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

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Abstract

1   Motor learning and adaptation are guided by the attribution of errors to internal or
2   external sources. When errors are clearly external, we should not update our
3   internal models for movement or state estimation, i.e. there should be no implicit
4   learning. However, measures of implicit learning are the same whether or not we
5   induce explicit adaptation with instructions about the nature of the perturbation.
6   Here we make errors even more clearly external by either demonstrating the
7   rotation on every trial, or showing the hand itself throughout training. Implicit
8   reach aftereffects persist, but are reduced in both groups. Only for the group
9   viewing the hand, state estimates suggest that predicted sensory consequences
10 are not updated, but only rely on recalibrated proprioception. Our results show
11 that state estimation of the hand incorporates source attribution during motor
12 learning, but recalibrated proprioception is an implicit process unaffected by
13 external error attribution.

Introduction

14 People have an almost limitless ability to learn a wide range of skills and adapt these in
15 dynamic conditions. When we experience movement errors within these changing
16 conditions, we correct for errors in subsequent movements. Large errors not only evoke
17 more explicit learning (Werner et al., 2015; Neville and Cressman, 2018; Modchalingam
18 et al., 2019), but are also believed to lead people to attribute errors as more likely to be
19 caused externally, i.e. not by oneself (Berniker and Kording, 2008; 2011; Wei and
20 Kording, 2009; Wilke et al., 2013; Kong et al., 2017). Previous research found that
21 adaptation of reach movements to visual or mechanical perturbations leads to changes
22 in proprioceptive estimates of hand location (Cressman and Henriques, 2009, 2015;
23 Ostry and Gribble, 2016). While intuitively it would not make sense for people to update
24 hand location estimates when errors are unambiguously caused by external factors, this
25 is unknown, and we test this here.

26   If a visual or mechanical perturbation is small, or introduced gradually, the
27 adaptation or resulting change in reaching movements is traditionally considered as
28 largely implicit (Krakauer et al., 2000; Krakauer, 2009). Implicit adaptation is manifested
29 by reach aftereffects, persistent deviations in hand movements even when the
30 perturbation is removed, suggesting that an internal representational remapping has
31 occurred in the brain (Krakauer, 2006; 2009; Krakauer et al., 2019). Reach aftereffects
32 also occur when participants are aware of the nature of the perturbation. For this case,
33 however, a part of the resulting adaptive change can be attributed to explicit processes
34 (Mazzoni and Krakauer, 2006; Taylor et al., 2010; Benson et al., 2011; Werner et al.,
35 2015; Modchalingam et al., 2019). Thus, it seems that both explicit and implicit
36 processes contribute to adaptation (Taylor and Ivry, 2011, 2012; Taylor et al., 2014;
37 Bond & Taylor, 2015). In the current study, we quantify explicit and implicit contributions
38 to learning with responses to different types of visual manipulations. These
39 manipulations differentially demonstrate to the participants the nature and source of
40 error they experience, thus varying the extent that they attribute the error to the cursor.

41   Motor adaptation leads not only to changes in motor performance but in
42 proprioceptive-based estimates of hand location as well. This proprioceptive
43 recalibration emerges quickly in response to altered visual feedback (Ruttle et al., 2016)
44 and reflects about 20% of the visual misalignment of the hand (Cressman and
45 Henriques, 2009; 2015). The recalibration of proprioception is preserved as people age
46 (Cressman et al., 2010) and in different forms of perturbations (rotations and
47 translations: Cressman and Henriques, 2009, force fields: Ostry et al., 2010, gains:
48 Cameron et al., 2012, locomotion: Leech et al., 2018; Sombric et al., 2019). Thus,
49 proprioceptive recalibration is ubiquitous, and seems to improve motor performance.

50   Apart from afferent proprioceptive information, hand location estimates are also
51 based on predicted sensory consequences of the movement calculated by internal
52 forward models that use a copy of the outgoing motor command, known as an efference
53 copy (Blakemore et al., 1998; Wolpert & Kawato, 1998). These efferent-based updates
54 to the forward model are considered a pre-requisite for implicit adaptation (Bastian,
55 2008; Haith & Krakauer, 2013), and seem to contribute to reach aftereffects separately
56 from recalibrated proprioception ('t Hart & Henriques, 2016; Ruttle et al., 2018; Mostafa
57 et al., 2019). Non-visual afferents and efferents should both be present when testing
58 hand location after self-generated 'active' movements, and robot-generated 'passive'
59 movements should only allow afferent based proprioceptive hand localization. While
60 using active and passive movements in a hand localization task allows assessing the
61 relative contributions of afferent and efferent signals to state estimates (Cameron et al.,
62 2012; 't Hart and Henriques, 2016; Modchalingam et al., 2019), both signals should be
63 implicit.

64   Since both contributions to hand location estimates should be implicit, they should
65 be reduced or not occur when errors are attributed externally, such that implicit learning
66 is engaged less or not at all. However, Modchalingam and colleagues (2019) found that
67 modulating explicit knowledge, by providing instructions or increasing the perturbation

size, does not affect persistent shifts in both proprioceptive recalibration and updating of predicted sensory consequences. In the current study, we instead investigate the effect of the external attribution of errors on both afferent and efferent-based changes. To do this, we vary the extent that people attribute the error they experience to the cursor, while holding a robot manipulandum and training with a 30° rotated hand-cursor (Fig. 1A-1D). 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. 1A), 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. 1B) or a view of the actual hand of the participant is present along with the rotated cursor (Hand View group; Fig. 1C). These manipulations should make clear to participants that the cursor errors are caused externally. We then use a localization task (Fig. 1E) and no-cursor reaches (Fig. 1F) to investigate how our manipulations affect changes in hand location estimates and motor behavior, respectively. We hypothesize that with increased external error attribution, both changes in motor behavior and shifts in afferent and efferent-based estimates of hand localization will decrease.
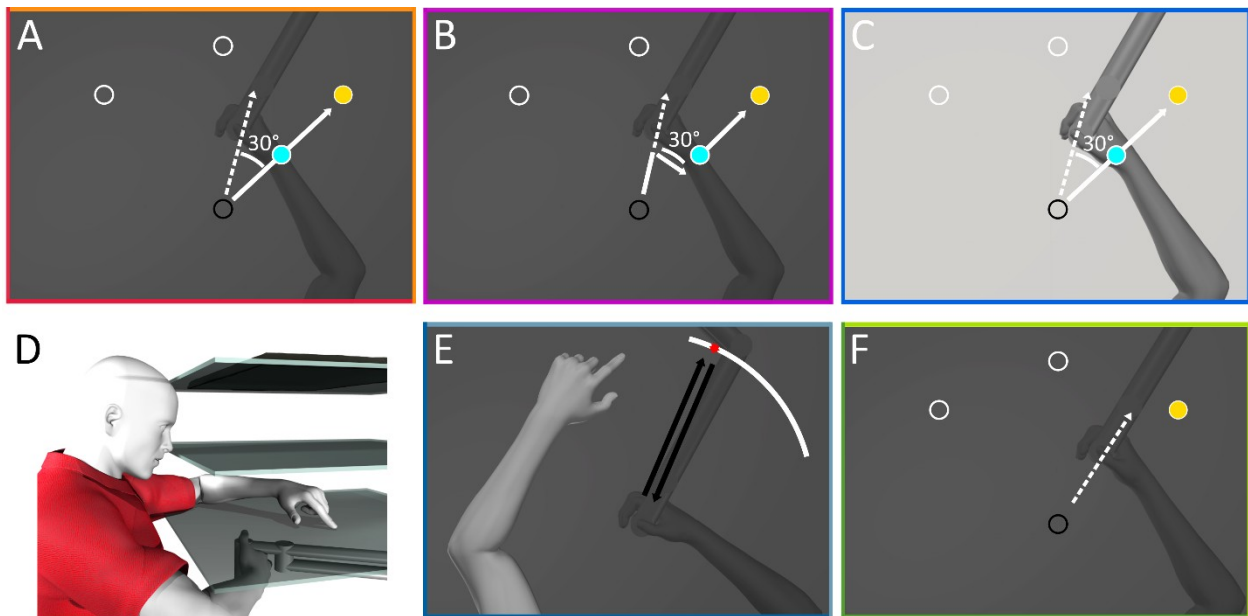

