Chapter 2: Research Article

External error attribution dampens efferent-based predictions but not proprioceptive changes in hand localization

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Abstract

In learning and adapting movements in changing conditions, people attribute the errors they experience to internal or external sources. When errors are clearly due to external conditions, we should not update our internal models for movement or estimating the position of the effector, i.e. there should be no implicit learning. However, measures of implicit learning are the same whether or not we induce explicit adaptation by telling participants about the nature of the perturbation. Here we evoke clearly external errors by either demonstrating the rotation on every trial, or showing the hand itself throughout training. Implicit reach aftereffects persist, but are reduced in both groups. Only for the group viewing the hand, changes in hand position estimates suggest that predicted sensory consequences are not updated, but rely on recalibrated proprioception. Our results show that estimating the position of the hand incorporates source attribution during motor learning, but recalibrated proprioception is an implicit process unaffected by external error attribution.

Introduction

Knowing our limbs' positions is crucial for our ability to move competently. Moreover, changing circumstances may cause movement errors, which require us to adapt our motor control to restore performance (Martin et al., 1996; Krakauer et al., 2000; Bastian, 2008; Shadmehr et al., 2010; Krakauer et al., 2019). When errors are not caused by our own motor system, but are instead externally caused, the way in which movements are adapted to counter them should change (Berniker and Kording, 2008; 2011; Wei and Kording, 2009; Wilke et al., 2013; Kong et al., 2017). Externally caused errors should also affect our estimate of limb position, but this has not been directly investigated yet. Here, we introduce two types of movement feedback to investigate how our limb position estimates may be affected when errors are clearly not caused by the individual.

In reaching movements, adaptive changes that result from small or gradually introduced visual or mechanical perturbations are traditionally considered as largely implicit (Krakauer et al., 2000; Krakauer, 2009). Implicit adaptation is manifested by reach aftereffects, persistent deviations in hand movements after perturbation removal, suggesting an internal representational remapping has occurred in the brain (Krakauer, 2006; 2009; Krakauer et al., 2019). Reach aftereffects also occur with larger and more abruptly introduced perturbations, as well as when participants are made aware of the nature of the perturbation. In these cases, explicit processes account for a part of the resulting adaptive change (Mazzoni and Krakauer, 2006; Taylor et al., 2010; Benson et al., 2011; Werner et al., 2015; Neville and Cressman, 2018; Modchalingam et al., 2019). Thus, both explicit and implicit processes contribute to adaptation (Taylor and Ivry, 2011; 2012; Taylor et al., 2014). Here, we first quantify implicit and explicit contributions to learning in response to different visual manipulations. These manipulations differentially

demonstrate the nature and source of errors experienced, thereby varying the extent of external error attribution.

Previous research has found that adapting reach movements to visual or mechanical perturbations leads to changes not only in motor performance, but also in proprioceptive estimates of hand location (Cressman and Henriques, 2009; 2015; Ostry and Gribble, 2016). This proprioceptive recalibration emerges quickly (Ruttle et al., 2016) and reflects about 20% of the visual misalignment of the hand (Cressman and Henriques, 2009; 2015). Recalibrated proprioception is also preserved in aging (Cressman et al., 2010) and in different perturbations (rotations and translations: Cressman and Henriques, 2009, force fields: Ostry et al., 2010, gains: Cameron et al., 2012, locomotion: Leech et al., 2018; Sombric et al., 2019). Thus, proprioceptive recalibration is ubiquitous, and seems to improve motor performance.

Apart from afferent proprioceptive information, hand localization is also based on predicted sensory consequences of the movement, calculated by internal forward models that use an efference copy of the outgoing motor command (Blakemore et al., 1998; Wolpert and Kawato, 1998). These efferent-based updates are considered a pre-requisite for implicit adaptation (Bastian, 2008; Haith and Krakauer, 2013), and seem to contribute to reach aftereffects separately from recalibrated proprioception ('t Hart and Henriques, 2016; Ruttle et al., 2018; Mostafa et al., 2019). Efferents and non-visual afferents should both be present when estimating hand location after self-generated 'active' movements, while robot-generated 'passive' movements should only allow afferent-based proprioceptive signals. Thus, active and passive movements assess the relative contributions of afferent and efferent signals to hand position estimates (Cameron et al., 2012; 't Hart and Henriques, 2016; Modchalingam et al., 2019).

Since both afferent and efferent contributions to hand location estimates should be implicit, they should be reduced or not occur when errors are attributed externally, as implicit learning is engaged less or not at all. In other words, it would be intuitive for people to not update estimates of their hand location, when it is clear that the error is being caused by an external source. However, modulating explicit knowledge about the nature of the perturbation, by providing instructions or increasing the perturbation size, does not affect persistent shifts in both proprioceptive recalibration and updating of predicted sensory consequences (Modchalingam et al., 2019). Therefore, in the current study, we investigate how external error attribution affects implicit changes in motor behaviour and hand location estimates.

To investigate our research question, we vary the extent that people attribute the error they experience to the cursor, while holding a robot manipulandum and training in a visuomotor rotation task. The experiment consists of two sessions: a baseline, aligned session, where visual feedback of the cursor matched the actual hand position, and a rotated session where participants adapt to a 30° rotated hand-cursor (Fig. 3a-3d). In addition to two groups either receiving instructions about the nature of the rotation and a strategy to counter for it or not (Instructed and Non-instructed groups; Fig. 3a), we test two other groups where either visual feedback of the hand-cursor jumps to the imposed rotation mid-reach on every training trial (Cursor Jump group; Fig. 3b) or a view of the actual hand of the participant is present along with the rotated cursor (Hand View group; Fig. 3c). These manipulations should make clear to participants that the cursor errors are caused externally. We interleave different tasks across blocks of cursor training in both the aligned and rotated sessions: a localization task (Fig. 3e) to investigate how our manipulations affect afferent and efferent contributions to hand localization, and no-cursor reaches (Fig. 3f) to assess the implicit and explicit contributions to learning in response to the

different manipulations. We hypothesize that with increased external error attribution, implicit

changes in motor behaviour and shifts in afferent and efferent-based estimates of hand
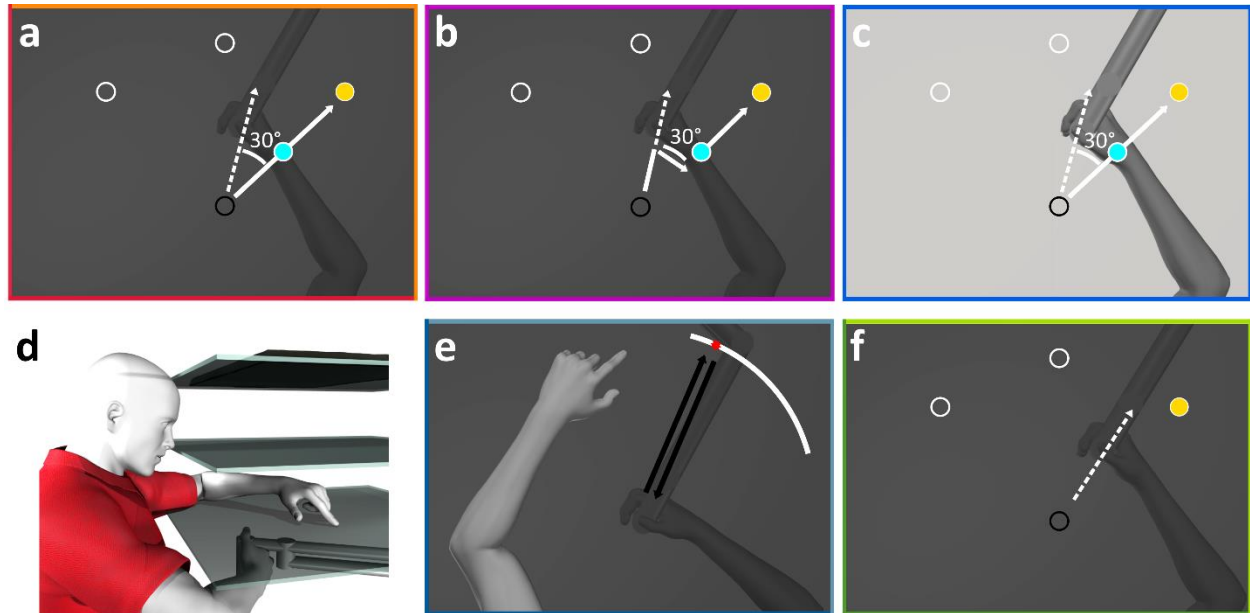
localization will decrease.

