

Concurrent adaptation to opposing visuomotor rotations by varying hand and body postures

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Abstract When reaching towards objects, the human central nervous system (CNS) can actively compensate for two different perturbations simultaneously (dual adaptation), though this does not simply occur upon presentation. Dual adaptation is made more difficult when the desired trajectories and targets are identical and hence do not cue the impending perturbation. In cases like these, the CNS requires contextual cues in order to predict the dynamics of the environment. Not all cues are effective at facilitating dual adaptation. In two experiments, we investigated the efficacy of two contextual cues that are intrinsic to the CNS, namely hand as well as body posture in concurrently adapting to two opposing visuomotor rotations. For the hand posture experiment, we also look at the role of extended training. Participants reached manually to visual targets with their unseen hand represented by a cursor that was rotated either 30° clockwise or counterclockwise, determined randomly on each reach. Each rotation was associated with a distinct hand posture (a precision or power grip, respectively) in one experiment and a distinct body rotation (10° leftward or rightward turn of the seat, respectively, while fixating straight) in the second experiment. Critically, the targets (and thus, the required cursor trajectories) were identical in both rotations. We found that how people held the tool or oriented their body while

reaching is sufficient for concurrently adapting separate visuomotor mappings such that over time, reach errors significantly decrease. Extended practice did not lead to further benefits though. These findings suggest that when the required cursor movements are identical for different visuomotor mappings, dual adaptation is still possible given sufficient intrinsic contextual cues.

Keywords Motor learning · Dual adaptation · Visuomotor rotation · Reaching · Internal model · Cerebellum

Introduction

The ability to switch between tasks accurately and efficiently is an impressive human feat afforded by a flexible and adaptive motor system. We can manipulate a tool, correct for our movement errors as we use it, and anticipate the consequences of switching to a completely different tool or environment. Although we make errors when first reaching towards a desired target, our motor system allows us to adapt to the novel condition so that eventually we are able to produce smooth, accurate movements despite perturbations to the direction or visual feedback of movement.

When visuomotor adaptation occurs, the brain forms distinct “internal models”, in order to reliably predict the outcome of specific motor commands in that context and the sensory consequences of executing those commands (Wolpert and Ghahramani 2000). We can probe the ability of the central nervous system (CNS) to maintain and recall multiple internal models simultaneously by introducing variants of the same environment serially (i.e. ABA paradigm) or concurrently. While ABA designs typically investigate whether the learning of one internal model will be affected by the subsequent learning of another, concurrent

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designs allow us to see simultaneous learning, acquisition, and switching between two or more internal models (also known as “dual adaptation”). A typical example of a concurrent paradigm is a task in which participants make out-and-back reaches in alternating trials of clockwise-perturbed and counter clockwise-perturbed hand cursors, within the same experimental block. Often, adaptation to both visuomotor variants does not proceed when there is a lack of predictability regarding the impending perturbation from trial to trial. Indeed, this has been found in several studies that examine the successive adaptation to two or more perturbations in which the adaptation to one perturbation fully interferes with the acquisition of another (Brashers-Krug et al. 1996; Caithness et al. 2004; Donchin et al. 2003; Karniel and Mussa-Ivaldi 2002; Krakauer et al. 1999).

One theoretical model, the Modular Selection and Identification for Control (MOSAIC) theory, suggests that a contextual switching mechanism must exist in order to change between internal models of specific motor commands and sensory states. Thus, in order for dual adaptation to proceed, a specific contextual cue must be associated with each of the visuomotor variants experienced. This predictive cue provides information about the impending sensorimotor mapping via responsibility predictors that add greater weighting on the probability of encountering one of the perturbed environments over the others (Haruno et al. 2001; Kawato 1999). Here, we use the dual adaptation task but adopt a broader definition of visuomotor adaptation to include both implicit and explicit processes, yet we did not inform subjects about the nature of the opposing perturbations. Thus, our findings implicate the efficacy of certain cues on overall concurrent visuomotor adjustment to distinct sensorimotor contexts.

