Differential contributions of implicit and explicit learning mechanisms to various contextual cues in dual adaptation

Maria N. Ayala & Denise Y. P. Henriques

Abstract

The ability to switch between different tasks accurately and efficiently is an invaluable feature to a flexible and adaptive human motor system. This can be examined in dual adaptation paradigms where the motor system is challenged to perform under randomly switching, opposing perturbations. Typically, dual adaptation doesn't proceed unless each mapping is trained in association with a predictive cue. To investigate this, we first explored whether dual adaptation occurs under a variety of contextual cues including active follow-through movements, passive follow-through movements, active three-part lead-in movements, and static visual cues. In a final intervention, we provided our Instructed group with a compensatory strategy about the perturbations (30° CW/CCW rotations) and their relationships to each context (static visual cues). This allowed us to explore the extent by which dual learning is supported by both implicit and explicit mechanisms, regardless of whether or not they elicited dual adaptation across all the various cues. To this end, following perturbed training, participants from all experiments were asked to either use or ignore the strategy as they reached without visual feedback. This Process Dissociation Procedure teased apart the implicit and explicit contributions to dual adaptation. We found that active movement cues, but not passive ones, elicited dual adaptation. Expectedly, static visual cues didn't elicit dual adaptation, but those in the Instruction group compensated by implementing aiming strategies. Critically, we found no implicit contributions in this Instruction group, but an effect of instruction, suggesting that explicit aiming strategies inhibit implicit mechanisms in dual adaptation. Thus, by implementing conscious strategies, dual adaptation can be easily facilitated even in cases where learning would not occur otherwise.

28 While it has always been imperative for humans to learn to manipulate new tools, with the
29 rise of modern technologies we are often required to operate and switch under multiple different
30 visuomotor mappings. This ability to switch between different tasks accurately and efficiently is
31 an invaluable feature to a flexible and adaptive human motor system. We can skillfully use a tool,
32 correct for any movement errors while we use it, and then anticipate the consequences of switching
33 to a completely different tool or environment. Often times we make large errors when first learning
34 to move under novel circumstances, but our motor systems quickly adapt, such that eventually,
35 and rather quickly, we produce smooth, accurate movements despite behavioural or environmental
36 constraints.

37 To study the ability of the motor system to switch between learned visuomotor maps,
38 variants of the same environment can be introduced serially (i.e. ABA paradigm) or concurrently
39 (i.e. dual adaptation paradigm). ABA paradigms probe how an internal model can be affected by
40 the subsequent learning of another, while dual adaptation paradigms have the advantage of
41 challenging the motor system to learn, acquire, and switch between multiple internal models,
42 mimicking its daily demands. Typically, when faced with unpredictable perturbations to
43 movement that vary from trial to trial, the motor system fails to adapt, leading to interference
44 (Brashers-Krug, Shadmehr, & Bizzi, 1996; Caithness et al., 2004; Donchin, Francis, & Shadmehr,
45 2003; Karniel & Mussa-Ivaldi, 2002; Krakauer, Ghilardi, & Ghez, 1999). However, adaptation to
46 two or more visuomotor perturbations (i.e. dual adaptation) can proceed when each visuomotor
47 map has been sufficiently cued during training, although what makes a cue sufficient is still
48 unclear. Usually, the relevance of the cue to the task and possibly the “intrinsic” or motor-based
49 nature of the cue appears to facilitate dual adaptation (e.g. (Ayala, ‘t Hart, & Henriques, 2015;

Howard, Wolpert, & Franklin, 2013)), while cues that are more “extrinsic” or less pertinent to the task lead to mixed findings (e.g. (Baldeo & Henriques, 2013; Gupta & Ashe, 2007; Hinder, Woolley, Tresilian, Riek, & Carson, 2008; Osu, Hirai, Yoshioka, & Kawato, 2004)).

Adaptation to a single perturbation can be characterized by at least two qualitatively different learning mechanisms: (1) an explicit, or conscious process which arises due to the implementation of aiming strategies (Heuer & Hegele, 2008; Taylor, Krakauer, & Ivry, 2014), and (2) an implicit process which is thought to function without awareness, reflect adaptation of internal models in the cerebellum, and largely produce reach aftereffects (Heuer & Hegele, 2008; Taylor, Klemfuss, & Ivry, 2010). Explicit and implicit contributions can also be elicited when adapting to opposing visuomotor rotations for some contextual cues, such as when targets are displayed in different workplaces (a cue that usually leads to dual adaptation rates similar to that for single-rotation adaptation (Baldeo & Henriques, 2013; Woolley, Tresilian, Carson, & Riek, 2007)), and when the perturbations are large and blocked, as demonstrated by Schween and colleagues (Schween, Taylor, & Hegele, 2018). In one of their dual adaptation experiments, Schween and colleagues showed that overlapping strategies led to interference, but when provided with compensatory strategies, participants showed overall learning and reach aftereffects (Schween et al., 2018). Still, it’s unclear to what extent these underlying processes are engaged, so here we break down the explicit and implicit contributions to dual adaptation across a diverse set of contextual cues.