Fig. 3: Experimental apparatus and stimuli. a-c: Top-down view displaying the different manipulations for the reach-training tasks, where the cursor (light blue) is rotated 30° CW. Reaches were made to one of three possible target locations (indicated as hollow white circles), but only one target appeared on every trial (yellow circle) **a:** In both the Instructed and Non-instructed groups, participants did not see their hand, and the cursor had a constant rotation throughout each trial. **b:** Participants in the Cursor Jump group saw the cursor "jump" to the 30° CW rotation mid-reach on every trial. **c:** In the Hand View group, participants saw both their actual, illuminated hand and the cursor. **d:** Participants sat on an adjustable chair in a dark room and held a robot manipulandum located below a touch screen (bottom surface), while viewing stimuli through a reflective screen (middle surface) which projected stimuli generated from a downward facing computer screen (top surface). **e:** Active and Passive Localization trials: Participants used their visible left hand to indicate on the touch screen where they have crossed the arc with their unseen right hand, after voluntarily generating a right-handed movement (active) or after a robot-generated movement (passive). **f:** No-cursor trials: Reaches were made to the same three targets in the absence of visual feedback of the cursor or hand.

Results

Before investigating how external error attribution affects changes in motor behaviour and hand localization, we first confirmed that all groups appropriately countered the perturbation by the end of 90 training trials (Fig. 4a) and observed that reach trajectories were not qualitatively different (Fig. 5). We tested for group differences at different time points during adaptation training (three blocks: trials 1-3, 4-6, 76-90) using a 3X4 mixed design ANOVA, with block as a within-subject factor (blocks 1, 2, and 3) and group as a between-subject factor (Non-instructed, Instructed, Cursor Jump, Hand View). We found main effects of group ($F(3,86) = 5.678$, $p = .001$, generalized eta squared (η^2_G) = .092) and block ($F(2,172) = 78.411$, $p < .001$, $\eta^2_G = .307$), and a group X block interaction ($F(6,172) = 7.856$, $p < .001$, $\eta^2_G = .118$). This suggests that, as expected, group differences in learning rates were modulated by the block of trials. Follow-up tests compared each group to the control Non-instructed group, and showed the expected initial advantage of instructions in reducing reach direction error within block one (Fig. 4a-4b), as only the Instructed group significantly differed from the Non-instructed group ($t(148) = 4.632$, $p < .001$, eta squared (η^2) = .127). In the second block (Fig. 4c), no groups significantly differed from the Non-Instructed group (Instructed: $t(148) = 1.922$, $p = .295$, $\eta^2 = .024$; Cursor Jump: $t(148) = 2.538$, $p = .071$, $\eta^2 = .042$; Hand View: $t(148) = 0.910$, $p = .934$, $\eta^2 = .006$). For the last block (Fig. 4a, 4d), an ANOVA on the effect of group on angular reach deviations showed that group differences were not statistically significant from each other ($F(3,86) = 0.561$, $p = .642$, $\eta^2_G = .019$), suggesting that our manipulations did not affect the asymptotic level of adaptation. Thus, any effects of training on changes in motor behaviour and hand localization cannot be explained by levels of adaptation in the different groups.
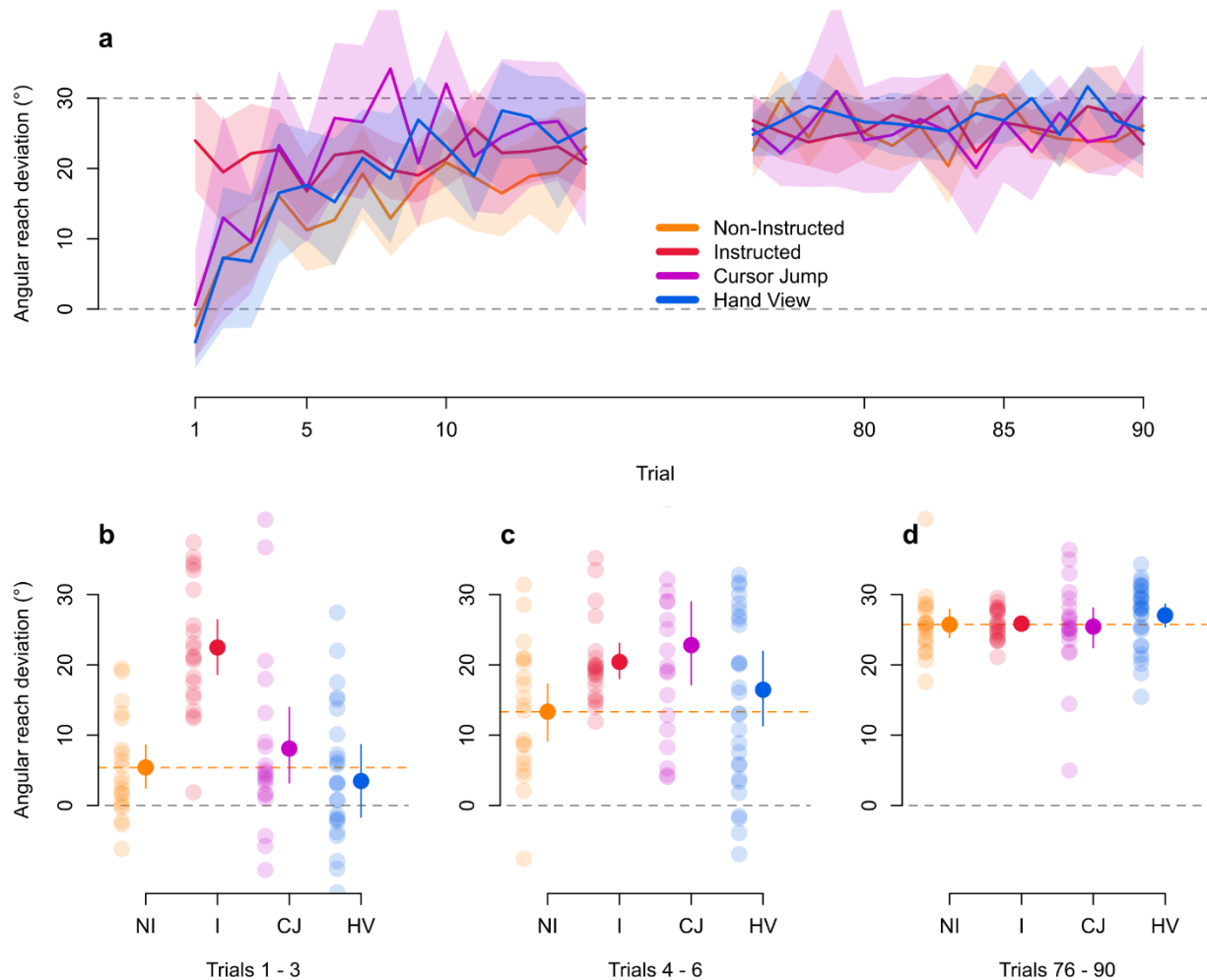
Fig. 4: Rate of learning during adaptation training. a: Only the first and last 15 trials of adaptation training are shown. Grey dashed line at the 30° mark indicates the direction that the hand must deviate in order to fully and successfully counter for the perturbation. The grey dashed line at the 0° mark indicates reach directions similar to those in the baseline, aligned session (i.e., no compensation). The Instructed group showed an initial advantage in successfully countering for the perturbation as early as the first trial. There were no statistically significant differences in reaches performed by participants from all groups for the last 15 trials. Solid lines are group means and shaded regions are corresponding 95% confidence intervals. **b-d:** Individual participant data from each group are shown, separated in three blocks of trial sets during adaptation training. Orange dashed line indicates mean for the Non-instructed, control group. Solid dots and error bars correspond to the group mean and bootstrapped 95% confidence intervals.
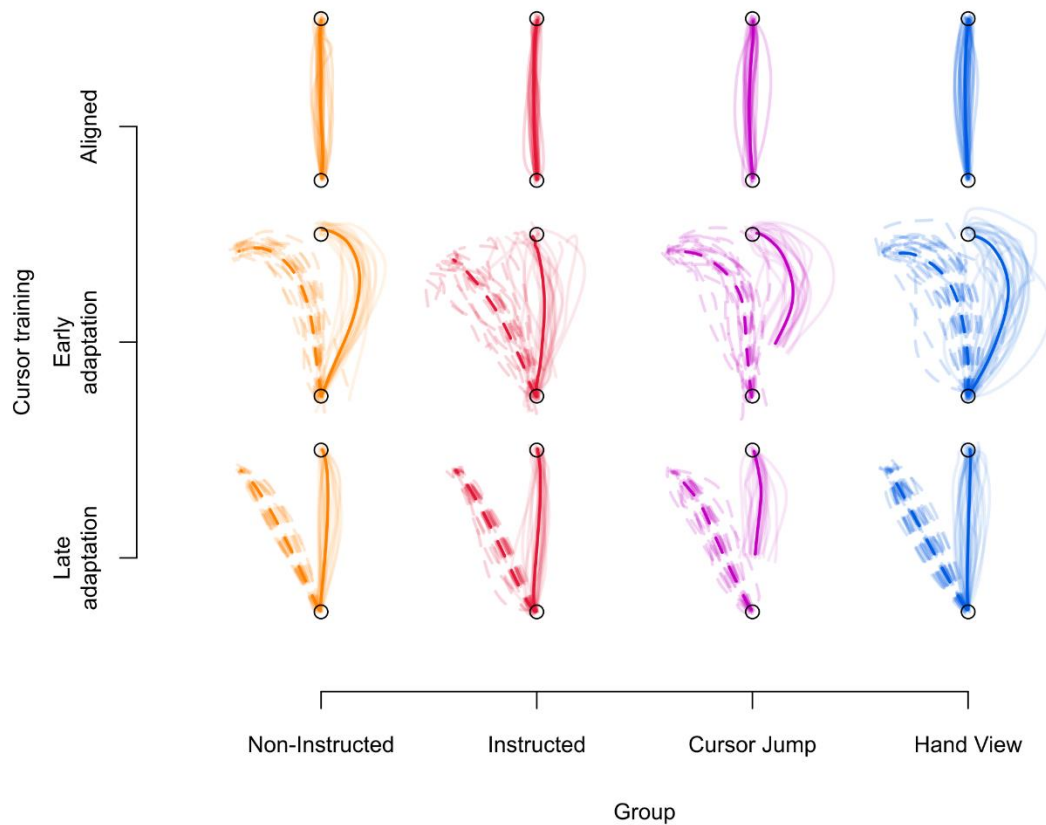
Fig. 5: Individual and average reach trajectories. The trajectory of reaches across all participants within their respective groups are shown with light coloured lines. Each participant's trajectory combines reaches during the last three trials of the first block of cursor training in the aligned session (**top**), as well as the first three (**middle**) and last three (**bottom**) trials of the first block of cursor training in the rotated session. Light solid lines indicate the trajectory of the hand-cursor and light dashed lines indicate the trajectory of the hand. Only solid lines are shown in the aligned session, as both hand and hand-cursor trajectories were similar. Group means for the hand trajectories are indicated with the dark dashed line, and dark solid lines indicate the mean hand-cursor trajectory. All groups seem to have produced similar reach trajectories, across the different time points in the experiment, regardless of condition. Moreover, despite curved reaches during early adaptation training, reach trajectories were straight towards the end of adaptation training.