Fig. 1: Experimental Apparatus and Stimuli.A-C: Top-down view displaying the different manipulations for the reach-training tasks, where the cursor (light blue) is rotated 30° CW. Reaches are made to one of three possible target locations (yellow circle). **A:** In both the Instructed and Non-instructed group, participants do not see their hand, and the cursor has a constant rotation throughout each trial. **B:** Participants in the Cursor Jump group see the cursor "jump" to the 30° CW rotation mid-reach on every trial. **C:** In the Hand View group, participants see both their actual, illuminated hand and the cursor. **D:** Participants hold a robot manipulandum located below a touch screen (bottom surface), while viewing stimuli through a reflective screen (middle surface) which projects stimuli generated from a downward facing computer screen (top surface). **E:** Active and Passive Localization trials: Participants use their visible left hand to indicate on the touch screen where they have crossed the arc with their unseen right hand, after voluntarily generating the right hand movement (active) or after a robot-generated movement (passive). **F:** No-cursor trials: Reaches are 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 behavior and hand localization, we first confirm that all groups appropriately counter the perturbation by the end of 90 training trials (Fig. 2A) and observe that reach trajectories are not qualitatively different (Fig. 3). We test 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
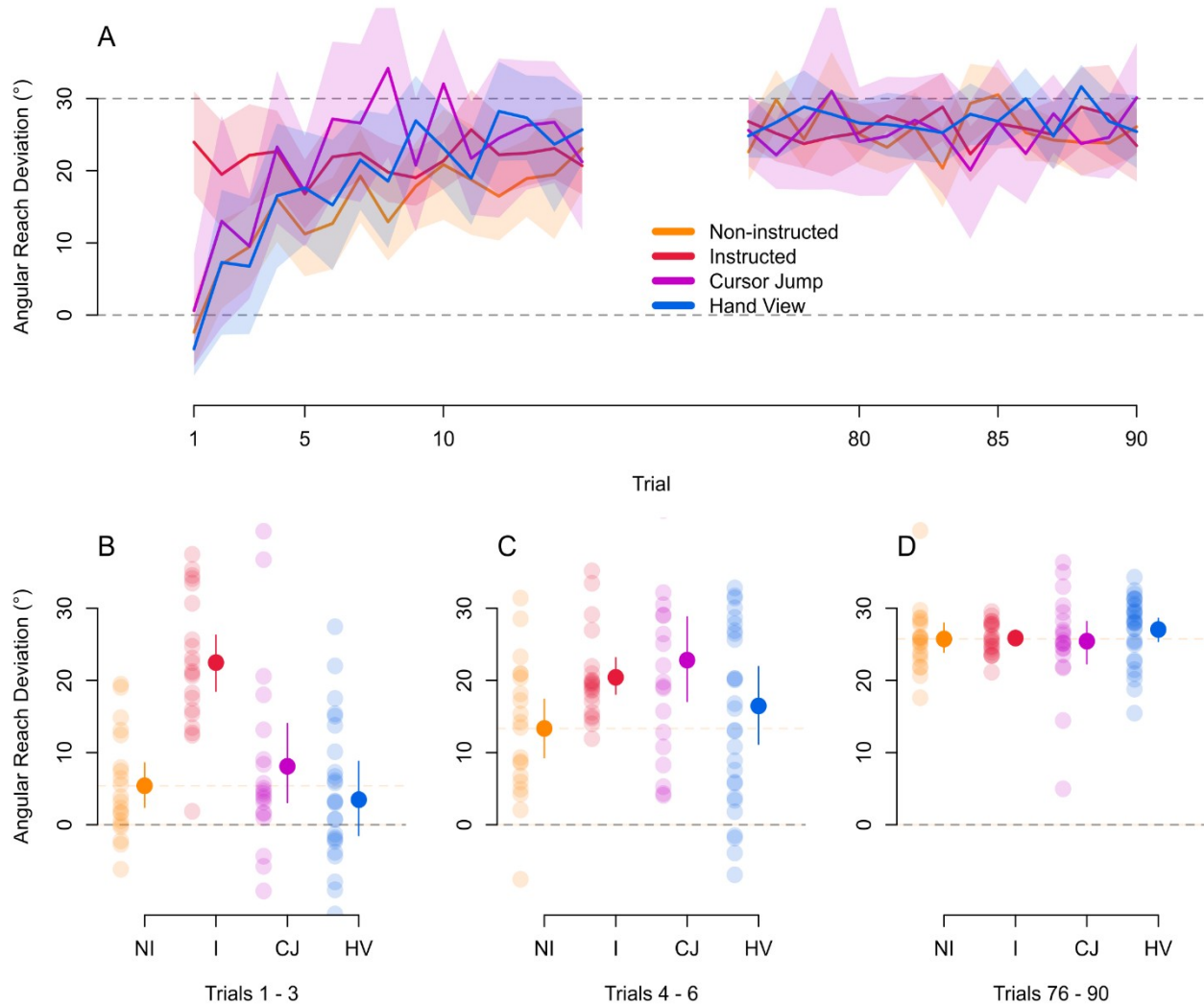

Fig 2: Rate of Learning During Adaptation Training. A: Only the first and last 15 trials of adaptation training are shown. Grey dashed line at the 30° mark indicates the direction that the hand must deviate in order to fully and successfully counter for the perturbation. Grey dashed line at the 0° mark indicates where aligned reaches are directed. The Instructed group shows an initial advantage in successfully countering for the perturbation as early as the first trial. There are no 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 to three blocks of trial sets during adaptation training (See Data Analysis). Orange dashed line indicates mean for the Non-instructed, control group. Dots and error bars correspond to the group mean and bootstrapped 95% confidence intervals.

between-subject factor (Non-instructed, Instructed, Cursor Jump, Hand View). We find 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, η^2_G=.307), and a group X block interaction ($F_{(6,172)}$=7.856, p<.001, η^2_G=.118). This suggests that, as expected, group differences in learning rates are modulated by the block of trials. Follow-up tests comparing each group to the control Non-instructed group, show the expected initial advantage of instructions in reducing reach direction error within block one (Fig. 2A and 2B), as only the Instructed group differs from the Non-instructed group ($t_{(148)}$=4.632, p<.001, eta squared (η^2)=.127). In the second block (Fig. 2C), no groups differ from the Non-Instructed group
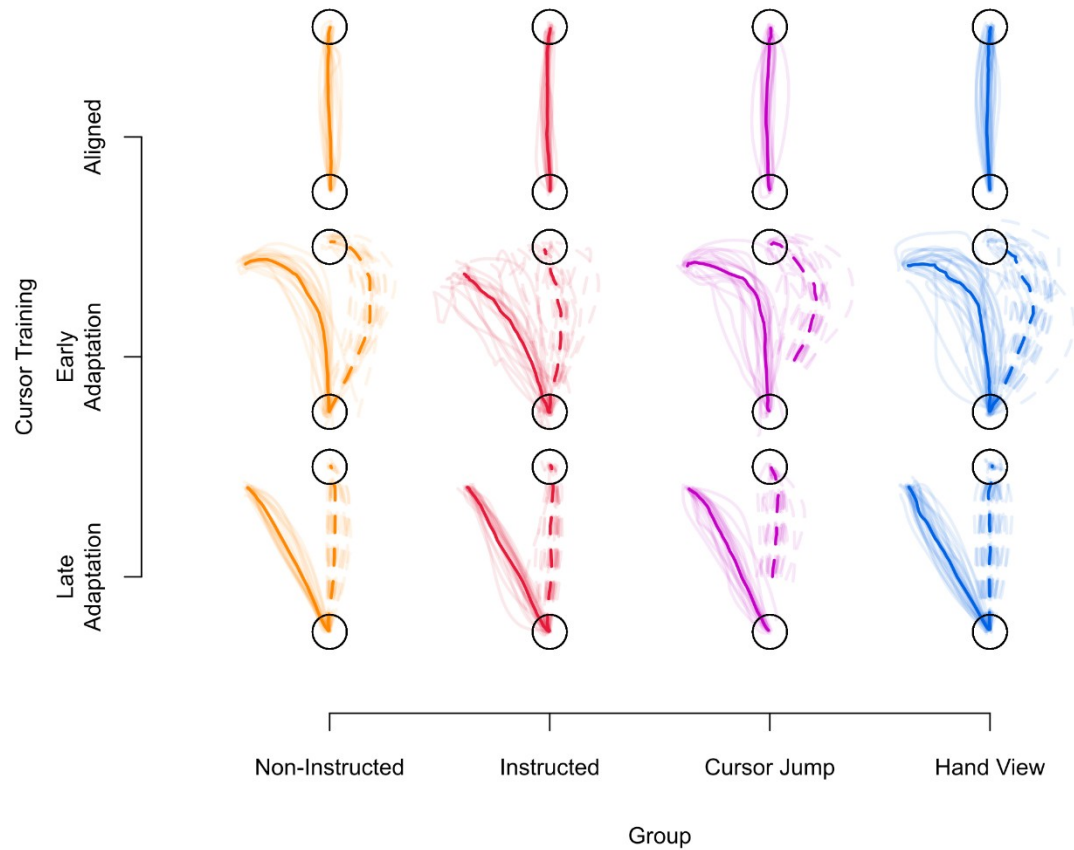

Fig 3: Individual and Average Reach Trajectories. The trajectory of reaches across all participants within their respective groups are shown with light solid lines. Each participant's trajectory combines reaches during the last three trials of the first block of cursor training in the aligned session (**Top**), first three trials of adaptation training (**Middle**), and last three trials of adaptation training (**Bottom**). Light dashed lines indicate the trajectory of the hand-cursor. Group means are indicated with the dark solid line, and dark dashed lines indicate the mean hand-cursor trajectory. All groups seem to perform similar patterns of reaches, across the different time points in the experiment, regardless of condition. Moreover, despite curved reaches during early adaptation training, reach trajectories are straight towards the end of adaptation training.