In this series of experiments, we explore the efficacy of various cues to dual adaptation, including one involving an explicit aiming strategy. First, we looked at whether distinct active movement sequences (i.e. follow-through movements) and more complex lead-in sequences can facilitate adaptation to opposing visuomotor rotations. This has been similarly demonstrated under

force-field paradigms (Howard, Ingram, Franklin, & Wolpert, 2012; Howard, Wolpert, & Franklin, 2015), but it's unclear whether the active component of the contextual cue drove dual adaptation, so in the following experiment we isolated the active movement component (i.e. the self-generated follow-through component) and replaced it with a passive visual consequence that mimicked that motion. We found that active, but not passive, movement sequences elicited dual adaptation. We then equipped a separate Instruction group with a compensatory strategy about the perturbations (30° CW and 30° CCW rotations) and their relationships to each context (visual cues), and compared their performance to an uninstructed group with the same visual cues. Using a Process Dissociation Procedure (PDP; adapted from (Werner et al., 2015), we teased apart the implicit and explicit contributions to dual adaptation and found that visual cues didn't elicit dual adaptation, but those in the Instruction group compensated by implementing aiming strategies. Critically, we found no implicit contributions for those who were instructed, but an effect of instruction, suggesting that explicit aiming strategies inhibit implicit mechanisms in dual adaptation. Thus, by implementing conscious strategies, dual adaptation can be easily facilitated even when learning would not occur otherwise.

Method

Participants

One-hundred and thirty-five participants (85 females, 20.40 ± 3.23 years old, mean $\pm$ SD) were recruited and assigned to participate in the following experiments and were granted a bonus credit for either an undergraduate psychology or kinesiology course. All participants were right-handed, had normal or corrected-to-normal vision, and were naïve to the purpose of the experiment. Participants provided written consent in accordance with York University's Human

Participant Review Committee. Two participants withdrew from the experiment due to discomfort and were thus excluded from all analyses.

Apparatus

Participants sat on an adjustable chair facing a digitizing tablet (Wacom Intuos3, 12" x 12" surface, resolution resampled by 1440 x 900 pixels at 60 Hz) and a monitor (Dell Technologies, 22" P2217 LED screen) located approximately 55 cm from the tablet workspace. The tablet was placed at waist level so that hand movements were made along the horizontal plane (Figure 1A). To prevent participants from seeing their arm movements, an adjustable opaque shield was placed above the tablet (Baldeo & Henriques, 2013; Balitsky Thompson & Henriques, 2010; Dionne & Henriques, 2008). All tasks required participants to reach to a target disc (1.5 cm in diameter) by moving a digitizing pen that moved a hand-cursor (1 cm in diameter) in a 1:1 ratio. Some tasks required a secondary reach from the target disc to a final target box (3 x 3 cm, e.g. Figure 1B). The target disc was radially-spaced and located at either 75°, 90°, or 105°. In all experiments but one, the target disc was flanked by a target box located 7.5 cm to its left or right, but never both at once. All target discs began at a common starting point located 10.5 cm away from the home position.

Experiment”), we implemented a more complex sequence of movements to cue the perturbations; participants make an unseen leftward or rightward reach, then back to the home position, and finally to the target disc, completing a three-part motion (Figure 1F). In the fourth experiment (**“Instruction Experiment”**), participants were given instructions about the nature of the perturbation and the relationship of the perturbations to the target boxes, although no movements to the target boxes were required (Figure 1E). In the final experiment (**“Static Visual Cue Experiment”**), like in the other experiments, left and right target boxes were coupled with different perturbations, but no instructions were given and no secondary movement to the target boxes occurred (i.e. purely visual cue; Figure 1E). Two groups, Single **“CW-only”** and **“CCW-only”** served as control groups and learned only a single perturbation (thus, under only *one* context; Figure 1B). Across all conditions, the presence of a left-flanking box was predictive of a 30° CCW rotation while the right-flanking box was predictive of a 30° CW rotation.

All participants started at the same home position and were told to make smooth and direct reaches to the target disc. For trials involving visual feedback of the hand-cursor (also referred to as “closed-loop trials”), participants simply reached towards the target disc. For trials involving no visual cursor feedback (also referred to as “open-loop trials”), participants reached towards the target disc with their unseen cursor, and remained stationary for 500 ms until the home position appeared. In order to facilitate returning to the home position and proceed to the next trial during open-loop trials, a line on the home position changed in orientation depending on the position of the pen. A solid edge was also placed just below the home position to help participants find the home position. Likewise, visual feedback of the hand-cursor appeared when participants were within a 2 cm radius of the home position.

157 For each experiment, participants completed pre-training, training, and post-training
158 sessions (Figure 2). For the **CW-only** and **CCW-only** control conditions, participants completed
159 the task in approximately one hour (Figure 2A). For the rest of the experiments, participants
160 completed the task in approximately two hours (Figure 2B - C). With the exception of the
161 **Instructions Experiment**, participants were not informed about the presence or nature of the
162 rotation at the start of the experiments. After the experiment, participants answered a series of
163 questions to assess their awareness of the rotation and the experimental objectives.