Implicit aftereffects persisted despite external error attribution

To investigate the effects of external error attribution on changes in motor behaviour, we used no-cursor trials both before and after adaptation (Fig. 3f). After adaptation, however, we adopted a process dissociation procedure (PDP, Werner et al., 2015; see also Neville and

Cressman, 2018; Modchalingam et al., 2019), where we asked people to make open-loop reaches to targets, while either including or excluding any strategy they learned to counter for the perturbation. We expected a difference between these reaches, as including a strategy comprises explicit and implicit contributions to learning, while excluding a strategy reflects only implicit contributions.

We first compared no-cursor trials in the aligned session and without strategy no-cursor reaches after adaptation, to test for implicit reach aftereffects (Fig. 6). We conducted a 2X4 mixed design ANOVA with session (aligned or rotated) as a within-subject factor and group as a between-subject factor. We confirmed the presence of reach aftereffects with a main effect of session ($F(1,86) = 373.023$, $p < .001$, $\eta^2_G = .530$). Moreover, we found a main effect of group ($F(3,86) = 16.576$, $p < .001$, $\eta^2_G = .230$) and an interaction between session and group ($F(3,86) = 22.605$, $p < .001$, $\eta^2_G = .170$), suggesting that the effect of session was modulated by group. Follow-up tests showed that aligned and without strategy reach deviations differed within each group (Instructed: $t(86) = -11.830$, $p < .001$, $\eta^2 = .619$; Non-Instructed: $t(86) = -12.912$, $p < .001$, $\eta^2 = .660$; Cursor Jump: $t(86) = -9.050$, $p < .001$, $\eta^2 = .488$; Hand View: $t(86) = -4.037$, $p < .001$, $\eta^2 = .159$). This means that implicit reach aftereffects were present in each group. To address how the effect of session was modulated by group, follow-up tests compared reach aftereffects for each group to those in the Non-instructed group. We found that the Instructed group was not significantly different from the Non-instructed group ($t(86) = -0.722$, $p = .922$, $\eta^2 = .006$), but the Cursor Jump ($t(86) = -3.419$, $p = .004$, $\eta^2 = .120$) and Hand View ($t(86) = -7.538$, $p < .001$, $\eta^2 = .398$) groups were, suggesting that external error attribution in the Cursor Jump and Hand View groups led to reduced implicit reach aftereffects, compared to the Instructed and Non-instructed groups. Furthermore, the reduction in aftereffects was more pronounced for the Hand View
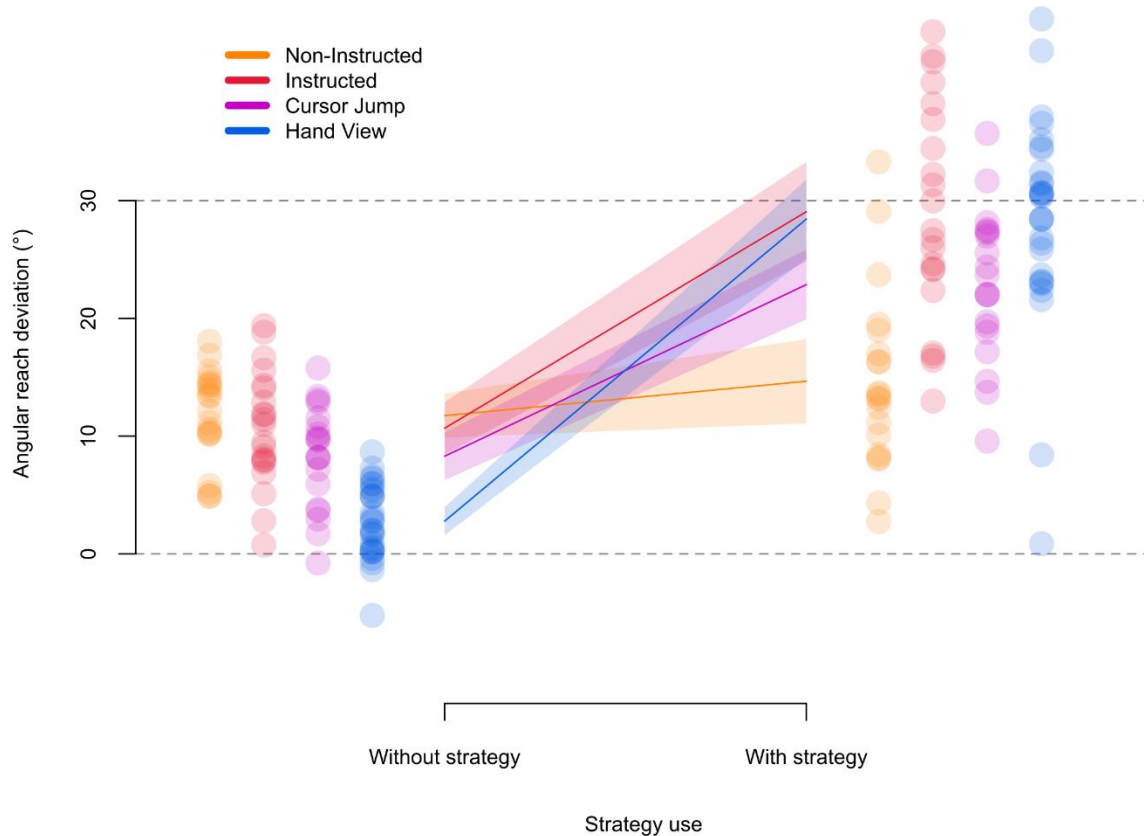
Fig. 6: No cursor reaches and strategy use. Angular reach deviations of the hand per group, while either excluding (without strategy) or including (with strategy) any strategies developed during adaptation training. Grey dashed line at the 30° mark indicates angular reach deviations equivalent to full compensation for the perturbation, and grey dashed line at the 0° mark indicates reaches that did not correct for the perturbation. Only the Non-instructed group was unable to switch between excluding and including a strategy to counter for the perturbation. Implicit reach aftereffects, indicated by without strategy angular reach deviations, were reduced for the Cursor Jump group and were further reduced in the Hand View group. Solid lines are group means and shaded regions are corresponding 95% confidence intervals. Individual participant data from each group are shown for both types of strategy use.