(Instructed: $t_{(148)}$=1.922, p>.05, η^2=.024; Cursor Jump: $t_{(148)}$=2.538, p>.05, η^2=.042; Hand View: $t_{(148)}$=0.910, p>.05, η^2=.006). For the last block (Fig. 2A and 2D), an ANOVA on the effect of group on angular reach deviations shows that the groups do not differ from each other ($F_{(3,86)}$=.561, p>.05, η^2_G=.019), suggesting that our manipulations do not affect the asymptotic level of adaptation. Thus, any effects of training on changes in motor behavior and hand localization can't be explained by levels of adaptation in the different groups.

Implicit aftereffects persist despite external error attribution

To investigate the effects of external error attribution on changes in motor behavior, we use no-cursor trials both before and after adaptation (Fig. 1F). After adaptation, however, we adopt a process dissociation procedure (PDP; from Werner et al., 2015; see also Neville & Cressman, 2018; Modchalingam et al., 2019), where we ask people to make open-loop reaches to targets, while either including any strategy they learned to counter for the perturbation or excluding it. Including a strategy includes explicit and implicit contributions to learning, while excluding a strategy reflects only implicit contributions.

We first compare aligned no-cursor trials and without strategy no-cursor reaches after adaptation, to test for implicit reach aftereffects (Fig. 4). We conduct a 2X4 mixed design ANOVA with session (aligned or rotated) as a within-subject factor and group as a between-subject factor. We confirm the presence of reach aftereffects with a main effect of session ($F_{(1,86)}$=373.023, p<.001, η^2_G=.530). Moreover, we find a main effect of group ($F_{(3,86)}$=16.576, p<.001, η^2_G=.230) and an interaction between session and group ($F_{(3,86)}$=22.605, p<.001, η^2_G=.170), suggesting that the effect of session is modulated by group. Follow-up tests show that aligned and without strategy reach deviations differ within each group (Instructed: $t_{(86)}$=-11.830, p<.001, η^2=.619; Non-Instructed: $t_{(86)}$=-12.912, p<.001, η^2=.660; Cursor Jump: $t_{(86)}$=-9.050, p<.001, η^2=.488; Hand View: $t_{(86)}$=-4.037, p<.001, η^2=.159). This means that implicit reach aftereffects are present in each group. To address how the effect of session is modulated by group, follow-up tests compare reach aftereffects for each group to those in the Non-instructed group. We find that the Instructed group doesn't differ from the Non-instructed group ($t_{(86)}$=-.722, p>.05, η^2=.006), but the Cursor Jump ($t_{(86)}$=-3.419, p<.004, η^2=.120) and Hand View ($t_{(86)}$=-7.538, p<.001, η^2=.398) groups do, suggesting that external error attribution in the Cursor Jump and Hand View groups lead to reduced implicit reach aftereffects, compared to the Instructed and Non-instructed groups. Furthermore, the reduction in aftereffects is more pronounced for the Hand View group compared to the Cursor Jump group ($t_{(86)}$=3.818, p<.001, η^2=.145). In short, reach aftereffects persist across groups, but are greatly reduced for the Hand View group.
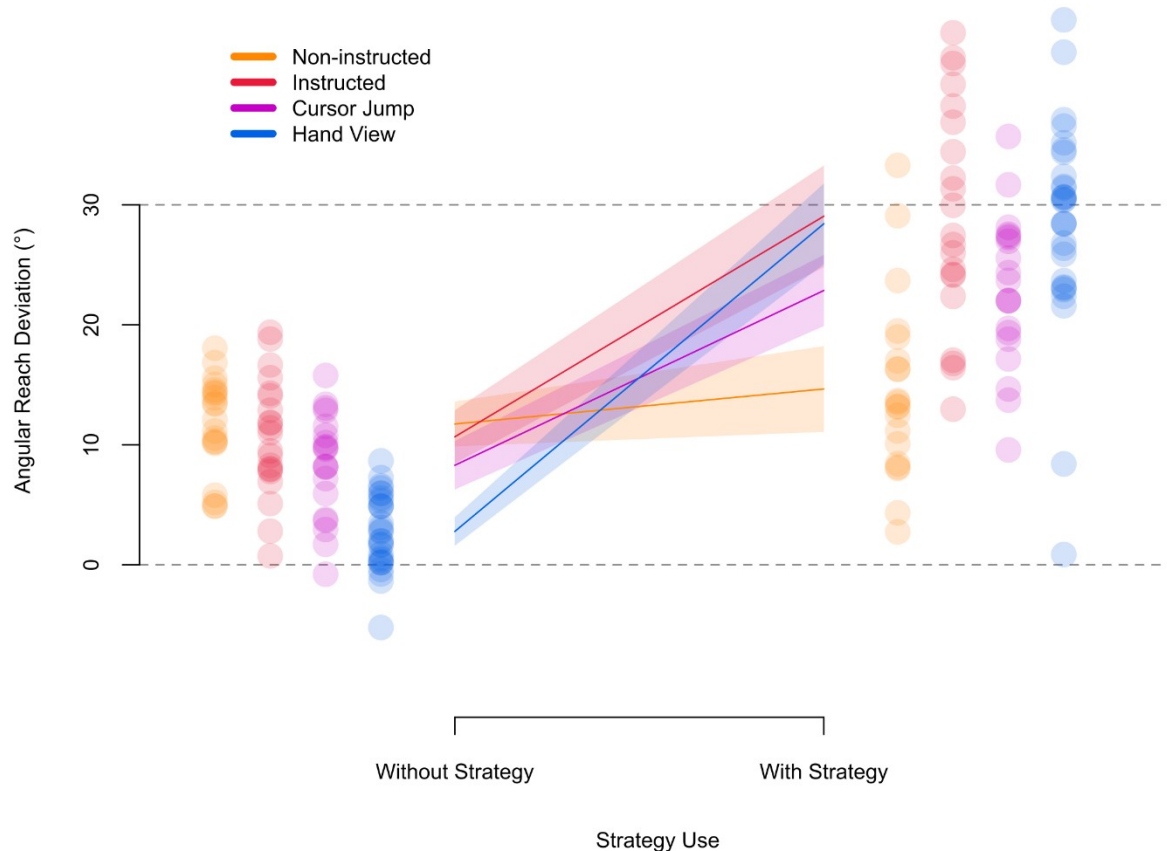
Fig 4: No Cursor Reaches and Strategy Use. Angular reach deviations of the hand per group, while either excluding (without strategy) or including (with strategy) any strategies developed during adaptation training. Grey dashed line at the 30° mark indicates angular reach deviations equivalent to full 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, are reduced for the Cursor Jump group and are 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.

135   After confirming the presence of reach aftereffects, we use the PDP to assess
136 explicit contributions to learning, by comparing with and without strategy no-cursor
137 reaches (Fig. 4). We conduct a 2X4 mixed design ANOVA with strategy use as a within-
138 subject factor (without strategy or with strategy) and group as a between-subject factor.
139 We find main effects of strategy use ($F_{(1,86)}$=285.493, p<.001, η^2_G=.592) and group
140 ($F_{(3,86)}$=6.779, p<.001, η^2_G=.118), and a strategy use and group interaction
141 ($F_{(3,86)}$=28.678, p<.001, η^2_G=.304). This suggests that angular reach deviations for at
142 least one group differ from the other groups. Follow-up tests compare with and without

strategy angular reach deviations for each group separately. We find no difference between angular reach deviations in with and without strategy no-cursor trials in the Non-instructed group ($t_{(86)}$=-1.529, p>.05, η^2=.026), but do see a difference in the other groups (Instructed: $t_{(86)}$=-9.877, p<.001, η^2=.531; Cursor Jump: $t_{(86)}$=-7.637, p<.001, η^2=.404; Hand View: $t_{(86)}$=-16.185, p<.001, η^2=.753). Thus, despite receiving no instructions, both Cursor Jump and Hand View groups can evoke an explicit strategy like the Instructed group.