Not every cue can sufficiently facilitate dual adaptation. When contextual cues are insufficient or unavailable, the CNS is unable to predict the sensorimotor consequences of the impending visuomotor perturbation. While theoretical models provide us with a mechanism for understanding how humans are able to dually adapt, they do not inform us on what qualifies as an effective contextual cue or the actual cues themselves. Here, we examine whether contextual cues that tend to be motor-based (e.g. hand and body posture) are sufficient for facilitating dual adaptation despite identical desired cursor trajectories (i.e. using identical target sets), as well as the role of extended training.

What qualifies a contextual cue to be an effective facilitator of dual adaptation? One possible property might be the visual features of the target or hand cursor. Extrinsic contextual cues refer to cues that are not motor-based, such as target or background colour. Dual adaptation as facilitated by extrinsic cues has been found to occur (Krouchev and Kalaska 2003; Osu et al. 2004), or not occur (Baldeo

and Henriques 2013; Gupta and Ashe 2007; Hegele and Heuer 2010; Hinder et al. 2008; Hirashima and Nozaki 2012; Woolley et al. 2007). One study by Gupta and Ashe (2007) had participants concurrently adapt to two opposing, velocity-dependent force fields with each perturbation associated with a colour cue, an external, non-motor-based property of a context, with the same set of visual targets and found no evidence for dual adaptation. Likewise, Woolley and colleagues used background colour as a predictive cue but found no evidence for dual adaptation while training with opposing visuomotor rotations when there is an overlap in the visual workspace (Hinder et al. 2008; Woolley et al. 2007). Baldeo and Henriques (2013) integrated target and cursor colour as predictive visual cues and found that it still does not facilitate dual adaptation. Interestingly, using a more explicit approach with colour cues to facilitate dual adaptation, Osu et al. (2004) found that participants were able to dual adapt to opposing force-field perturbations after distributed training over two consecutive days although these results may have been influenced by enhanced consolidation. Thus, while dual adaptation is difficult to achieve with extrinsic cues on shorter timescales, Osu and colleagues suggest that perhaps extended practice may allow for significant learning.

In contrast to extrinsic cues, intrinsic or motor-based cues involving distinct muscle recruitment patterns, change in the end-effector, or previous behavioural context have shown to be more promising in facilitating dual adaptation (Baldeo and Henriques 2013; Galea and Miall 2006; Gandolfo et al. 1996; Wang and Musseler 2014; Woolley et al. 2011). This may be due to the idea that the generalization of motor learning depends on context, which is determined based on the history of the prior movement of that end-effector (Baraduc and Wolpert 2002; Krakauer et al. 2006). Indeed, Krakauer et al. (2000) initially demonstrated that when adapting to visuomotor rotations, the extent by which this adaptation generalizes depends on the proximity of the novel target direction compared with the trained direction. Baraduc and Wolpert (2002) further showed that even when the target or hand path direction is identical, reach after-effects (and thus, generalization) become smaller when reaches are made with increasingly different arm postures than the one used during training with a visuomotor rotation (i.e. as the upper arm becomes more adducted relative to the arm posture used during training). Likewise, Krakauer et al. (2006) suggested that using different effectors can function as intrinsic contextual cues for retrieving specific internal models. In this ABA study (serial adaptation blocks to opposing perturbations), participants made pointing movements with a rotated cursor using either their arm (shoulder and elbow) or wrists. When both body parts were serially exposed to opposite cursor rotations,