A. Non-instructed single perturbation experiments

B. Non-instructed dual perturbation experiments

C. Instructed dual perturbation experiment

164

165 *Figure 2. Perturbation schedule. A. Non-instructed single perturbation experiments. Two*
 166 *experimental groups follow this perturbation schedule: CW-only and CCW-only control groups.*
 167 *B. Non-instructed dual perturbation experiments. Four experiments fall into this perturbation*
 168 *schedule category: Active Movement Sequence Experiment, Passive Movement Consequence*
 169 *Experiment, Active Lead-in Sequence Experiment, and Static Visual Cue Experiment. B.*
 170 *Instructed Dual Perturbation experiment. Only the Instruction Experiment followed this*
 171 *perturbation schedule. All PDP trials, shaded in green, were counterbalanced.*
 172

Active Movement Sequence Experiment

Twenty-eight participants completed the **Active Movement Sequence Experiment**. In this experiment, participants reached towards the target disc followed by a reach to either its LEFT or RIGHT to a target box (Figure 1B). After acquiring the target disc, the hand-cursor was visually clamped to only show the horizontal component of movement as they moved towards the target box.

Pre-training (Baseline measures)

The aim of the pre-training session was to obtain baseline performance and familiarize participants with the task. Participants reached towards the target disc 60 times with visual feedback of the aligned cursor (veridical), followed by 24 reaches with no visual feedback of the cursor (i.e. No-Cursor) in order to record baseline open-loop reach errors (Figure 2B, Pre-training).

Rotated Training (Adaptation)

The aim of reach training was to expose participants to a visuomotor rotation in order to assess the learning rate and later, reach aftereffects. Participants reached 360 times with interleaved 30° CW and CCW rotated cursors followed by 12 “Within-Training” No-Cursor reaches (Figure 2B, Training). This was repeated for a total of 720 rotated training trials. During training, each rotation was associated with either a LEFT or RIGHT target box (Figure 1B), in order to determine whether dual adaptation can occur when cued by different movement sequences. At the beginning of every trial, participants saw both the initial and final targets. CW and CCW trials were presented in a pseudo-randomized order such that participants encountered all three possible targets for each cursor rotation before any target location was repeated.

Post-training (Analysis for awareness)

195 Immediately after Training, it was confirmed with participants that the cursor would not
196 move in the same direction as their hand, and that they needed to compensate and keep that
197 compensatory strategy in mind (Figure 2B, Confirmation, in orange), as they will later be prompted
198 by the screen to either use a “strategy” (Include-Strategy) or *not* use a “strategy” (Exclude-
199 Strategy). This Process Dissociation Procedure (PDP; adapted from Werner et al., 2015) allowed
200 us to make inferences about the participants’ awareness, which in turn allowed us to tease apart
201 implicit and explicit contributions to dual adaptation. After Confirmation, participants reached
202 with both CW- and CCW-rotated cursors for 24 trials to preserve any dual adaptation. This was
203 followed by 12 Include-Strategy No-Cursor trials, then 12 Exclude-Strategy No-Cursor trials
204 (Figure 2B, Post-training). Finally, they again reached with both CW- and CCW-rotated cursors
205 for 24 trials, followed by another 12 Include-Strategy trials and 12 Exclude-Strategy trials. All
206 post-training tasks were counterbalanced.

207 Recall that we also collected No-Cursor reaches amidst training (Within-Training No-
208 Cursor trials). Previous dual adaptation work from our lab did not differentiate between Include-
209 Strategy or Exclude-Strategy No-Cursor trials; participants simply made open-loop reaches,
210 identical to our Within-Training No-Cursor trials here (Ayala et al., 2015; Ayala & Henriques,
211 2018; Baldeo & Henriques, 2013). Thus, to confirm that these previously found reach
212 aftereffects are indeed implicit in nature and to ensure that participants do not use any explicit
213 strategies without being reminded to do so, we will compare our Within-Training No-Cursor
214 trials (i.e. reach aftereffects after training) with Exclude-Strategy No-Cursor trials (i.e. reach
215 aftereffects after training *and* being told not to use any strategies).

216 **Single CW-only and CCW-only Control Experiments**

Twenty participants served as **CW-** or **CCW-only** controls for all experiments. The task is identical to the **Active Movement Sequence Experiment**, except participants in these groups experienced either a 30° CW *or* 30° CCW rotation of the cursor during training. Participants reached towards the target disc followed by a reach to either the left or right target box. Again, after acquisition of the target disc, cursor movement was visually clamped to show only the horizontal component of movement. The experiment began with a Pre-training session, consisting of 60 aligned reaches followed by 12 No-Cursor reaches.

Rotated Training (Adaptation)

The aim of reach training was to expose participants to a visuomotor rotation in order to assess the learning rate and later, reach aftereffects. During training, participants in the SINGLE groups reached 180 times with a rotated cursor (30° CW *or* 30° CCW) followed by 15 No-Cursor reaches twice (Figure 2A, Training). This was repeated for a total of 360 rotated training trials. Since participants in these groups only experienced a single perturbation, they only saw either a left or a right target box across training. Trials were presented in a pseudo-randomized order such that participants encountered all three possible targets before any target location was repeated.