Changes in afferent-based estimates of hand localization persist

We then investigate the effects of external error attribution on afferent and efferent-based shifts in hand location estimates. We use localization trials (Fig. 1E), where hand localization is either based on both afferent and efferent contributions (active localization) or based mainly on afferent contributions (passive localization). All groups appear to show shifts in hand localization, despite external error attribution (Fig. 5A). Moreover, these shifts seem larger in active than passive localization for each group, except for the Hand View group (Fig. 5B-5C). We conduct 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 find a main effect of session ($F_{(1,86)}$=82.972, p<.001, η^2_G=.199) and group ($F_{(3,86)}$=10.214, p<.001, η^2_G=.195), an interaction between session and group ($F_{(3,86)}$=2.895, p=.040, η^2_G=.025) and between session and movement type ($F_{(1,86)}$=16.802, p<.001, η^2_G=.004). This suggests that estimates of hand position do shift despite external error attribution, but the extent of these shifts are modulated by group and movement type. Thus, we analyze 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 find a main effect of movement type ($F_{(1,86)}$=16.802, p<.001, η^2_G=.016) and group ($F_{(3,86)}$=2.895, p=.040, η^2_G=.085), but no interaction ($F_{(3,86)}$=2.425, p>.05, η^2_G=.007). We therefore investigate group differences for active and passive localization shifts separately.

For shifts in hand location estimates during active localization, that measures both afferent and efferent-based contributions (Fig. 5B), we conduct an ANOVA to test for an effect of group. We find an effect of group ($F_{(3,86)}$=4.361, p=.007, η^2_G=.132), suggesting that mean active localization shifts differ for at least one group. Follow-up tests, comparing mean active localization shifts for each group to the Non-instructed group, show that only the Hand View group differs ($t_{(86)}$=3.577, p=.002, η^2=.130). For shifts in hand location estimates during passive localization, that measures mainly afferent-based contributions (Fig. 5C), we conduct an ANOVA to test for an effect of group, and find no significant differences across groups ($F_{(3,86)}$=1.482, p>.05, η^2_G=.049). Moreover, we confirm the persistence of passive localization shifts (Fig. 5C) across all groups with follow-up one-tailed t-tests that compare the mean passive localization shifts of each group to zero (Instructed: $t_{(20)}$=-4.614, p<.001, d=1.007; Non-Instructed:
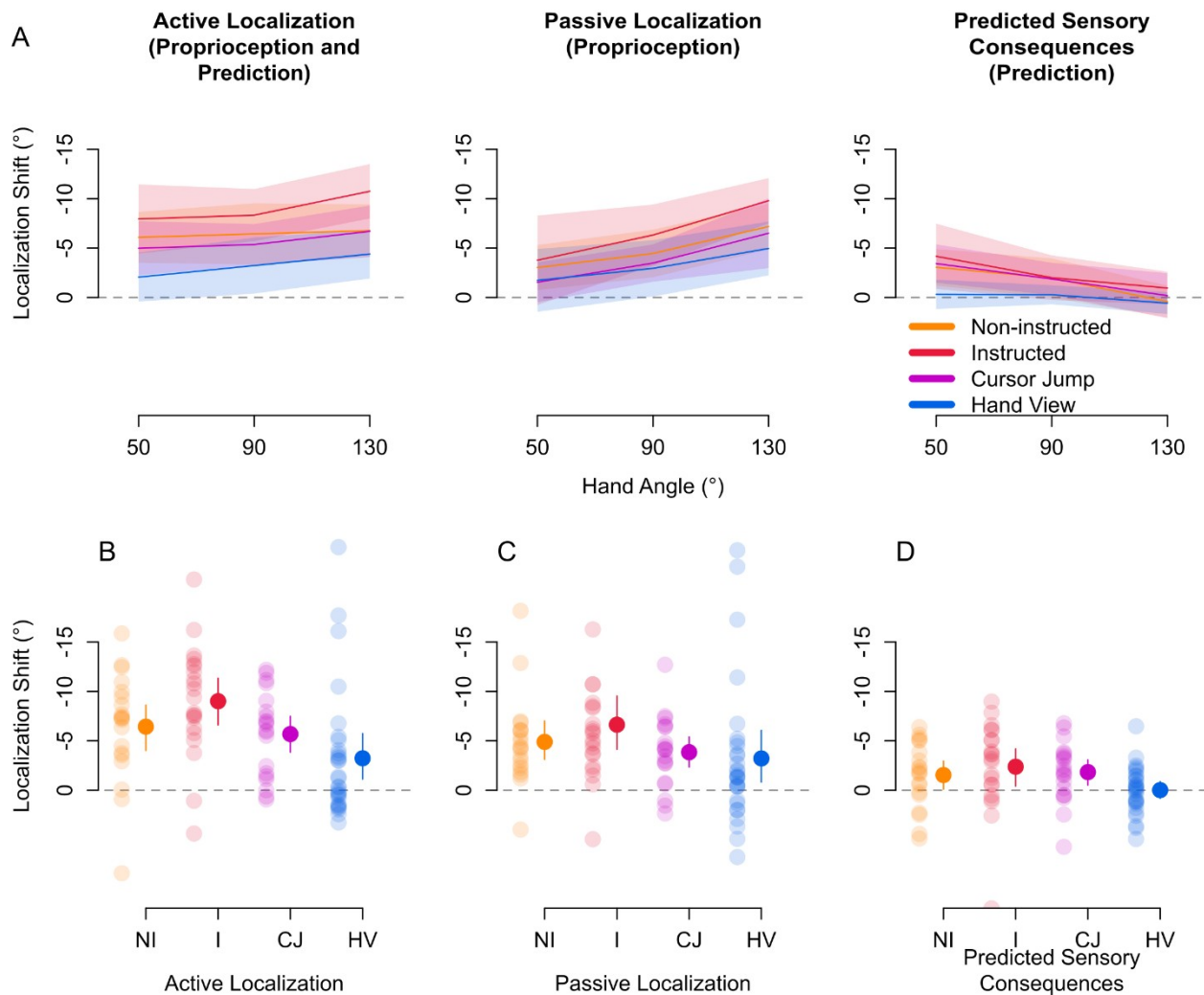
Fig 5: Afferent and Efferent-Based Changes in Hand Location Estimates. A: Shifts in localizing the unseen right hand following adaptation training after self-generated movements (**Left:** active localization), robot-generated movements (**Middle:** passive localization), and the difference between active 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 angle, while 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.

$t_{(19)}$=-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=.440). Since passive localization shifts should rely mainly on updated afferents, or recalibrated proprioception, these tests show that the attribution of error to external sources surprisingly does not reduce proprioceptive recalibration.

Given that passive localization shifts reflect updated afferents, a difference between active and passive localization shifts is likely due to efferent-based contributions. Thus, we measure efferent-based contributions or updates in predicted

sensory consequences by removing afferent-based contributions (active minus passive; Fig. 5D). We conduct an ANOVA on the effect of group on updates in predicted sensory consequences, and find no difference between the groups ($F_{(3,86)}$=2.425, p>.05, η^2_G=.078). We then confirm the presence of updates in predictions for all groups with follow-up one-tailed t-tests comparing the mean shifts for each group to zero. We find that updates in predictions do not differ from zero for only the Hand View group ($t_{(28)}$=-.037, p>.05, d=.007; Instructed: $t_{(20)}$=-2.411, p<.013, d=.526; Non-Instructed: $t_{(19)}$=-2.101, p<.025, d=.470; Cursor Jump: $t_{(19)}$=-2.751, p<.006, d=.615). This suggests that the Hand View group's different active localization shifts could be due to updates in prediction not emerging for this group. Thus, both these results and our analysis of active localization shifts suggest that external error attribution affects efferent-based contributions to hand localization.

We then investigate whether afferent and efferent-based estimates of hand localization contribute to behavior. 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. 6A-6B), we find that both share a small relationship with implicit aftereffects (passive-aftereffects: p<.001, r^2=.121; prediction-aftereffects: p=.004, r^2=0.089). Moreover, a multiple regression with both variables as predictors and angular reach deviations in without strategy no-cursor trials as the dependent variable, shows that both passive localization shifts (β=-.430, p<.001,
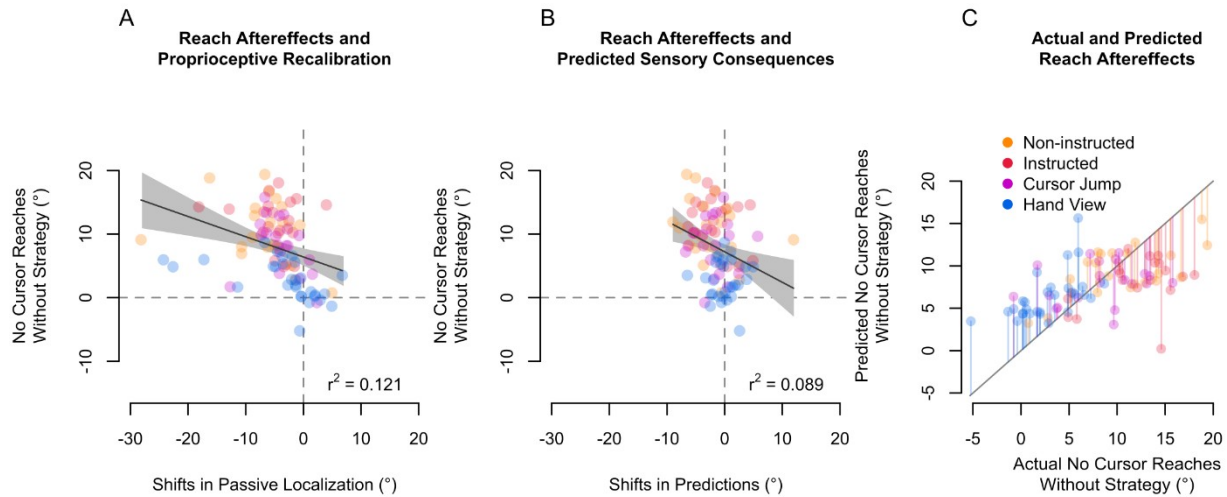

Fig 6: Contributions of afferent and efferent-based hand localization changes to implicit aftereffects. A-B: Relationship between afferent and efferent-based changes in hand location estimates and reach deviations when no visual feedback of the cursor is presented, while excluding any strategies used 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 from the multiple regression model, plotted against observed values for reach aftereffects. Points falling along the diagonal represents perfect prediction. Individual data points are colour-coded according to group, and lines represent the distance of each point from the diagonal.