there was no interference between the effectors, but when exposed to the same rotation, the wrist benefitted from the previous adaptation of the arm, although not vice versa. Thus, distinct association with the context, in this case different arm segments, reduces the likelihood of interference and allows the CNS to dissociate between different adaptive states. Likewise, Gandolfo et al. (1996) used a block-wise concurrent design (switch hand posture every 48 movements) that showed that associating a specific hand grasp posture with each of two opposing force-field perturbations allowed for dual adaptation to identical target sets across perturbations. Participants were able to compensate for these opposing perturbations and produced after-effects consistent with the type of grip and the associated perturbation (Gandolfo et al. 1996). However, when participants instead change their thumb position (i.e. vertical or horizontal) as a cue, no adaptation or after-effects were found. In sum, they were only able to elicit dual adaptation to opposing force fields by changing the joint angles and joint torques associated with each perturbation. This study indicates that grasp posture that ultimately leads to differences in joint angles and torques facilitate dual adaptation, which is supported by a study showing that even an illusory grasp that indicated whether the robot was gripped by the end-effector (or not) can also facilitate dual adaptation (Cothros et al. 2009). To test the hypothesis of whether eliciting distinct muscle recruitment patterns are able to cue the retrieval of learned adaptive states, we used a concurrent paradigm in which we associated distinct hand and body postures as predictive cues for opposing visuomotor rotations.

Not surprisingly, when hand path trajectories overlap, dual adaptation may proceed at a slower rate and require more training than adaptation to a single perturbation. This is evidenced by a less steep learning curve for adaptation to reaches that required completely overlapping hand paths compared to when the required hand path overlapped partially or not at all (Baldeo and Henriques 2013; Wang and Musseler 2014; Woolley et al. 2011). While reaching with distinct hand path trajectories requires distinct motor programming, planning movement with identical or overlapping trajectories is more ambiguous to the CNS and requires context to dissociate between associated internal models. Indeed, Hirashima and Nozaki (2012) showed that multiple environments (e.g. opposing force fields) can be learned simultaneously for physically identical movements if each is associated with a distinct motor plan. As with the studies on posture cues, this work using different and overlapping trajectories also suggests that dual adaptation benefits from having different motor plans associated with each of multiple perturbations, and this might be facilitated through the enhancement of the association between the cues and internal models.

In sum, not all motor-based cues are adequate sources of contextual information for facilitating concurrent motor learning. When desired cursor trajectories overlap in cases where reach targets are similar or identical, contextual cues and extended training need to be employed in order for multiple adaptations to proceed. Here, we expand on previous findings to show that the way in which the hand and body are configured can allow for concurrent learning of opposing rotations despite overlapping desired cursor motion. Our first objective is to determine whether participants can dually adapt to opposing visuomotor rotations with the same desired cursor trajectory when only cued by intrinsic cues including minor changes in hand or body and limb posture. Our second objective is to explore the effect of extended training on adapting to two opposing visuomotor rotations. In the experiment using hand posture as a cue, we gave participants double the amount of training to increase practice with learned associations between context and visuomotor mapping.

Methods

Participants

Seventy-eight right-handed participants (57 females, mean age 20.48, ranging from 17 to 34 years) with normal or corrected-to-normal vision were recruited and participated in exchange for a bonus credit in an undergraduate psychology course. Participants provided written consent in accordance with York University's Human Participants Review Committee and were subsequently assigned to either the single or dual visuomotor distortion group prior to the experiment.

Apparatus

Participants were seated on an adjustable chair facing a digitizing tablet (Wacom Intuos3, 12" × 12" surface, resolution of 5080 lines/in., sampled at 50 Hz). The chair was adjusted so that the tablet was at waist level, allowing for hand movements along the horizontal plane (see Fig. 1a). An Epson 3LCD projector rear-projected an image onto a screen located approximately 60 cm from the tablet work space. An opaque shield occluded the participant's view of their hand (Cf. Baldeo and Henriques 2013; Balitsky Thompson and Henriques 2010; Dionne and Henriques 2008). Participants reached to targets, which were 1.5 cm in diameter, by moving the stylus across the surface of the tablet which moved a cursor (1 cm in diameter) that was projected on the screen. The corners of the screen were masked and replaced with a circle-shaped edge so as to discourage participants from using the screen corners as cues