group compared to the Cursor Jump group ($t(86) = 3.818$, $p = .001$, $\eta^2 = .145$). In short, reach aftereffects persisted across groups, but were greatly reduced for the Hand View group.

After confirming the presence of reach aftereffects, we used the PDP to assess explicit contributions to learning, by comparing with and without strategy no-cursor reaches (Fig. 6). We

conducted a 2X4 mixed design ANOVA with strategy use as a within-subject factor (without strategy or with strategy) and group as a between-subject factor. We found main effects of strategy use ($F(1,86) = 285.493$, $p < .001$, $\eta^2_G = .592$) and group ($F(3,86) = 6.779$, $p < .001$, $\eta^2_G = .118$), and a strategy use and group interaction ($F(3,86) = 28.678$, $p < .001$, $\eta^2_G = .304$). This suggests that strategy use had an effect on angular reach deviations and that this effect differed across groups. Follow-up tests compared with and without strategy angular reach deviations for each group separately. We found no effect of strategy in the Non-instructed group ($t(86) = -1.529$, $p = .427$, $\eta^2 = .026$), but found significant differences in the other groups (Instructed: $t(86) = -9.877$, $p < .001$, $\eta^2 = .531$; Cursor Jump: $t(86) = -7.637$, $p < .001$, $\eta^2 = .404$; Hand View: $t(86) = -16.185$, $p < .001$, $\eta^2 = .753$). Thus, despite receiving no instructions, both Cursor Jump and Hand View groups were able to evoke an explicit strategy like the Instructed group.

Persistent changes in afferent-based estimates of hand localization

We then investigated the effect of external error attribution on afferent and efferent-based shifts in hand location estimates. We used localization trials (Fig. 3e, 7), where hand localization was either based on both afferent and efferent contributions (active localization) or based mainly on afferent contributions (passive localization). All groups appeared to show shifts in hand localization, despite external error attribution (Fig. 7a). Moreover, these shifts seemed larger in active than passive localization for each group, except for the Hand View group (Fig. 7b-7c). To test if training affected hand location estimates, we conducted a 2X2X4 mixed design ANOVA on localization error with session (aligned or rotated) and movement type (active or passive) as within-subject factors and group as a between-subject factor. We found a main effect of session ($F(1,86) = 82.972$, $p < .001$, $\eta^2_G = .199$) and group ($F(3,86) = 10.214$, $p < .001$, $\eta^2_G = .195$), an interaction between session and group ($F(3,86) = 2.895$, $p = .040$, $\eta^2_G = .025$) and between
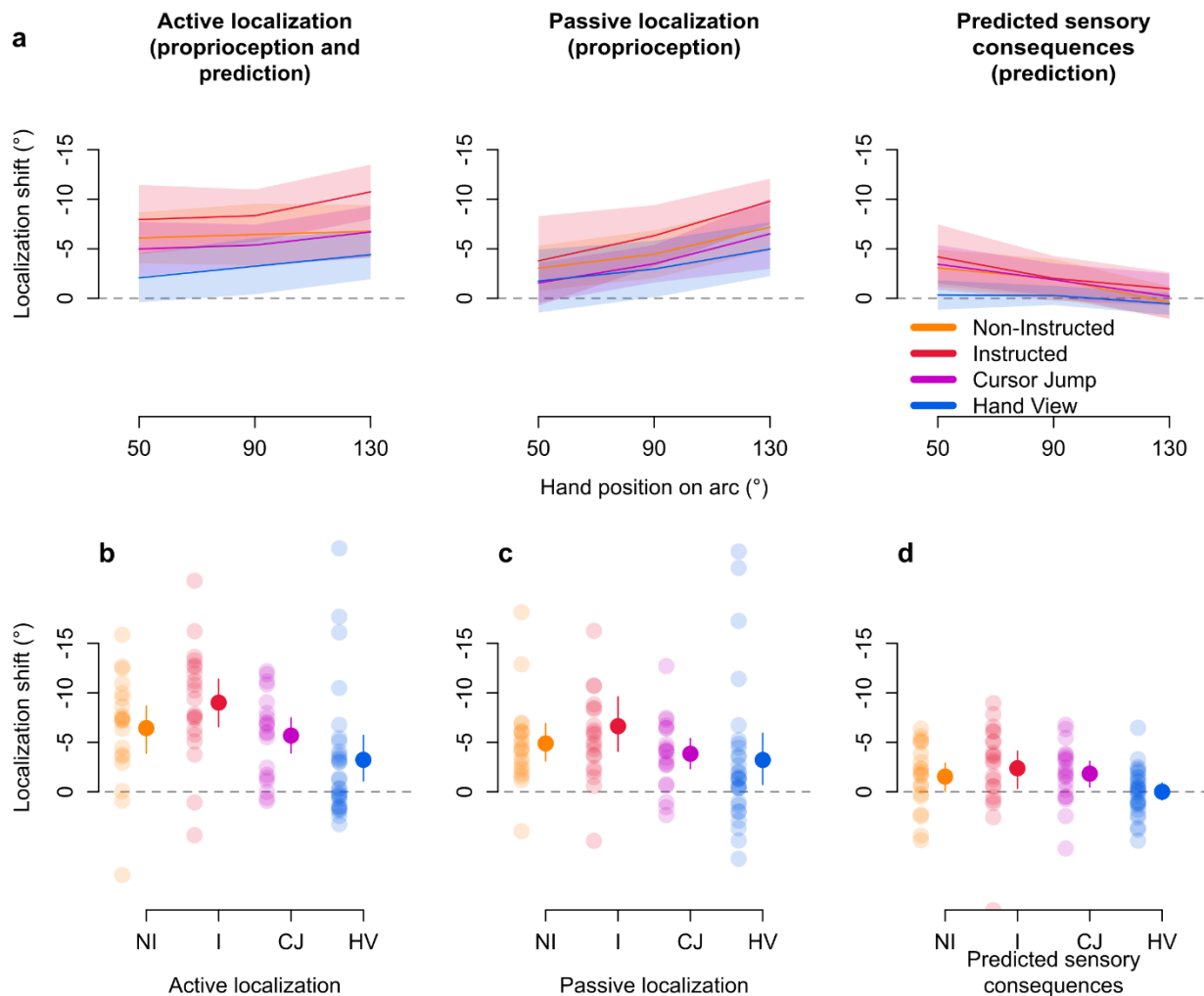
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Fig. 7: Afferent and efferent-based changes in hand location estimates. During localization trials, the arc stimulus was presented and participants either moved, or were moved, towards different points on the arc. **a:** Shifts in localizing the unseen right hand following adaptation training after self-generated movements (**left:** active localization), robot-generated movements (**middle:** passive localization), and the difference between active and passive localization as a measure of updates in efferent-based estimates (**right:** predicted sensory consequences). Grey dashed line at the 0° mark indicates the absence of shifts, while positive and negative values indicate the direction of shifts. Solid lines correspond to group means at each hand position on the arc, which mark the position in polar coordinates of where the arc stimuli were centred on during these trials. These positions closely match the target locations during adaptation training and no-cursor reaches. Shaded regions are corresponding 95% confidence intervals. **b-d:** Individual participant data for shifts in hand localization are shown, separated according to group and movement type in transparent dots. Solid dots and error bars to the side of individual data correspond to group means and bootstrapped 95% confidence intervals.