Post-training (Awareness analysis)

As in the **Active Movement Sequence Experiment**, immediately after Training it was confirmed with participants that the cursor would not move in the same direction as their hand and that they needed to compensate (Figure 2A, Confirmation). They were told to follow screen prompts that would state when (Include-Strategy) and when *not* to use a “strategy” (Exclude-Strategy) to compensate for the odd movement of the cursor.

After Confirmation, participants reached with both CW- *or* CCW-rotated cursors for 24 trials to preserve any dual adaptation. This was followed by 12 Include-Strategy No-Cursor trials,

then 12 Exclude-Strategy No-Cursor trials (Figure 2A, Post-training). All post-training tasks were counterbalanced.

Passive Movement Consequence Experiment

Thirty participants completed the **Passive Movement Consequence Experiment**. Unlike the **Active Movement Sequence Experiment**, participants simply had to reach to the initial target and stay stationary until the initial target has made its complete migration into the final target (Figure 1C). When participants failed to remain still, a high-pitched beep and a visual message “Stay still!” signaled them to stop moving until all stimuli disappear.

Figure 2B shows the perturbation schedule for the **Passive Movement Consequence Experiment**. Pre-training, training, and post-training followed the same protocol as in the **Active Movement Sequence Experiment** (Figure 2B).

Active lead-in Sequence Experiment

Thirty-one participants completed the **Active Lead-In Sequence Experiment**. Instead of making a secondary movement to the box target, participants made a three-part movement sequence: first, an unseen initial reach to the left or right along a physical edge, followed by a visually-clamped reach to the home position, then finally to the target disc (Figure 1F). Three participants fell in the extreme outlier range and were excluded from analysis.

Figure 2B shows the perturbation schedule for the **Active Lead-in Sequence Experiment**. Pre-training, training, and post-training followed the same protocol as in the **Active Movement Sequence Experiment** (Figure 2B).

Instruction Experiment

Twelve participants completed the **Instruction Experiment**. Here, participants did not reach towards the boxes or see any visual motions toward the boxes. Participants simply had to

reach to the target disc and stay stationary (Figure 1E). When they failed to remain still, a high-pitched beep and a visual message “Stay still!” signaled them to stop moving until all stimuli disappear. Critically, participants were instructed about the nature of the perturbations and their relationship to the static visual cues (i.e. boxes). They were explicit given a strategy on how to counter the perturbations.

Figure 2C shows the perturbation schedule for the **Instructions Experiment**. During Pre-training, participants reached towards the initial and final targets 60 times with visual feedback of the aligned cursor, followed by 24 reaches with no visual feedback of the cursor (Figure 2C, Pre-training). After Pre-training, participants were informed about the nature of the rotations and were provided with a strategy to counteract the rotation so that they can move the cursor in a straight path to the targets (Figure 2C, Instruction, shaded in blue). More specifically, they were instructed to visualize the location of the home position as the center of a clock face. They were told that for trials where they saw the box on the left side, reaching towards a number on the clock would result in the cursor heading an hour behind, so they should aim an hour ahead to make a straight path to the target. They were told that the opposite was true for trials where they saw the box on the right side.

During training, participants reached 720 times with interleaved CW- and CCW-rotated cursors (Figure 2C, Training). Post-training followed the same protocol as in the **Active Movement Sequence Experiment** (Figure 2C, Post-training).

Static Visual Cue Experiment

Twelve participants completed the **Static Visual Cue Experiment**. This experimental group served as controls for the Instruction Experiment; participants only saw the final target and were not informed about the rotations, the coupling between the rotation and target box, nor were

they given any compensatory strategy (Figure 1E). Participants reached to the target disc and stayed stationary (and were otherwise alerted as described above in the **Instruction Experiment** if they failed to do so). Figure 2B shows the perturbation schedule for the **Static Visual Cue Experiment**. Pre-training, training, and post-training followed the same protocol as in the **Active Movement Sequence Experiment** (Figure 2B).

Analysis

Cursor movement data was digitally smoothed using a first-order, low-pass Butterworth filter with a frequency cut-off of 2.5 Hz. Movement onset was fixed at 10% of peak velocity. The experimental data was analyzed offline using R (preprocessing and analysis scripts can be found in <https://github.com/ayalamar/sequence>), using kinematic error (operationalized as angular deviation at maximum velocity) during training and No-Cursor trials. Angular error at maximum velocity refers to the angular difference of the target and cursor at peak velocity relative to the home position. For all our analyses involving blocks, we averaged across blocks of 3 trials in order to include a movement to each target.

Visuomotor adaptation

Classic analysis of reach adaptation typically includes comparisons between single-perturbation groups and dual-perturbation groups to compare rates of learning. However, as it has been shown in the literature, dual adaptation rarely parallels the learning rate to that of single adaptation, so we opted to report only dual learning statistics for brevity. For those who are interested, omnibus tests are available on OSF and can be analyzed with scripts found in (<https://github.com/ayalamar/sequence>).