210   sr^2=.204) and updates in predicted sensory consequences (β=-.694, p<.001, sr^2=.171)
211   significantly predict reach aftereffects. Importantly, pooling data from all individuals
212   across groups is justified, as both predictors are still statistically significant after
213   accounting for a group effect (see OSF: https://doi.org/10.17605/osf.io/xdgh6).
214   Furthermore, the two predictors are independent given our calculation of updates in
215   predictions (confirmed by a low collinearity: vif=1.087). Finally, we validate our
216   regression model by comparing predicted and observed values of reach aftereffects
217   (Fig. 6C). We find that model predictions are not perfect, but relatively close to observed
218   values. The model is likely incomplete, which would explain this disparity, but we don't
219   investigate this further. Overall, hand localization predicts implicit reach aftereffects to
220   some extent, and it seems that this contribution may be split into afferent and efferent-
221   based components.

Discussion

222   We test if manipulating the extent of external error attribution, by demonstrating the
223   visuomotor rotation to participants in various ways, affects changes in hand location
224   estimates. Particularly, the visual feedback of the hand-cursor either jumps to the
225   imposed rotation mid-reach on every training trial, or is present along with a view of the
226   actual hand of the participant. If it is clear to the participant that they are not causing
227   the errors, because the cursor is not where their hand is, adaptation to the perturbed
228   cursor should not lead to changes in hand location estimates. First, despite the Hand
229   View group being the clearest condition that the error source is external, afferent-based
230   (proprioceptive) estimates of hand location still shift following cursor-training. The extent
231   of these shifts doesn't differ from the other groups, including the Non-instructed group
232   where external error attribution is expected to be minimal. This was not the case for
233   estimates based on both afferent and efferent signals (active localization), where shifts
234   are smaller in the Hand View group compared to the others. Second, implicit reach
235   aftereffects persist across conditions, but external error attribution does reduce these
236   changes in motor behavior. Given the difference between their with-strategy and
237   without-strategy no-cursor reaches, the Instructed, Cursor Jump and Hand View groups
238   developed an explicit strategy. However, the persistent but decreased without-strategy
239   reach deviations in the Cursor Jump and further reduction in the Hand View groups,
240   suggest that the type of feedback in these groups leads to less implicit learning, as
241   could be expected with more external error attribution. Finally, we find that both afferent
242   and efferent-based changes in hand localization share a relationship with implicit
243   aftereffects. Given that both implicit motor changes and afferent-based changes in hand
244   position estimates persist across all our experimental groups, our findings suggest that
245   these processes are robust against external error attribution, while updating of efferent-
246   based predicted sensory consequences is not.

Persistent shifts in hand localization

247   In visuomotor rotation adaptation paradigms, visual feedback of the hand is
248 consistently shifted, which over time leads people to update estimates of their unseen
249 hand after a movement (Synofzik et al., 2008; Cressman and Henriques, 2009; 2015;
250 Cressman et al., 2010; Izawa et al., 2012; Ruttle et al., 2016). These updates of hand
251 location estimates rely on at least two components: an efferent-based component,
252 where the expected outcome of a given motor command is updated to reflect the
253 experienced, altered visual outcome of the movement, and an afferent component,
254 where a given proprioceptive signal is updated ("recalibrated proprioception") to
255 associate with the experienced, altered visual outcomes ('t Hart and Henriques, 2016;
256 Mostafa et al., 2019). But, when people know that the rotated cursor does not represent
257 their true hand location, they should not update any estimates of hand location. Yet, we
258 previously found that merely increasing explicit adaptation, by providing instructions or
259 increasing the rotation size, does not decrease updates of neither afferent nor efferent-
260 based hand location estimates (Modchalingam et al., 2019). Here, we ask if increased
261 external error attribution allows people to retain what they know are veridical hand
262 position estimates. Surprisingly, we find evidence of shifts in afferent-based
263 contributions to hand localization across all groups, despite the error source being
264 clearly external in the Hand View group. We also find evidence of an efferent-based
265 contribution to hand localization in the Instructed group, as we found previously
266 (Modchalingam et al., 2019), and in the Cursor Jump group, but not in the Hand View
267 group. This can be interpreted to indicate how heightened external error attribution in
268 the Hand View group leads to decreased efferent contributions to updated hand location
269 estimates. Proprioceptive recalibration, however, seems to be robust against varying
270 degrees of explicit adaptation and external error attribution.

271 Changes in afferent-based estimates of hand location seem to be a robust form of
272 sensory plasticity, as evidenced by its relatively quick emergence (Ruttle et al., 2016),
273 its persistence despite explicit adaptation (Modchalingam et al., 2019), and its
274 preservation despite aging (Cressman et al., 2010; Vachon et al., 2019) and within other
275 forms of perturbations (Cressman and Henriques, 2009; Ostry et al., 2010; Cameron et
276 al., 2012; Leech et al., 2018; Sombric et al., 2019). Furthermore, the recalibration of
277 proprioception is intact in people with mild cerebellar ataxia (Henriques et al., 2014),
278 despite the cerebellum playing a crucial role in adaptation (Martin et al., 1996; Bastian,
279 2006; 2008; Tseng et al., 2007; Synofzik et al., 2008; Taylor et al., 2010; Izawa et al.,
280 2012; Wong et al., 2019). This implies that proprioceptive recalibration relies on a signal
281 different from efferent-based contributions to hand localization, such as a visuo-
282 proprioceptive discrepancy ('t Hart and Henriques, 2016; Ruttle et al., 2018; Mostafa et
283 al., 2019). However, shifts in afferent hand location estimates persist in the Hand View
284 group, even though there should be no visuo-proprioceptive discrepancy, as they can
285 see and feel their own hand. It could be that the cursor still acts as a visual placeholder
286 for the actual hand, as the task is completed by bringing the cursor (not the hand) to the
287 target. Since proprioceptive feedback is veridical, that could lead to a sensory

discrepancy (between seen cursor and felt hand) and result in sensory recalibration. That is, the error signal that underlies proprioceptive recalibration may still be present in some form in the Hand View group. This may explain why the Hand View group does not show decreased shifts in afferent-based hand localization, even when they attributed the source of the errors externally. Regardless, given the persistence of proprioceptive recalibration but not the efferent-based contributions to hand localization when errors are attributed externally, it is likely that these two contributions to hand localization rely on different error signals.

External error attribution reduces implicit processes

In addition to robust sensory recalibration, visuomotor adaptation also leads to implicit motor behavior changes. Previous studies have shown that awareness of the nature of the perturbation increases the contribution of explicit learning during adaptation, on top of rather stable implicit learning (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 we measure implicit and explicit learning using a process dissociation procedure (PDP; adapted from Werner et al., 2015), which we and others have done before (Neville and Cressman, 2018; Maresch and Donchin, 2019; Modchalingam et al., 2019) and is consistent with findings from a similar task quantifying explicit learning (Hegele and Heuer, 2013). We ask people to make open-loop reaches to targets after adaptation, while either using the strategy they just learned (implicit and explicit), or not using it (only implicit). We use this measurement task as it doesn't seem to evoke additional explicit learning itself, as other methods do (Leow et al., 2017; de Brouwer et al., 2018; Maresch and Donchin, 2019), and to keep results comparable to earlier work from our lab (Modchalingam et al., 2019). While explicit learning does not necessarily lead to external error attribution, it is likely that external error attribution is accompanied with more explicit adaptation. In the groups that received visual feedback designed to enable external error attribution (Cursor Jump and Hand View), the PDP method shows evidence of explicit learning, as in the Instructed group. Conversely, while external error attribution does not necessarily have to lead to more explicit learning, it seems advantageous to suppress implicit learning when perturbations are external and hence likely to disappear quickly (Berniker and Kording, 2008; 2011; Wei and Kording, 2009; Wilke et al., 2013; Kong et al., 2017). Consequently, it is easier to revert to non-adapted behavior if adaptation is largely explicit or strategy-based (Ong and Hodges, 2010; Ong et al., 2012). That is, we expect increased external error attribution to decrease implicit learning, which leaves more room for explicit learning. Although we see persistent implicit learning across all conditions, we observe the pattern of implicit and explicit adaptation marginally in the Cursor Jump group, and even more pronounced in the Hand View group. The cursor jump task, however, seems able to elicit explicit learning without the need for elaborate instructions or setups, and is also able to decrease implicit learning due to external error attribution. Nevertheless, we can be fairly certain that people in the Hand View group attribute the source of the error more externally than the other groups.