session and movement type ($F(1,86) = 16.802$, $p < .001$, $\eta^2_G = .004$). This suggests that estimates of hand position did shift despite external error attribution, but the extent of these shifts was

modulated by group and movement type. Thus, we analyzed the effects of group and movement

type further using a 2X4 mixed design ANOVA on localization shifts (i.e. difference in

localization error between rotated and aligned sessions), with movement type as a within-subject

factor and group as a between-subject factor. We found a main effect of movement type ($F(1,86)$

$= 16.802, p < .001, \eta^2_G = .016$) and group ($F(3,86) = 2.895, p = .040, \eta^2_G = .085$), but no

interaction ($F(3,86) = 2.425, p = .071, \eta^2_G = .007$). The main effect of movement type was

expected because active movements contain afferent and efferent contributions to hand

localization, while passive movements only have afferent contributions. For follow-up tests on

the group effect, we compared the localization shifts of each group to the other groups regardless

of movement type, and found that the Hand View group significantly differed from the

Instructed group ($t(86) = 2.901, p = .028, \eta^2 = .089$). Regardless, given the persistent shifts in

hand position estimates, we investigated the afferent and efferent contributions for each group

separately.

Passive localization should rely mainly on updated afferents, or recalibrated

proprioception. We confirmed the persistence of passive localization shifts across all groups with

one-tailed t-tests that compared the mean passive localization shift of each group to zero

(Instructed: $t(20) = -4.614, p < .001, d = 1.007$; Non-Instructed: $t(19) = -4.869, p < .001, d =$

1.089; Cursor Jump: $t(19) = -4.832, p < .001, d = 1.080$; Hand View: $t(28) = -2.372, p = .012, d =$

0.440). These tests show that the attribution of error to external sources surprisingly did not

reduce proprioceptive recalibration. Given that passive localization shifts reflect proprioceptive

recalibration, a difference between active and passive localization shifts is likely due to efferent-

based contributions. Thus, we measured efferent-based contributions or updates in predicted

sensory consequences by removing afferent-based contributions (active minus passive; Fig. 7d).

We confirmed the presence of updates in predictions for all groups with one-tailed t-tests comparing the mean shift for each group to zero. We found that updates in predictions differed from zero for three groups (Instructed: $t(20) = -2.411$, $p = .013$, $d = 0.526$; Non-Instructed: $t(19) = -2.101$, $p = .025$, $d = 0.470$; Cursor Jump: $t(19) = -2.751$, $p = .006$, $d = 0.615$), but was not statistically significant for the Hand View group ($t(28) = -0.037$, $p = .485$, $d = 0.007$). This suggests that active and passive localization shifts were not much different in the Hand View group, due to the greatly reduced updates in prediction for this group. Taken together, these results show that external error attribution affected efferent-based contributions to hand localization, but not afferent-based contributions.

We then investigated whether afferent and efferent-based estimates of hand localization contribute to behaviour. When considering either passive localization shifts or updates in predictions and their respective relationships with angular reach deviations in without strategy no-cursor trials (Fig. 8a-8b), we found that both had a weak, but significant, correlation with implicit aftereffects (passive-aftereffects: $p < .001$, $r^2 = .121$; prediction-aftereffects: $p = .004$, $r^2 = .089$). Moreover, a multiple regression with both variables as predictors and angular reach deviations in without strategy no-cursor trials as the dependent variable, showed that both passive localization shifts ($\beta = -0.430$, $p < .001$, $sr^2 = .204$) and updates in predicted sensory consequences ($\beta = -0.694$, $p < .001$, $sr^2 = .171$) were statistically significant predictors of reach aftereffects. Importantly, pooling data from all individuals across groups is justified, as both predictors were still statistically significant after accounting for a group effect (see Gastrock et al., 2020). Furthermore, given that we calculated afferent and efferent contributions to hand localization as additive (see Methods), the two predictors were necessarily independent from each other (confirmed by a low collinearity: $vif = 1.087$). Finally, we validated our regression

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model by comparing predicted and observed values of reach aftereffects (Fig. 8c). We found that model predictions ($r^2 = .293$) were not perfect, but relatively close to observed values. The model is likely incomplete, which would explain this disparity, but we did not investigate this further. Overall, hand localization predicts implicit reach aftereffects to some extent, and it seems that this may be split into afferent and efferent-based components.
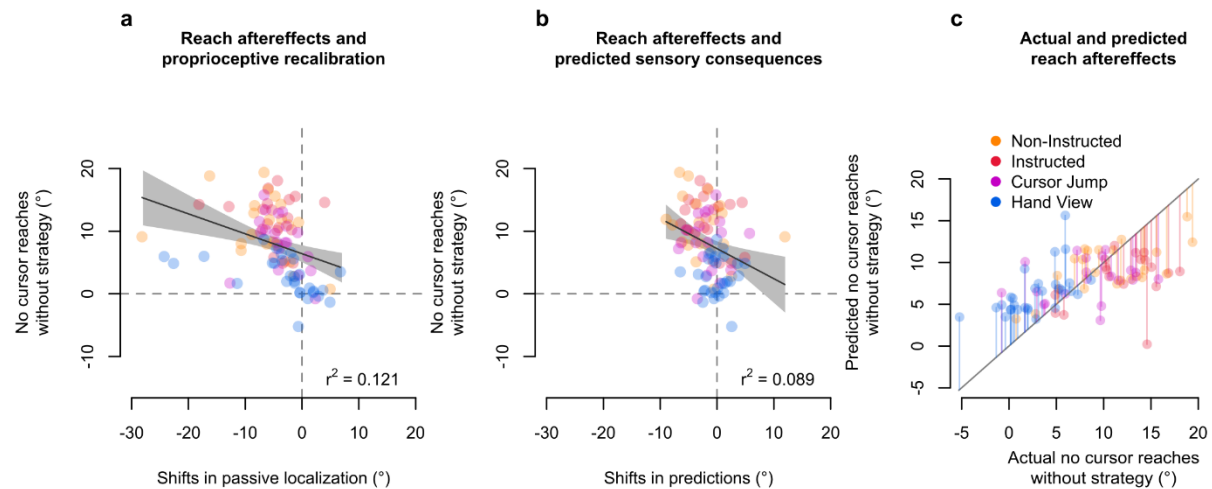

Fig. 8: Contributions of afferent and efferent-based hand localization changes to implicit aftereffects. a-b: Relationship between afferent and efferent-based changes in hand location estimates and reach deviations when no visual feedback of the cursor was presented, while excluding any strategies used during adaptation training. Individual data points from all participants are colour-coded according to their respective groups. Solid line corresponds to a regression line, while the grey shaded region corresponds to 95% confidence intervals. **c:** Predicted values for reach aftereffects based on a multiple regression using both shifts in afferent and efferent-based hand localization, plotted over observed values for reach aftereffects. The diagonal represents perfect prediction. Individual data points are colour-coded according to group, and lines represent residual errors.