The overall difference in reaching error between the first trial and the last block reflect the extent of learning. Since CW and CCW rotations were not expected to elicit different rates of

learning, we analyzed normalized errors, but we provide visualizations of signed errors to show whether compensation occurs in the expected directions. A planned repeated-measures t-test (first block vs. final block; one-sided) was used to show whether adaptation has occurred within each experimental group. In addition, we compared performance from the beginning of rotation training (substituted as 30 to reflect the size of the rotations) to the final block of experiencing the rotation. We quantified this Percent Improvement (PI) below:

$$\text{Percent Improvement} = \frac{\text{Initial block error} - \text{Final block error}}{30} \times 100$$

Positive PIs indicate reduction in errors over time while negative PIs indicate worsening of errors over time. PI was analyzed for every experimental group using a one-sample t-test, one-sided.

Reach Aftereffects

An alternative measure to test whether adaptation has occurred is the presence of reach aftereffects during No-Cursor trials. Reach aftereffects refer to rotation-dependent, deviated reaching in the absence of visual feedback of the cursor. Using the PDP (Werner et al., 2015), reach aftereffects can be segmented to its explicit and implicit components. It is thought that implicit learning is reflected in No-Cursor trials where participants are told not to implement any strategy in their movements (i.e. Exclude-Strategy No-Cursor trials). To this end, we subtracted any biases from the final block of No-Cursor trials following aligned training from the first Exclude-Strategy No-Cursor trial, and determined whether this was significant from zero using a one-sample t-test (one-sided) for all experimental groups. To assess whether participants were using a compensatory strategy, we compared the first Include-Strategy No-Cursor trials and the first Exclude-Strategy No-Cursor trials, after accounting for baseline biases, using a repeated-measures t-test (one-sided) for all experimental groups.

To confirm that Within-Training No-Cursor trials do not include explicit strategies, we also compared whether errors during Within-Training No-Cursor trials differed from Exclude-Strategy No-Cursor trials. Using a repeated measures t-test (one-sided), we found no differences in the magnitude of reach aftereffects between the first Exclude-Strategy No-Cursor trial with the first Within-Training No-Cursor trial, in both the **Active Movement Sequence Experiment** and **Active Lead-In Sequence Experiment**.

The role of instruction

In this final set of analyses we set off to understand the role of explicit strategy in dual learning by comparing the results between the **Instruction Experiment** (Instructed group) and the **Static Visual Cue Experiment** (Uninstructed group). To confirm that participants in the **Instruction Experiment** were able to implement the strategy, we compared their first block of training to those from the **Static Visual Cue Experiment** using an Welch independent-measures t-test.

First, to assess whether any implicit learning occurs following training, we ran a 2 X 2 Mixed Repeated-Measures ANOVA comparing reach aftereffects across Pre-training No-Cursor tasks and Exclude-Strategy No-Cursor tasks between the Instructed and Non-instructed groups. A significant effect would indicate the presence of reach aftereffects even when participants are excluding strategy, suggesting the presence of an implicit learning mechanism.

Then, to examine the effect of instruction, we ran a 2 X 2 Mixed Repeated-Measures ANOVA comparing across Exclude-Strategy No-Cursor tasks and Include-Strategy No-Cursor tasks between the Instructed and Non-Instructed groups. If participants are aware and are using the instructed strategy, we would see a significant difference between Include-Strategy No-Cursor trials (in the expected directions) and Exclude-Strategy No-Cursor trials. Finally, this analysis will

be followed by planned comparisons within each group (Instructed and Non-instructed groups) to determine whether having instructions significantly affects the magnitude of reach aftereffects.

Results

To investigate the underlying mechanisms behind dual adaptation, we implemented various contextual cues, and in one case, provided detailed instructions on how to counter the perturbations given the contexts. In the **Active Movement Sequence** and **Active Lead-in Movement Sequence** experiments, participants made two-part and three-part reaches that cued the perturbations, respectively. In the **Passive Movement Consequence**, participants reached to a target and saw the target move to a secondary target whose location cued the perturbation. In the **Instruction Experiment**, participants were given a compensatory aiming strategy to dual adapt, while those in the **Static Visual Cue Experiment** were left uninstructed. Across all experiments, a leftward sequence (or visual location of the box) was indicative of a 30° CCW rotation, while a rightward sequence (or visual location of the box) was indicative of a 30° CW rotation.

Participants in the **Single CW-only and CCW-only control groups** exhibited typical visuomotor adaptation since they only encountered one perturbation, with large errors approximately the size of the rotation at the beginning of training that gradually reduced to baseline levels (Figure 3A), and rotation-dependent reach aftereffects (Figure 5A).

Visuomotor adaptation

Active movement sequence experiment

Participants made a two-part, active movement sequence involving a reach to the target disc followed by a secondary, visually-clamped reach to the target box. Figure 3B (green) shows the learning curves for **Active Movement Sequence Experiment**. We saw a small, significant reduction in reaching errors across training ($t(27) = 2.45$, $p = 0.01$). Distinct active sequences led

to significantly improved performance for both rotations as seen in Figure 4 (green bar). On average, participants significantly improved by a modest 16.25% across training ($t(27) = 1.86$, $p = 0.04$; Figure 4, green bar).