Although we expect minimal implicit learning and changes in hand location estimates when movement errors are attributed externally, we still observe the presence of these changes across all groups, but reduced for the Hand View group. A reduction of sensory prediction error-based learning may explain both patterns of reduced reach aftereffects and of efferent-based hand localization shifts in the Hand View group. First of all, motor-control policies in both the with and without strategy no-cursor reaches, rely on implicit adaptation 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). Explicit strategies then only contribute to behavior in the with strategy no-cursor reach deviations. The balance between sensory prediction error-based learning and explicit strategy contributions to behavior is changed in the Hand View group. It has been shown that sensory prediction error-based learning is an automatic process 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). Consistent with studies implementing a similar condition to our 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. Second, hand location estimates should make use of available efferent-based information, or updated predicted sensory consequences. When sensory prediction error-based learning is decreased, its effect on state estimates should also be minimal. This in turn could explain reduced efferent-based contributions to hand localization shifts in the Hand View group. Thus, while changes in 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 when errors are clearly external, only sensory prediction error-based learning is reduced.

Afferent and efferent-based hand location estimates contribute independently to behavior

Reach aftereffects are considered evidence that people have updated their internal model, and efferent-based predictions, during adaptation (Krakauer, 2006; 2009; Krakauer et al., 2019). That is, people learn to use a different movement to achieve the same desired outcome. Recalibrated proprioception also informs movements, as we and others have shown that paradigms preventing updates of internal models, while allowing for proprioceptive recalibration, do lead 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). Moreover, the Non-instructed group's different localization shifts for active and passive localization show both afferent and efferent-based contributions to behavior. Here we show that both afferent and efferent changes independently predict reach aftereffects in our without strategy no-cursor task. People in this task are asked to consciously suppress their explicit strategies, which means that both changes can be considered implicit. First, the hand localization shifts allow separate gauging of the

afferent and efferent-based changes that occur in the brain. If both these changes separately contribute to behavioral changes, then they should be independent predictors in a multiple regression. The way we calculate them here, by considering them to be additive in hand localization, necessarily makes them statistically independent (perhaps an oversimplification). However, there is additional behavioral evidence for the independent contributions of afferent and efferent-based processes to reach aftereffects. We see that suppressed efferent-based changes, as in the Hand View group's hand localization shifts, is tied to reduced implicit reach aftereffects. The remaining reach aftereffects in the Hand View group could then be solely based on afferent changes. Regardless of the precise changes in afferent and efferent-based hand location estimates as a result of more external error attribution, our data confirms that changes in motor behavior after learning depend to some degree on updates of our internal estimate of hand location.

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 behavior. 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) changes in hand localization, we show that afferent-based changes persist, despite external error attribution, but efferent-based changes are reduced. This suggests that changes in afferent-based estimates of hand location are robust against external error attribution. Moreover, adaptation proceeds to be more strategy-based, such that there is less reliance on sensory prediction error-based learning. Thus, aside from the reduced efferent-based changes, implicit aftereffects are greatly reduced when the source of the error is clearly external in nature. Since attributing the errors externally leads to persistent but reduced implicit aftereffects, as well as the persistence of changes in afferent-based estimates of hand location, both afferent- and efferent-based components to hand localization seem to independently contribute to changes in motor behavior. Taking all our findings together, it seems that sensory recalibration is impervious to external error attribution, while sensory prediction error-based processes are not.

Methods

Participants

Ninety right-handed participants (64 female, M_{Age} = 20.79, SD_{Age} = 3.88) from York University participated in the experiment, in exchange for course credit for their introductory Psychology course. All participants reported having normal or corrected to normal vision, and gave prior, written, informed consent. All procedures used in this study have been approved by York University's Human Participants Review Committee (e2017-238).

Experimental Set-up

Apparatus

Participants sat on an adjustable chair and held the handle of a 2-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA) that both guided and recorded movements of the hand. While holding the handle with their right hand, participants were instructed to place their thumb on top of the handle. A black cloth covered their right arm and shoulder in order to occlude visual feedback from these body parts. A downward facing computer screen (Samsung 510 N, 60 Hz) located 28 cm above the robot handle projected visual stimuli on a reflective screen, located in between the computer screen and robot manipulandum (14 cm above the robot manipulandum). Below the reflective screen is a touchscreen (2 cm above the manipulandum), where participants responded to some tasks using their left hand (Fig. 1D). Viewing stimuli on the reflective screen made it appear as if projected images from the computer screen were on the same plane of depth as the hand of the participant (Fig. 1A-1C for an example). The left hand of each participant was always illuminated by a lamp and thus remained visible in the areas above the touchscreen panel (Fig. 1D-1E). For one group of participants (the Hand View group), the right hand was also illuminated to make it clearly visible to the participant (Fig. 1C). All trials were conducted in a dark room.

Stimuli

Each trial started with the right hand of the participant at the "home position", which was located along the body midline, about 20 cm in front of the participant (black circle in Fig. 1A-1C, 1F). Participants made 12 cm out-and-back reaching movements from the home position, as smooth and straight as possible, in a block consisting of one of several trial types. The three targets (or arcs, see below) the reaches were made toward, were presented in a pseudorandom order: all three targets (or arcs) were presented once in a shuffled order before being presented again. This way the order appears unpredictable to the participant, but reach directions remain distributed evenly across the trial types. All trial types consist of a multiple of three trials.

Cursor Training Trials

At the start of each block of trials with a cursor (cursor training, Fig. 7), participants saw the words "Reach to Target" displayed on the screen. Afterwards, the participants saw a cursor (green circle, 1 cm diameter) representing their right thumb and kept it at the home position for 300 ms, so that a target (yellow circle, 1 cm diameter) appeared at one of three possible locations. The targets were located 12 cm away from the home position and were positioned either straight ahead at 90°, or to either side at 45° or 135° in polar coordinates. Participants reached for and acquired the target by holding the cursor for 300 ms within 0.5 cm of the target's centre. Once the target was acquired, both the cursor and target disappeared. Participants then returned their hand straight to the home position through a constrained path. If the participants deviated from this
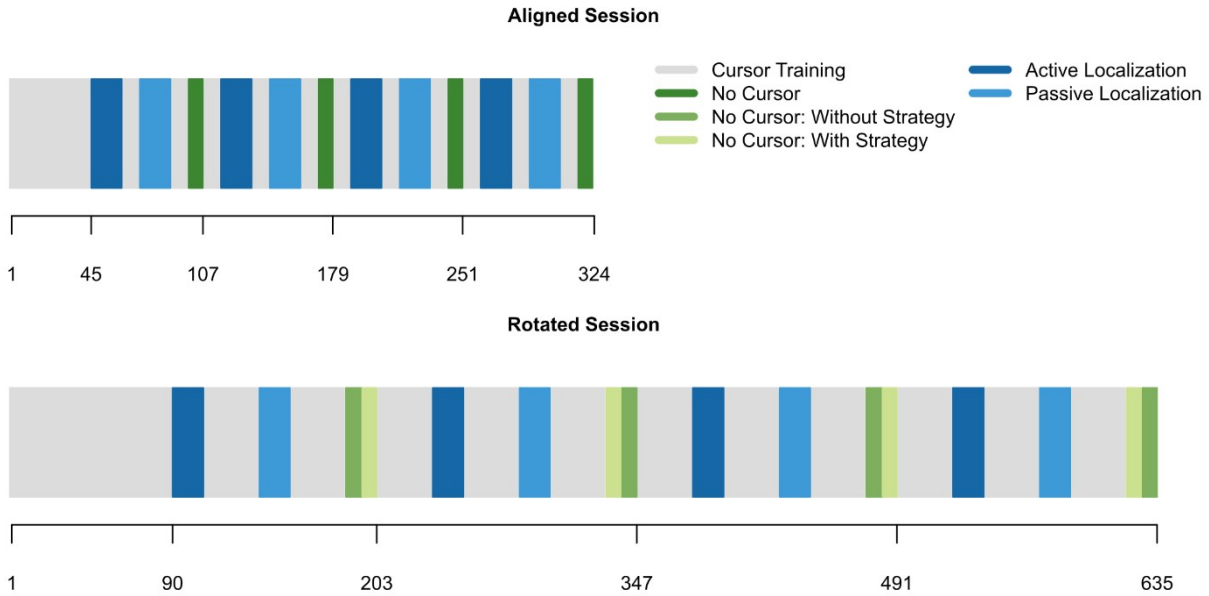
Fig 7: Experiment Schedule. Top: First session, and considered as baseline, where the cursor was aligned with the position of the right hand. Participants performed 45 cursor training trials followed by blocks of active localization (18 trials/block), passive localization (18 trials/block), and no-cursor 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.