Discussion

We test if manipulating the extent of external error attribution affects both changes in motor behaviour and hand location estimates after visuomotor adaptation training. Particularly, the visual feedback of the hand-cursor either jumps to the imposed rotation mid-reach on every training trials, or is present along with a view of the actual hand of the participant. Given the mismatch between cursor and hand positions, errors should be attributed externally and not lead to changes in hand location estimates. In the Hand View group, despite the error source being clearly external, afferent-based (proprioceptive) hand location estimates still shift to the same extent as in other groups where external error attribution should be minimal. With both afferent and efferent-based estimates (active localization), shifts are smaller in the Hand View group compared to other groups. Furthermore, we find evidence that the Instructed, Cursor Jump, and Hand View groups developed an explicit strategy. However, the persistent but reduced implicit reach aftereffects in the Cursor Jump and Hand View groups, suggest that the feedback in these groups leads to less implicit learning, as could be expected with more external error attribution. Finally, we find that both afferent and efferent-based changes in hand localization share a relationship with implicit aftereffects. The persistent implicit motor changes and afferent-based changes in hand position estimates suggest that these are robust against external error attribution, while updating of efferent-based predicted sensory consequences is not.

In visuomotor adaptation, visual feedback of the hand is consistently shifted, which eventually updates estimates of the unseen hand after a movement (Synofzik et al., 2008; Cressman and Henriques, 2009, 2015; Cressman et al., 2010; Cameron et al., 2012; Izawa et al., 2012; Ruttle et al., 2016). These updates rely on at least two components: an efferent-based component, where the expected outcome of a motor command is updated to reflect the

experienced, altered visual outcome of the movement, and an afferent component, where a proprioceptive signal is recalibrated to the experienced visual outcome ('t Hart and Henriques, 2016; Mostafa et al., 2019). People should not update either hand location estimate when the rotated cursor does not represent their true hand location. Yet, our previous results suggest that when explicit adaptation increases, due to instructions or increased rotation size, there is no concomitant decrease in updates of afferent and efferent-based estimates (Modchalingam et al., 2019). In the current study, despite the error source being clearly external in the Hand View group, we surprisingly find shifts in afferent-based hand location estimates across all groups. We also find evidence of efferent-based contributions to hand localization in the other three groups, but not in the Hand View group, which suggests that heightened external error attribution in the Hand View group decreases efferent contributions to hand location estimates. Proprioceptive recalibration, however, seems to be robust against varying degrees of explicit adaptation and external error attribution.

Changes in afferent-based hand location estimates seem to be a robust form of sensory plasticity, given its relatively quick emergence (Ruttle et al., 2016), persistence despite explicit adaptation (Modchalingam et al., 2019), and its preservation despite aging (Cressman et al., 2010; Vachon et al., 2019) and within other forms of perturbations (Cressman and Henriques, 2009; Ostry et al., 2010; Cameron et al., 2012; Leech et al., 2018; Sombric et al., 2019). Furthermore, recalibrated proprioception is intact in people with mild cerebellar ataxia (Henriques et al., 2014), despite the cerebellum's crucial role in adaptation (Martin et al., 1996; Bastian, 2006; 2008; Tseng et al., 2007; Synofzik et al., 2008; Taylor et al., 2010; Izawa et al., 2012; Wong et al., 2019). This implies that proprioceptive recalibration relies on a signal different from efferent-based contributions to hand localization, such as a visuo-proprioceptive

discrepancy ('t Hart and Henriques, 2016; Ruttle et al., 2018; Mostafa et al., 2019). Although there should be no visuo-proprioceptive discrepancy in the Hand View group, as they see and feel their hand, our findings suggest otherwise. Since the task is completed by bringing the cursor to the target, the cursor could be acting as a visual placeholder for the actual hand, while proprioceptive feedback is still veridical. This could create a sensory discrepancy, between seen cursor and felt hand, leading to sensory recalibration. Thus, the Hand View group does not show decreased shifts in afferent-based hand localization, despite external error attribution. Regardless, given the persistence of proprioceptive recalibration but not efferent-based contributions when errors are attributed externally, it is likely that these two contributions to hand localization rely on different error signals.

Aside from sensory recalibration, visuomotor adaptation also leads to implicit motor behaviour changes. Implicit learning is rather stable, but awareness of the perturbation's nature increases explicit contributions during adaptation (Heuer and Hegele, 2008; Benson et al., 2011; Taylor and Ivry, 2011, 2012; Taylor et al., 2014; Bond and Taylor, 2015; McDougle et al., 2015; Werner et al., 2015; Modchalingam et al., 2019). Here, participants make open-loop reaches with (implicit and explicit) or without (implicit) the strategy they learned. This process dissociation procedure (PDP, Werner et al., 2015) is consistent with similar tasks (Hegele and Heuer, 2013), has been used in previous studies (Neville and Cressman, 2018; Modchalingam et al., 2019; Maresch et al., 2020),), and does not seem to evoke additional explicit learning unlike other methods (Leow et al., 2017; de Brouwer et al., 2018; Maresch et al., 2020). While explicit learning does not necessarily correspond to external error attribution, it is likely that external error attribution is accompanied by more explicit adaptation. Despite no elaborate instructions, the Cursor Jump and Hand View groups exhibit explicit learning like the Instructed group.

Furthermore, it seems advantageous to suppress implicit learning with external and likely transient perturbations (Berniker and Kording, 2008, 2011; Wei and Kording, 2009; Wilke et al., 2013; Kong et al., 2017), making adaptation largely explicit or strategy-based (Ong and Hodges, 2010; Ong et al., 2012). Here, although implicit learning persists, we observe a decrease in implicit adaptation in the Cursor Jump group, which is more pronounced in the Hand View group. We take this as evidence that the Hand View group attributes the source of the error more externally than other groups.

A reduction of sensory prediction error-based learning may explain the reduced reach aftereffects and efferent-based hand localization shifts in the Hand View group. Implicit adaptation is based on sensory prediction errors (Mazzoni and Krakauer, 2006; Bastian, 2008; Synofzik et al., 2008; Shadmehr et al., 2010; Izawa et al., 2012; Wong et al., 2019), that both healthy individuals and people with cerebellar damage involuntarily engage in (Martin et al., 1996; Tseng et al., 2007; Bastian, 2008; Taylor et al., 2010; Wong et al., 2019). In the Hand View group, the balance between sensory prediction error-based learning and explicit strategy contributions to behaviour is changed. Consistent with previous studies using a similar condition as the Hand View group (Ong and Hodges, 2010; Ong et al., 2012; Wong et al., 2019), our data suggests that increased external error attribution leads to reduced sensory prediction error-based visuomotor adaptation. Furthermore, efferent-based updates in predicted sensory consequences contribute to hand location estimates. The decreased sensory prediction error-based learning should have minimal effects on state estimates, which in turn could explain the reduced efferent-based contributions to hand localization in the Hand View group. Thus, while afferent-based contributions to hand localization rely on visuo-proprioceptive discrepancy signals, changes in

efferent-based contributions depend on sensory prediction error-based learning. Consequently, it seems that external error attribution only reduces sensory prediction error-based learning.

Reach aftereffects are evidence that people have updated their internal model, and efferent-based predictions, to adapt movements (Krakauer, 2006; 2009; Krakauer et al., 2019). Recalibrated proprioception also informs movements, as preventing updates of internal models while allowing for proprioceptive recalibration, leads to reach aftereffects that mimic this proprioceptive shift (Cressman and Henriques 2010; Cameron et al., 2012; Salomonczyk et al., 2013; Henriques et al., 2014; Mostafa et al., 2019). Here, we show with a multiple regression that both afferent and efferent changes independently predict reach aftereffects in without strategy no-cursor reaches. In other words, changes in hand location estimates separately contribute to behavioural changes. Given that we consider afferent and efferent contributions as additive in hand localization (see Methods), these contributions are necessarily statistically independent from each other. Moreover, our behavioural evidence shows that suppressed efferent-based changes in the Hand View group is tied to reduced implicit reach aftereffects. Based on these results, we speculate that the remaining reach aftereffects for the Hand View group are solely based on afferent changes. Regardless, our data shows that changes in motor behaviour after learning take into account updates to our internal estimates of hand location.