When we removed visual feedback of the cursor but kept the cues intact, we found significant reach aftereffects in their expected directions ($t(27) = 5.13$, $p < 0.001$; Figure 5B, exclude strategy). When asked to implement a compensatory strategy, participants do not change their reaching behaviour ($t(27) = -2.1942$, $p > 0.05$; Figure 5B, include strategy). These findings further support that active movement sequences can facilitate dual adaptation, but this compensation is largely implicit. This was further supported when we compared the size of reach aftereffects during Within-Training No-Cursor trials and Exclude-Strategy No-Cursor trials and found no difference ($t(27) = -1.0626$, $p > 0.05$). This suggests that participants do not implement any explicit strategies during Within-Training No-Cursor trials, nor by the end of full dual training (when we directly compare Exclude-Strategy and Include-Strategy reach aftereffects).

Figure 3. Visuomotor adaptation across training blocks. Colored translucent lines represent individual learning curves. A. Single CW- and CCW-only control groups. B. Active Movement Sequence Experiment. C. Passive Movement Consequence Experiment. D. Active Lead-in Sequence Experiment. E. Instructions Experiment. F. Static Visual Cue Experiment. Dashed lines represent the rotation magnitude. Error bars represent SEM.

Figure 4. Percent improvement across training for all experiments. Grey dots represent individual improvement scores. Positive values reflect improvement, and vice-versa. Error bars represent SEM.

403

404 *Figure 5. Reach aftereffects in post-training. Grey dots represent individual participant errors.*
 405 *Red bars represent CW errors and blue bars represent CCW errors. Dashed lines represent*
 406 *rotation magnitude experienced during training (30° CW and 30° CCW). A. Single CW- and*
 407 *CCW-only control groups. B. Active Movement Sequence Experiment. C. Passive Movement*
 408 *Consequence Experiment. D. Active Lead-in Sequence Experiment. E. Instructions Experiment.*
 409 *F. Static Visual Cue Experiment. Error bars represent SEM.*

410

411 *Passive movement consequence experiment*

412 In contrast to the **Active Movement Sequence Experiment**, in the **Passive Movement**

413 **Consequence Experiment** participants were required to reach to the target disc with a CW- or

CCW-rotated cursor, and then observe their target disc move towards the target box. Training performance is illustrated in Figure 3C (pink). This cue was insufficient at facilitating dual adaptation as evidenced by their large reaching errors that persist across training ($t(29) = 0.58$, $p > 0.05$). This cue did not lead to any improvement over training ($t(29) = 1.18$, $p > 0.05$; Figure 4, pink bar). Expectedly, reach aftereffects were not in the expected directions, and were not significant from baseline ($t(31) = 1.34$ $df = 31$, $p > 0.05$; Figure 5C). Furthermore, participants did not implement strategies in the correct directions ($t(31) = -0.39$, $p > 0.05$). Thus, merely viewing the movement sequence does not elicit dual adaptation.

Active lead-in sequence experiments

To explore whether a more complex sequence of movements can elicit dual learning, we had participants make a three-part movement sequence where the final portion of the reach was perturbed but the preceding motions were predictive of that perturbation. In the **Active Lead-in Sequence Experiment**, participants reached along an edge from the home position, back to the home position, and finally, to the target disc. This active, three-part sequence was able to elicit significant dual learning ($t(27) = 4.16$, $p < 0.001$; Figure 3D). On average, participants reduced their errors by 19.57%, and this improvement was significant from zero ($t(26) = 2.34$, $p = 0.01$; Figure 4, purple bar).

Reach aftereffects for the **Active Lead-in Sequence Experiment** were in the expected directions (Figure 5D). When asked to exclude any explicit strategy used, participants showed significant reach aftereffects in their expected directions, suggesting the involvement of an implicit mechanism ($t(29) = 2.23$, $p = 0.02$). Conversely, when asked to implement an aiming strategy, participants did not show any additional reach deviations in the expected directions as would be expected if they had used a strategy ($t(29) = -0.76$, $p > 0.05$).

The role of instruction in dual adaptation

To examine the explicit and implicit contributions to dual adaptation, we instructed a group about the nature of the perturbations and how to compensate for them given the contextual cue (**Instruction Experiment**) and compared their performance to a group who completed an identical task but were not provided any instruction (**Static Visual Cue Experiment**). In the **Static Visual Cue Experiment**, we eliminated any active or passive sequences; participants merely saw the box targets but only reached towards the target discs. Expectedly, reaching errors did not reduce across training ($t(10) = -1.81$, $p > 0.05$; Figure 3F). On average, percent improvement was -24.45% for those who only received a static cue, which suggests that not only did participants fail to adapt, they also performed worse over time (Figure 4, yellow bar).

Participants in the **Instruction Experiment** showed immediate benefits of strategy-use such that they made smaller errors right at the beginning of training. On average, those with instructions only had a 13.23° error in the first block of training, which is significantly smaller than that of the **Static Visual Cue Experiment** at 32.54° ($t(20.80) = 7.79$, $p < 0.001$). This advantage was fleeting, however, as participants in the **Instruction Experiment** do not further reduce their reaching errors across training ($t(11) = -1.78$, $p > 0.05$), suggesting that instruction benefits are immediate and are not moderated by more training (Figure 3E). Those in the **Instruction Experiment** did not show any improvement over time ($t(11) = -2.18$, $p > 0.05$). Indeed, their average reaching error by the end of training was only 18.41° , compensating for only about 38.64% of the rotation, implying that the role of instruction is limited and exerts most of its effects in the early stages of learning (Figure 3E).