441 constrained path, the robot applied a perpendicular resistance force of 2 N/(mm/s) and
442 a viscous damping of 5 N/(mm/s). Only participants in the Hand View group saw their
443 right hand along with the cursor throughout these trials. For these trials, we calculated
444 angular reach deviations at the point of maximum velocity. This is the angular difference
445 between a line connecting the home position to the target and a line connecting the
446 home position to the participant's hand position at the peak of their movement velocity.
447 Thus, once the rotation is introduced (rotated session: cursor training, Fig. 7), full
448 adaptation should then result in angular reach deviations of 30°.

No-Cursor Trials

449 These trials invoke open-loop reach control and were done before and after visuomotor
450 adaptation training to measure reach aftereffects (aligned and rotated sessions: no-
451 cursor, Fig. 7). At the start of this block of trials in the aligned session, participants saw
452 the words "No Cursor" displayed on the screen. These trials proceeded similarly to

cursor training trials, however, participants in all groups reached to targets in the absence of visual feedback provided by the cursor (Fig. 1F). Participants in the Hand View group did not see their right hand as well during these trials. Once participants believed that they had acquired the target, they held their hand in place for 500 ms. Holding their hand in place triggered the end of the trial, making the target disappear. Participants then returned their hand to the home position via the same constrained path as in the cursor training trials.

During the rotated session, we used two variations of no-cursor trials (rotated session: no-cursor without and with strategy, Fig. 7). Participants completed these two variations in succession. At the start of each block, participants saw either the words "No Cursor, Reaching WITHOUT Strategy/Perturbation" or "No Cursor, Reaching WITH Strategy/Perturbation" displayed on the screen. This text instructed participants to either exclude or include any strategy they developed to counter for the visuomotor rotation during rotated cursor training trials. Similar to the process dissociation procedure (PDP) used in Werner et al. (2015) and Modchalingam et al. (2019), we expected that the magnitude of explicit awareness of the participant to the perturbation and the strategy they developed to compensate for it would have produced a difference between reaches, depending on whether they included or excluded this strategy. Hence, there would be both explicit and implicit contributions to learning in the with strategy no-cursor trials, and implicit contributions in without strategy no-cursor trials. These two variations of no-cursor trials were counter-balanced for both within and between participants. That is, blocks of with and without strategy trials alternate within one participant, and the particular variation that an individual starts with is also alternated between participants. For all no-cursor trials, we calculated the angular difference between a straight line from the home position to the point where the participant's hand movement ended, and a line from the home position to the target. Using the endpoint of the reach, rather than the point of maximum velocity, makes data more similar to those obtained in localization trials (see below).

Active Localization

During localization trials, participants in all groups did not receive visual feedback of the location of their right hand. The goal of these trials is to gauge both proprioceptive recalibration and updating of predicted sensory consequences (afferent and efferent-based contributions to hand location estimates). Participants saw the words "Right: Cross Arc and Back, Left: Touch Cross" displayed on the screen, before every block of this trial type. At the start of each trial, an arc (white in color, 0.5 cm thick), located 12 cm away from the home position, was displayed on the screen (Fig. 1E). The arc spanned 60°, and was centered on either the 50°, 90°, or 130° mark in polar coordinates. For each trial (active localization, Fig. 7), participants held the robot manipulandum with their unseen right hand and were instructed to make volitional hand movements from the home position to any point on the arc, as well as to vary their chosen crossing points across trials. Once the handle was moved 12 cm from the home

position, a force prevented the participant from moving the robot any further, giving them the sensation of hitting a cushion. They then returned their right hand to the home position via the same constrained path as in the cursor training trials. With the arc still displayed, participants used their visible left hand to indicate on the touchscreen the point at which they believed their unseen right hand had intersected the arc. After each touchscreen response, participants were instructed to place their left hand under their chin to avoid unwanted contact with the touchscreen.

Passive Localization

This trial type serves to investigate proprioceptive recalibration in the absence of voluntary movements. Before each block of this trial type, participants saw the words "Right: Robot Cross Arc and Back, Left: Touch Cross" displayed on the screen. The trials proceeded similarly to active localization trials, but now the robot manipulandum moved the participant's right hand towards the same points on the arc that their hand intersected during active localization trials in the preceding task (passive localization, Fig. 7). Participants then voluntarily returned their right hand to the home position. With the arc still displayed, they used their visible left hand to indicate on the touchscreen the point to which they believed the robot guided their right hand to intersect the arc.

Procedure

Data from three out of our four experimental groups were collected prior to updates with our experimental program. Thus, only the Hand View group began the experiment with a familiarization session. During this session, participants became comfortable with the apparatus and learned how to perform the reaching and localization trial types. This session included 18 aligned cursor training trials, followed by 18 active localization trials. Participants proceeded to the aligned session immediately.

The aligned session consisted of four cycles of each block of localization and no cursor trial types, and served as baseline data (aligned session, Fig. 7). The first cycle in the session started with 45 aligned cursor training trials, followed by blocks of active localization, passive localization, and no-cursor trials respectively. To account for any practice advantages provided by the familiarization session in the Hand View group, we only used the last 30 out of the first 45 aligned cursor training trials across all groups for further analyses. Furthermore, we also observe that reach trajectories in the aligned session do not qualitatively differ across groups (as shown in Fig. 3). To prevent decay in learning, we included shorter blocks of cursor training trials, which we call "top-up" cursor training trials, interleaved between localization and no-cursor blocks. Each block of top-up cursor training trials consisted of nine trials. After the first cycle, cursor training trials in the second up to the fourth cycle were all top-up trials, with the other trial types proceeding in the same order. For all four cycles, each block of active localization and passive localization trials consisted of 18 trials. For all four cycles, each block of no-cursor trials consisted of nine trials. The end of the last block of no-cursor trials during the fourth cycle marked the end of the aligned session.

531   After the aligned session, participants were given a mandatory five-minute break.
532 During the mandatory break, participants in the Instructed Group received instruction
533 about the nature of the perturbation that they will be experiencing as well as a strategy
534 to counter for it. Other participants did not receive this strategy, but were simply advised
535 that the cursor would be moving differently and that they needed to compensate for this
536 difference. For all groups, participants were instructed to keep in mind the strategy that
537 they developed to compensate for the perturbation, as they will be asked to either use
538 or not use this strategy later on in the experiment.

539   Participants then completed the rotated session, where the cursor (now a light
540 blue circle, 1 cm diameter) was perturbed for all cursor training trials (Fig. 1A-1C). The
541 perturbation consisted of a 30° CW rotation of the cursor, relative to their hand position.
542 Participants were still told to move the cursor as smooth and straight as possible to the
543 target location. Hence, the most optimal way to counter the 30° CW rotation is to reach
544 straight in a direction 30° CCW to the target. The rotated session consisted of the same
545 four cycles discussed in the aligned session (rotated session, Fig. 7). In this session,
546 however, we increased the number of cursor training trials in each block, to saturate
547 learning of the visuomotor rotation. The first cycle in the session started with 90 rotated
548 cursor training trials, while each block of top-up cursor training trials now consisted of 30
549 trials. For all cycles, each block of active localization and passive localization trials
550 consisted of 18 trials. For all cycles, each block of no-cursor trials consisted of nine
551 trials. In this session, however, each block of no-cursor trials was done twice, each in
552 one variation (either with strategy or without strategy). The end of the second variation
553 of no-cursor trials during the fourth cycle marked the end of the rotated session.

Experimental Groups

554 There were four groups in this experiment: Non-Instructed Group (n = 20, 14 females),
555 Instructed Group (n = 21, 13 females), Cursor Jump Group (n = 20, 14 females), and
556 Hand View Group (n = 29, 23 females). These groups were intended to vary in the
557 extent by which people externally attributed the error they experienced to the cursor
558 rotation. Although the groups experienced similar experimental conditions during the
559 aligned session, the stimuli and conditions presented to each group differed during
560 cursor training trials in the rotated session (Fig. 1A-1C).