The changes in both afferent and efferent-based hand location estimates that rely on different error signals, and independently contribute to changes in motor behaviour, are likely processed in different regions of the brain. While the relationship between implicit adaptation and sensory prediction error-based learning has been linked to the cerebellum (Mazzoni and Krakauer, 2006; Bastian, 2008; Synofzik et al., 2008; Shadmehr et al., 2010; Izawa et al., 2012; Wong et al., 2019), the visuo-proprioceptive discrepancy leading to recalibrated proprioception

has been linked to parietal areas (Ostry et al., 2010; Block et al., 2013; Ostry and Gribble, 2016; Munoz-Rubke et al., 2017). Particularly, parietal lesions that disrupt the angular gyrus in the posterior parietal cortex (PPC) affect visuo-proprioceptive realignment (Block et al., 2013), which in turn affects corresponding activity in somatosensory and motor areas (Ostry and Gribble, 2016; Munoz-Rubke et al., 2017). In the current study, the greatly reduced efferent-based changes and persistent afferent-based changes in hand location estimates, due to external error attribution in the Hand View group, show that processing for these two signals are dissociated to some degree in the brain. However, although afferent and efferent-based signals seem to be independently processed in brain, both the PPC and cerebellum project signals to premotor and motor cortical areas. Here, we do find that afferent and efferent-based hand location estimates share small but significant relationships with implicit reach aftereffects. Thus, our data suggests that the independent signals used in updating our hand location estimates are likely integrated within premotor and motor areas, and consequently affect our motor behaviours.

In summary, external error attribution affects changes in our internal estimates of hand location and motor behaviour. Particularly, afferent-based (proprioceptive) estimates of hand location are so susceptible to change, that the resulting recalibration is immune to external error attribution. However, external error attribution can be manipulated to change efferent-based, sensory prediction error-based learning. As adaptation becomes less reliant on sensory prediction error-based learning, implicit motor behaviour changes (reach aftereffects) are consequently reduced. We also find behavioural evidence that these afferent and efferent-based estimates contribute independently to motor behaviour changes. Taken together, it seems that proprioceptive plasticity plays an important role when updating our hand location estimates after

experiencing movement errors, as sensory recalibration is impervious to external error attribution, but sensory prediction error-based processes are not.

Methods

Participants

Ninety right-handed university students (64 female, $M_{Age} = 20.8$, $SD_{Age} = 3.88$) were assigned to one of four groups: Non-Instructed ($n = 20$, 14 females), Instructed ($n = 21$, 13 females), Cursor Jump ($n = 20$, 14 females), and Hand View ($n = 29$, 23 females). We conducted a statistical power analysis for sample size estimation. In this study, we investigated both the persistence of reach aftereffects as well as shifts in afferent and efferent-based estimates of hand location. We used effect sizes based on Cohen's (1988) criteria for a large effect (Cohen's f = .40, Cohen's d = .80), depending on the effect of interest (alpha = .05, power = .80). The projected sample size for the persistence of reach aftereffects was $n = 18$, while the sample size for the persistence of shifts in hand localization was $n = 11$ (R pwr package, Champely et al., 2020), which makes the larger sample size ideal. Furthermore, data for the Instructed and Non-instructed groups have been used in our earlier work (Modchalingam et al., 2019). In those two data sets, the sample (~20 participants per group) was large enough to detect differences between active and passive localization shifts. Thus, we matched the sample size of these reference groups with the Cursor Jump group. To our knowledge, no previous study has compared active and passive hand localization shifts after training with a full view of the hand, which could be used to decide on the sample size. Therefore, to ensure sufficient power to detect subtler effects, we increased the sample size of the Hand View group with roughly 10 participants. All participants gave written informed consent prior to participating. All procedures were in

accordance with institutional and international guidelines. All procedures were approved by York University's Human Participants Review Committee.

Experimental Set-up

Apparatus

Participants held the handle of a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA) with their right hand, while placing their thumb on top of the handle. A downward facing monitor (Samsung 510 N, 60 Hz) 28 cm above the manipulandum projected visual stimuli on a reflective screen (14 cm above the manipulandum), making the stimuli appear on the same horizontal plane as the participant's hand (Fig. 3a-3c). Participants responded using their visible left hand in some tasks on a touchscreen 2 cm above the manipulandum (Fig. 3d). The right hand was occluded from the participant's view and a black cloth was draped over their right arm and shoulder. For the Hand View group, the right hand was illuminated in some tasks, making it visible to the participant.

Stimuli

Participants made smooth and straight 12 cm out-and-back reaching movements from the "home position" to one of three targets (or arcs). Targets and arcs were presented once in a shuffled order before being presented again, such that reach directions were evenly distributed across trial types (Fig. 9).

Cursor Training Trials. Participants kept a green cursor (circle, 1 cm diameter), representing their right thumb, at the home position for 300 ms. A yellow target (circle, 1 cm diameter) then appeared at one of three possible locations: 45°, 90°, 135° in polar coordinates. Once the target was acquired, they held the cursor for 300 ms within 0.5 cm of the target's centre. Afterwards, both stimuli disappeared, and participants returned their hand to the home position via a robot-constrained path (perpendicular resistance force: 2 N/(mm/s); viscous damping: 5 N/(mm/s)).
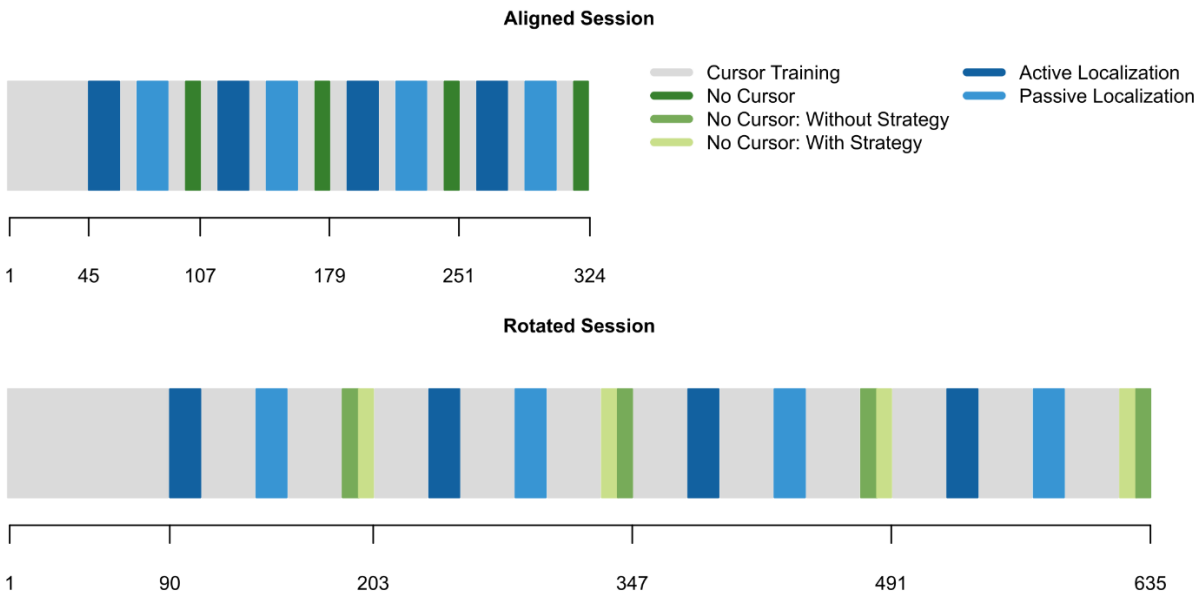

Fig. 9: Experiment schedule. Top: First session, and considered as baseline, where the cursor was aligned with the position of the right hand. Participants performed 45 cursor training trials followed by blocks of active localization (18 trials/block), passive localization (18 trials/block), and no-cursor trials (9 trials/block). Top-up cursor training trials (9 trials/block) were interleaved in between localization and no-cursor blocks. **Bottom:** Second session where the cursor was rotated 30° CW, relative to the position of the right hand. Participants performed 90 cursor training trials followed by blocks of active localization (18 trials/block), passive localization (18 trials/block), and two variations of no-cursor trials (with or without strategy; 9 trials/block). Top-up cursor training trials (30 trials/block) were interleaved in between localization and no cursor blocks. For both aligned and rotated sessions, passive localization always proceeded after active localization, as endpoint locations of the robot-generated movements in passive localization are based on locations that participants voluntarily moved towards during active localization. For no-cursor trials in the rotated session, the two variations are counterbalanced both within and between participants. That is, with and without strategy trials alternate within one participant, and the variation that an individual starts with is also alternated between participants.