Comparing No-Cursor trials across the **Instruction Experiment** (Figure 5E) and **Static Visual Cue Experiment** (Figure 5F), we found no implicit learning such that Exclude-Strategy

No-Cursor trials were no different from Pre-Training No-Cursor trials ($F(1,11) = 2.21, p > 0.05$). To probe the effect of instruction, we compared Exclude-Strategy and Include-Strategy No-Cursor trials between **Instruction** and **Static Visual Cue Experiments** and found that having instructions significantly elicits larger reach aftereffects in the expected directions ($F(1,11) = 10.72, p < 0.01$). Together, these findings suggest that when contextual cues convey no information, the motor system can instead rely on an explicit mechanism to support adaptation.

To assess whether explicit processes are engaged within *each* experimental group, we compared Include-Strategy No-Cursor trials with Exclude-Strategy No-Cursor trials for the instructed and non-instructed groups separately. For the **Instruction Experiment**, we found that explicit mechanisms are engaged such that Include-Strategy and Exclude-Strategy No-Cursor reaches significantly differed ($t(11) = 2.61, p = 0.01$; Figure 5E). Expectedly, we did not find the same for the **Static Visual Cue Experiment** ($t(10) = -0.98, p > 0.05$; Figure 5F). Together these findings suggest that when given an explicit compensatory strategy to dual adapt, the motor system likely relies on explicit processes exclusively.

Discussion

To better understand what allows for dual learning, we investigated various contextual cues including both actively-generated sequences and passive visual consequences. In a final experiment, we explicitly provided participants with a compensatory strategy. Across all these conditions, we teased apart the explicit and implicit mechanisms underlying dual adaptation by separating the influence of strategy. We found that active movement sequences, but not passive ones, facilitate dual adaptation. These simple active movement sequences were largely learned without awareness, since we found implicit but not explicit contributions in their reach aftereffects. Expectedly, static visual cues (a purely extrinsic cue), did not convey useful information to the

CNS, leading to interference. However, when given instructions about the rotations and their relationships to the static visual cues dual learning was able to proceed but only in the form explicit learning, evident in the lack of implicit reach aftereffects.

Active but not passive cues facilitate dual learning

Previous work on dual adaptation has largely demonstrated that motor-based or “intrinsic” cues tend to be more successful at reducing interference and facilitating learning (Ayala et al., 2015; Ayala & Henriques, 2018; Baldeo & Henriques, 2013; Galea & Miall, 2006; Schween et al., 2018; Wang & Musseler, 2014; Woolley, de Rugy, Carson, & Riek, 2011). We further explored this idea by investigating whether self-generated movement sequence cues, which are motor-based by nature, can facilitate dual adaptation. In both our **Active Movement Sequence** and **Active Lead-in Sequence Experiments** we found significant dual adaptation as evidenced by reduced reaching errors and significant reach aftereffects in the former experiment. Our findings support the force-field work by Howard and colleagues, who found that distinct follow-through motions can sufficiently cue the motor system to compensate for opposing force-field perturbations (Howard et al., 2015). Still, it was unclear if movement sequences needed to be self-generated in order to facilitate dual adaptation. To explore whether the *active* lead-in or *active* follow-through was the key component in this contextual cue, we removed that active component of the cue, as in the **Passive Movement Consequence Experiment**, and found no reduction in reaching errors or any reach aftereffects in the expected directions. This suggests that even dynamic visual cues—likely extrinsic like that used in the **Static Visual Cue Experiment**, are insufficient even when it is temporally linked as a consequence of the perturbed reach.

Research by Howard and colleagues also found that lead-in motions can be coupled with opposing force-fields to produce significant reach aftereffects (Howard et al., 2012). They found that in their most effective dwell condition that included a lead-in motion, participants were able to compensate up to 75% of the necessary force to overcome the perturbation. Here, we found that participants compensated for less than half the size of the rotation in the **Active Lead-in Sequence Experiment**. There are a few factors that may account for this. One key difference is the complexity of our lead-in cue—participants were asked to make a three-part motion in which the final reach was perturbed. So, not only did participants in the **Active Lead-in Sequence Experiment** have to access the past motion as a cue (second lead-in motion to the home position), they also had to go one step back to access the motion cue prior to that (first lead-in motion from the home position). Thus, one possibility is that cues that take longer to execute hampers its efficacy. Indeed, Howard and colleagues have found that a complex combination of lead-in and follow-through motion cues elicited dual adaptation to opposing force-fields, but only after intensive training across 5 days (Howard et al., 2015). Additionally, in a previous study of ours, we saw that doubling the training (from 360 to 720 trials) did not sufficiently induce greater improvement nor larger reach aftereffects (Ayala et al., 2015), so it's possible that this is the maximum level of dual adaptation for this specific cue. Thus, future work should investigate if, and to what extent, longer sequences elicit dual learning. An alternative and less prevalent account might be that certain cues are more effective at facilitating dual adaptation to more dynamic tasks (i.e. force-field perturbations), and less to visuomotor rotations like we saw in our present experiments. Together, these may account for a proportion of why we saw a smaller mean level of compensation compared to previous force-field work implementing similar cues.