Non-Instructed Group

561 During the mandatory break, participants in this group did not receive any strategy on
562 how to counter the perturbation they would experience in the following rotated session.
563 Participants were only advised that the cursor would move differently and that they
564 needed to compensate for it (Fig. 1A). They also did not receive different stimuli in the
565 rotated session, apart from the cursor rotation. Thus, this group is designated as our
566 control group.

Instructed Group

567 Participants in this group were explicitly informed about the nature of the perturbation
568 and were given a strategy on how to counter for it during the break. The strategy
569 involved presenting a clock face to the participant (Benson et al., 2011). The center of
570 the clock face was similar to the home position. If the target was located on the twelve
571 o'clock position, and a 30° CW rotation made the cursor move towards the one o'clock
572 position, participants were informed that moving towards the eleven o'clock position
573 would bring the cursor towards the target. Additionally, we presented an animation to
574 demonstrate the appropriate reach movements to the participant. The experimenter
575 ensured that the participant understood the strategy well, before moving on to the
576 rotated session. Like the Non-instructed Group, apart from the rotated cursor, this group
577 also did not receive any different stimuli in the rotated session.

578 Importantly, results for the Non-instructed and Instructed groups have been
579 published in our earlier work (Modchalignam et al., 2019; data: https://doi.org/10.17605/
580 osf.io/mx5u2). Here, we use these groups as controls and add two new groups, where
581 we further manipulate the extent of external error attribution, as described below.

Cursor Jump Group

582 This group did not receive any strategy and was instructed similarly to the Non-
583 instructed Group during the break. As they performed cursor training trials in the rotated
584 session, the cursor was perturbed differently. At the start of each trial, the cursor was
585 aligned with the position of the unseen right hand, as it did in the aligned session.
586 However, after moving for one-third of the home-target distance (i.e. when the hand is 4
587 cm away from the home position), the cursor shifted from an aligned trajectory to a
588 rotated trajectory, showing the 30° CW rotation to the participant on every single trial
589 (Fig. 1B). Presenting the cursor in this manner was expected to clearly demonstrate the
590 nature and source of the error for the participant.

Hand View Group

591 The hand view group did not receive any strategy and was instructed similarly to the
592 Non-instructed Group. Participants were able to see their actual right hand during cursor
593 training trials in both aligned and rotated sessions. Lamps beneath the touchscreen
594 illuminated and allowed the participant to see their right hand through the reflective
595 screen. Thus, participants were able to see that the cursor moved with their right hand
596 in the aligned session, but moved in a different direction than their right hand in the
597 rotated session (Fig. 1C). This veridical visual representation of the hand was expected
598 to be the clearest demonstration, among all groups, about the nature and source of the
599 error for the participant.

Data Analysis

600 In this experiment, we aimed to determine the effects of external error attribution on
601 changes in afferent and efferent-based hand localization. Thus, we compared all four

602 groups across the different trial types. Alpha level was set to 0.05 for all statistical tests
603 conducted and, when necessary, Greenhouse-Geisser corrections were applied. For
604 planned follow-up tests, we used the Sidak method to control for the family-wise error
605 rate when necessary. We note that degrees of freedom values for these follow-up tests
606 are larger than expected, as the tests were conducted using the emmeans package in R
607 (Lenth, 2019), which is based on the pooled information of a model that is fit into the
608 whole dataset. All data preprocessing and analyses were conducted in R version 3.6.0
609 (R Core Team, 2019). Data and analyses scripts are available on OSF
610 (https://doi.org/10.17605/osf.io/xdgh6).

Rate of Learning During Adaptation Training

611 First, we analyzed any group differences in rates of learning for reaches during cursor
612 training trials. Reaches in these trials, for both the aligned and rotated sessions, were
613 manually inspected for failing to perform the required reach, i.e. not reaching the target
614 with a smooth and straight movement. Trials deemed as unusable for further analyses
615 were removed for both aligned cursor training trials (Non-instructed: 2.67%; Instructed:
616 1.13%; Cursor Jump: 4.07%; Hand View: 0.05%) and rotated cursor training trials (Non-
617 instructed: 0.94%; Instructed: 1.38%; Cursor Jump: 0.33%; Hand View: 0.14%). For the
618 retained trials, we calculated angular reach deviation at the point of maximum velocity.
619 We corrected for individual baseline biases, by calculating the average reach deviation
620 for each target separately within each participant, during the last 30 out of the first 45
621 aligned cursor training trials, and subtracting this from cursor training trials in the rotated
622 session. Next, we investigated three specific blocks of trial sets from the initial 90
623 rotated cursor training trials. The first set consisted of the first three trials, the second
624 consisted of the next three trials, and the third consisted of the last 15 trials of training
625 (i.e., trials 1 to 3, 4 to 6, 76 to 90 respectively). We then compared measures of angular
626 reach deviation, for each of these three trial sets across all four groups, in order to
627 confirm whether all groups learned to counter for the perturbation and to investigate any
628 differences across groups.

Reach Aftereffects and Strategy Use

629 We then analyzed for any group differences in reaching movements without cursor-
630 feedback. Reaches in no-cursor trials for both aligned and rotated sessions were
631 manually inspected for failing to perform the required reach. Trials deemed as unusable
632 for further analyses were removed for both aligned no-cursor trials (Non-instructed:
633 1.67%; Instructed: 0.26%; Cursor Jump: 2.22%; Hand View: 0.86%) and rotated no-
634 cursor trials (Non-instructed: 0.83%; Instructed: 1.79%; Cursor Jump: 3.89%; Hand
635 View: 0.38%). For the remaining trials, we calculated angular reach deviations at
636 movement endpoints. Angular reach deviations from aligned no-cursor trials were
637 subtracted from without strategy no-cursor trials to confirm whether training with a
638 rotated cursor led to reach aftereffects.

22

Following analyses for reach aftereffects, we assessed the effect of our manipulations of external error attribution on awareness of the perturbation, using a process dissociation procedure (PDP; Werner et al., 2015; Modchalingam et al., 2019). First, we implemented a baseline-correction procedure, by subtracting no-cursor reaches in the aligned session from no-cursor with strategy and no-cursor without strategy trials, respectively. We then compared angular reach deviations per participant when either including any strategy they learned during adaptation training (no-cursor with strategy) or excluding such a strategy (no-cursor without strategy). We expect that our manipulations will increase participants' awareness of the external nature of the perturbation and, insofar as with strategy trials capture the explicitly available strategy, this should lead to a difference between without strategy and with strategy trials. On the other hand, a lack of awareness will not lead to a difference between the two types of trials.

Proprioceptive Recalibration and Updating Predicted Sensory Consequences

For our main research question, we investigated the effects of external error attribution on afferent and efferent-based changes in hand location estimates. To do this, we analyzed hand location estimates in active localization and passive localization trials, before and after adaptation training. We calculated the angular difference between a line connecting the home position to the point where the participant's unseen right hand movement ended, and a line connecting the home position to the participant's perceived hand location, i.e. their touchscreen response using the left hand. To account for potential inconsistencies in performing the localization tasks, we ensured that arc responses were centred on where the arc stimuli were expected to be displayed (12 cm from home position) by implementing a circle fitting procedure (see Mostafa et al., 2019 for details). This procedure ensured that any localization shifts we detected in our analyses were not due to technical issues or unwanted response biases. Furthermore, we conducted an outlier removal procedure for this fitted data, such that trials with hand movement endpoints beyond ±20° from the arc centre and angular errors beyond ±3 standard deviations from the mean angular error were removed (Non-instructed: 0.84%; Instructed: 0.17%; Cursor Jump: 1.44%; Hand View: 1.56%). As participants chose the points on the arc that they moved towards, their movements did not end on all possible points on the arc. To account for this, we used a kernel smoothing method (gaussian kernel with width = 15°) to interpolate changes in hand localization at specific points (50°, 90°, and 130°) for every participant. These locations are the same points where the arc stimuli are centred on in polar coordinates. We then used the mean of these interpolated values at each of the three points, to estimate hand localization errors in active and passive movements for both the aligned and rotated sessions.

After these pre-processing procedures, we first confirmed whether hand position estimates did shift after adaptation to a visuomotor rotation. To do this, we compared hand localization errors in the aligned session from those in the rotated session. We

23

678 then calculated the difference of localization errors between the two sessions to
679 represent shifts in hand localization. These shifts were compared across groups,
680 separately for active and passive localization. While active localization shifts are based
681 on both afferent and efferent contributions, passive localization shifts are based mainly
682 on afferent contributions. This means that a difference between active and passive
683 localization shifts shows that there is some efferent-based contribution on active
684 localization shifts. Thus, we used the difference between active and passive localization
685 shifts as a measure of efferent-based updates in predicted sensory consequences, and
686 passive localization shifts as a measure of the afferent-based recalibration of
687 proprioception. We then investigated whether these measures were distinguishable
688 from zero, across all groups. Finally, we investigated how both afferent and efferent-
689 based contributions to hand localization may contribute to implicit motor changes.

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