Participants in the Hand View group saw their right hand along with the cursor throughout these trials. For these trials, we calculated the angular difference between the hand position at the peak of movement velocity and the target, relative to the home position. Thus, once the rotation is introduced, full adaptation should then result in angular reach deviations of 30°.

No-Cursor Trials. These proceeded similarly to cursor training trials, but without visual feedback from the cursor or hand (Fig. 3f). Participants kept stationary for 500 ms once they believe they had acquired the target, making the target disappear. They returned to the home position via the constrained path.

During the rotated session, participants completed two variations of no-cursor trials in succession (with and without strategy; Fig. 9). We instructed participants to either include or exclude any strategy they developed to counter for the visuomotor rotation. The order of these blocks was counter-balanced within one participant and between participants (Fig. 9). For all no-cursor trials, we calculated the angular difference between the endpoint of the participant's hand movement and the target, relative to the home position. Considering reach endpoints makes this data comparable to those from localization trials.

Localization Trials. Participants saw a white arc (0.5 cm thick) 12 cm away from the home position (Fig. 3e), which spanned 60°, and was centred on either the 50°, 90°, or 130° mark in polar coordinates. The arc encouraged participants to generate movements throughout the trained area, making the responses across all trial types more comparable. In self-generated active localization trials, participants moved their unseen right hand from the home position to any point on the arc, and were instructed to vary their chosen crossing points across trials. In passive localization trials, the robot guided the participant's right hand towards the same points on the arc that they intersected during active localization trials in the preceding task. Regardless of

localization type, a cushion force prevented hand movements from moving beyond the arc

position. Participants then voluntarily returned their right hand to the home position via the

constrained path, and used their visible left hand to indicate on the touchscreen the point at

which they believed their unseen right hand intersected the arc.

Procedure

The aligned session served as baseline data, and started with aligned cursor training trials,

followed by blocks of active localization, passive localization, and no-cursor trials respectively

(Fig. 9). Localization and no-cursor blocks were repeated in the same order for three more times

during this session. To prevent decay in learning, we interleaved shorter blocks of "top-up"

cursor training trials between every localization and no-cursor block. The aligned session ended

upon completion of the fourth no-cursor block.

Participants were given a mandatory five-minute break. During this break, the Instructed

group was informed about the nature of the perturbation and was given a strategy to counter it

(see Benson et al., 2011; Modchalingam et al., 2019 for details). The other groups were simply

advised to compensate for the cursor moving differently.

In the following session, the cursor was rotated 30° clockwise (CW) relative to the hand

position for all cursor training trials. Hence, correcting for this perturbation requires straight

reaches in the 30° counterclockwise (CCW) direction. For the Cursor Jump group, the cursor

shifted to this rotated trajectory after participants moved for one-third of the home-target

distance (4 cm; Fig. 3b). For the Hand View group, illuminating the right hand allowed

participants to see the misalignment between cursor and hand, making this the clearest

demonstration that the error was caused externally (Fig. 3c). The rotated session proceeded

similarly to the aligned session. However, to saturate learning of the visuomotor rotation, we

increased the number of cursor training trials in each block (Fig. 9). Moreover, each block of no-cursor trials was done twice, each in one variation (with strategy or without strategy).

Data Analysis

We compared all four groups within the different trial types. All results are reported with an alpha level of 0.05. Greenhouse-Geisser corrections were applied when necessary. Planned follow-up tests used the Sidak method when it was necessary to control for multiplicity. Degrees of freedom for follow-up tests are larger than expected in some cases, as it uses a model fit on all the data (R emmeans package, Lenth, 2019). All data preprocessing and analyses were conducted in R version 3.6.0 (R Core Team, 2019).

Rate of Learning During Adaptation Training

We analyzed cursor training trials from both the aligned and rotated sessions. Trials were manually inspected for outlier reaches (0.94% of trials removed). We corrected for individual baseline biases by calculating the average reach deviation for each target separately within each participant, during the last 30 out of the first 45 aligned cursor training trials, and subtracting this from rotated cursor training trials. We compared angular reach deviation measures across all groups, within each one of three trial sets (rotated cursor training trials 1-3, 4-6, 76-90), to confirm learning and investigate any differences.

Reach Aftereffects and Strategy Use

We tested for group differences in reaches without cursor-feedback. Upon manual inspection, outlier reaches were removed (1.46% of trials). We confirmed the presence of reach aftereffects by comparing angular reach deviations from aligned no-cursor trials to without strategy no-cursor trials. For the PDP (Werner et al., 2015; Modchalingam et al., 2019), we implemented baseline-correction (aligned session no-cursor reaches subtracted from no-cursor

with and without strategy trials, respectively), before comparing angular reach deviations in with and without strategy trials.

Proprioceptive Recalibration and Updating Predicted Sensory Consequences

We investigated active and passive localization trials, before and after adaptation training. We calculated the angular difference between the endpoint of the participant's right hand movement and their left hand responses on the touchscreen, relative to the home position. Localization response biases were accounted for using a circle fitting procedure (see Mostafa et al., 2019 for details). Trials with hand movement endpoints beyond ±20° from the arc centre across all groups, and angular errors beyond ±3 standard deviations from the mean angular error per participant were removed (1.06% of angular errors). As participants actively directed their own movements to the arc, the reach end points were randomly dispersed. Thus, to compare participants, we calculated weighted averages from known data points to estimate values at specific locations. This involved the use of a kernel smoothing method (gaussian kernel with bandwidth = 15°) to interpolate changes in hand localization at specific points (50°, 90°, 130°) for every participant. Mean values at each of these points estimate active and passive hand localization errors for both the aligned and rotated sessions.

We compared hand localization errors in the rotated session to those in the aligned session. The difference of localization errors between the two sessions represents shifts in hand localization, and were compared across groups and movement type (active and passive). The difference between active and passive localization shifts were used as a measure of efferent-based updates in predicted sensory consequences, while passive localization shifts measured the afferent-based recalibration of proprioception. If afferent and efferent contributions to hand localization are optimally integrated (e.g. Bayesian integration), then variance in active

localization should be lower than passive localization ('t Hart and Henriques, 2016). However, this does not seem to be the case. Even when we compile results of these two localization tasks from several different studies to amass a sample of over 200 participants, we fail to see a reduction in variance for active localization when compared to passive localization in the baseline conditions ('t Hart and Henriques, 2016; Ayala et al., 2020). Thus, we take a parsimonious approach, and treat afferent and efferent contributions as additive in hand localization. We compared afferent and efferent contributions to hand localization for each group against zero, and investigated how both hand location estimates may contribute to implicit motor changes.

Data Availability

Data, analyses scripts, and preprint are available on Open Science Framework (https://doi.org/10.17605/osf.io/xdgh6, Gastrock et al., 2020).

Conclusion

After training with a visuomotor adaptation task, the attribution of errors to an external source affects changes in both our internal estimates of hand location, as well as motor behaviour. Given that updates to hand location estimates are based on both afferent (proprioceptive input from the effector) and efferent (computed from an efference copy of an outgoing motor command) contributions, we show that afferent-based changes persist, despite external error attribution, but efferent-based changes are reduced. The persistent changes in afferent-based estimates of hand location provides further evidence of how proprioceptive recalibration is a robust form of sensory plasticity. With external error attribution, it is more intuitive to deal with perturbations transiently, rather than relying on a more stable implicit form of learning. Thus, adaptation becomes more strategy-based, such that there is less reliance on sensory prediction error-based learning. Behaviourally, this is observed as a reduction in both efferent-based changes and implicit aftereffects. Given that implicit aftereffects are reduced but still present, along with the persistence of only afferent-based estimates of hand location, it seems that afferent and efferent-based components to hand localization independently contribute to changes in motor behaviour. These findings show that although both are implicit processes, sensory recalibration is impervious to external error attribution, but sensory prediction error-based processes are not.

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