Interestingly, knowledge about the perturbations alone does not seem to dictate whether dual adaptation will occur. While not reflected in *larger* Include-Strategy reach aftereffects, post-experimental interviews revealed that a large proportion of those in the **Active Lead-in Sequence Experiment** were aware of the perturbations. In fact, in the **Active Lead-in Sequence Experiment**, nearly 42% (13 out of 31) of participants were able to explain the nature of the perturbations and their relationships with the cues, compared to 8 out of 28 participants (28.57%) in the **Active Movement Sequence Experiment**. This didn't seem to lead to any advantage as both *active* experiments achieved a similar level of percentage improvement. For the experiments where dual adaptation did not occur, only one participant in the **Static Visual Cue Experiment** and an intriguing 8 out of 30 (26.67%) participants in the **Passive Movement Consequences Experiment** were able to explain the nature of the perturbations and their relationships to the cues. Thus, it seems that even with a sizeable portion of participants having knowledge about the nature of the perturbation, we still do not see significant strategy application. Possibly, insufficient cues might require the implementation of explicit aiming strategies to be successful.

Dual reach aftereffects are implicit by default

In our previous dual adaptation experiments, we collected reach aftereffects during No-Cursor trials without prompting participants that the rotations have been removed and thus, without any reminder to ignore any strategy they may have been implementing during training (Ayala et al., 2015; Ayala & Henriques, 2018; Baldeo & Henriques, 2013). To validate our previous findings, here we confirm that Within-Training reach aftereffects (i.e. following training but without prompt to exclude strategy) do not differ in magnitude compared to Exclude-Strategy reach aftereffects (i.e. following training but with instructions to exclude any

strategies) in both the **Active Lead-in Sequence Experiment** and **Active Movement Sequence Experiment**. This suggests that reach aftereffects from our previous experiments are likely due to implicit mechanisms and excludes any conscious aiming strategies. Thus, when reaching without visual feedback of the cursor, regardless of whether or not they are asked to, participants tend to disregard any strategies by default. Still, it's possible that this applies only for moderately effective cues, while stronger, more predictive cues such as workspace location (Baldeo & Henriques, 2013; Schween et al., 2018) are able to recruit not only implicit, but also explicit mechanisms.

Insufficient cues can be salvaged by aiming strategies

As expected, static visual cues did not show any predictive strength, so in addition we provided participants in the **Instruction Experiment** with aiming strategies that depended on that context. This implementation led to significant learning which suggests that when cues are insufficient (e.g. static visual cues), the CNS can tap into explicit mechanisms to support dual learning. This purely explicit learning, however, comes at a cost. We saw that those in the **Instruction Experiment** were able to immediately compensate by implementing the aiming strategy, but they failed to improve, only retaining a small portion of the aiming strategy by the end of the training session, and later reflected in the lack of implicit reach aftereffects. In contrast, using a strongly predictive cue of target workspace separation, Schween et al. (2018) nicely demonstrated significant implicit reach aftereffects in their group that received verbal instructions about how to counter their blocked 60° CW and CCW rotations (Schween et al., 2018) that were otherwise shown to interfere. Indeed, we found a similar effect whereby dual adaptation as cued by separated target sets were able to elicit reach aftereffects that decreased in size as a function of the distance between workspaces (Baldeo et al., 2013). Critically, we show

here that moderately predictive cues can indeed elicit implicit learning, but in the case of the **Static Visual Cue** and **Instruction Experiments**, an ineffective cue even in conjunction with aiming strategies will be unsuccessful.

Finally, it should be emphasized that our instructed participants are by proxy provided some explicit component of learning (i.e. through the aiming strategy), while those uninstructed groups (e.g. in Schween et al., (2018)) were able to derive it from visuomotor learning alone. In fact, their participants had relatively decent estimates of the rotations, estimating over half of the rotations' magnitudes in their explicit judgment task, while our explicit reach aftereffects in the **Instruction Experiment** only reached about a third of the size of our rotations. In light of these key differences, these findings bring up critical points that (1) explicit strategies can support dual learning but only to a limited extent, (2) potentially, that the mechanisms behind dual adaptation differ for smaller and larger rotations, and (3) the possible influence of rotation presentation schedules (pseudo-randomized trial-by-trial vs. alternating blocks of 8 trials per rotation).

Altogether our findings show that while intrinsic cues provide an avenue for the motor system to learn two or more visuomotor maps at the same time, it is single-handedly the underlying explicit mechanism that drives learning when the cues are insufficient. This has significant implications in short-term rehabilitation where time is constrained and the motor system must rely on explicit processes to re-learn multiple motor skills, so future studies should investigate how to enhance this explicit process so that learning can be retained over extended periods of time.

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