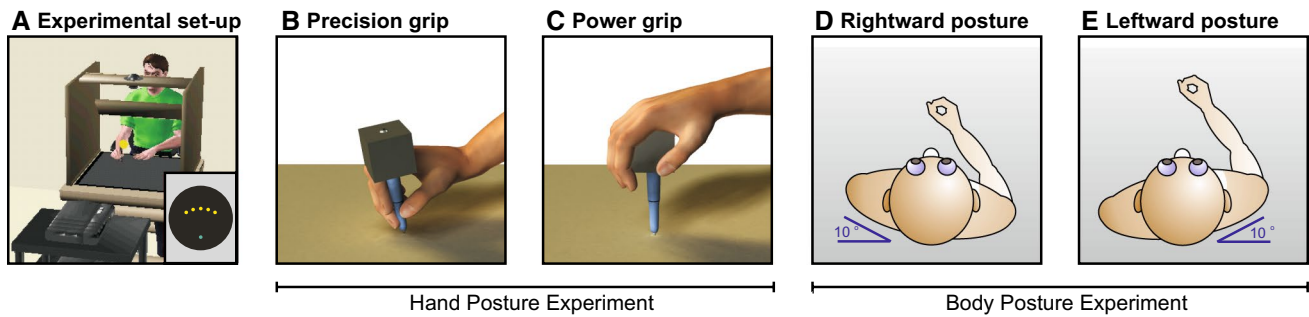


Fig. 1 **a** Experimental apparatus and target display. Stimuli were projected onto the vertical screen by a projector located approximately 60 cm behind the screen. Participants reached towards targets using a stylus on a digitizing tablet along the horizontal plane while viewing a projected image of the targets and visual feedback of their hand on a circular, vertical screen. An opaque chipboard occluded visual feedback of the participants' hands during the task. *Inset* The home position was depicted as a *green disc*, and the par-

ticipant's hand was depicted as a *white disc*. The *yellow discs* depict all five possible locations of the target. The equipment was calibrated so that the hand–cursor ratio was approximately 1:1. **b** Hand posture “BOTTOM” or “precision” grip, associated with a CCW rotation, **c** Hand posture “TOP” or “power” grip, associated with a CW rotation. **d** Body posture with a rightward 10° body rotation, associated with a CCW rotation, **e** Body posture with a leftward 10° body rotation, associated with a CW rotation (colour figure online)

(see Fig. 1a, inset). Reaching movements were made to one of five radially spaced targets (located at 60°, 75°, 90°, 105°, 120°), always starting at a common origin located 12 cm away. The hand–cursor relationship was similar to using a desktop computer so that movements were made with a 1:1 ratio.

General procedure

In the first experiment (hereafter referred to as the hand posture experiment), we examined the role of hand posture and extended training in facilitating dual adaptation. In the second experiment (hereafter referred to as the body posture experiment), we investigated whether the direction of body rotations 10° to the left or right was a sufficient contextual cue for dual adaptation. Participants were asked to make smooth and direct out-and-back reaches toward individually presented targets located 12 cm away. Targets appeared in one of the five locations, in a pseudo-randomized order (i.e. each target appeared once before appearing again). During trials with visual feedback of the hand cursor (closed-loop trials), reaches were complete when participants overlapped the hand cursor with the visible target. During trials without visual feedback of the hand cursor (open-loop trials), participants estimated the location by reaching towards the visible target, remaining stationary for 500 ms until the target disappeared. While returning to the home position, participants' hand remained unseen so they were instead shown a smiley-face that changed orientation roughly relative to the direction of the cursor, as a guide to help their return movement. In addition, visual feedback of the hand cursor became available within a 2 cm radius around the home position. A cardboard edge located just below the home position aided

participants with returning to the home position in order to proceed to the next trial.

For both experiments, participants completed pre-training, training, and post-training sessions (see Fig. 2a, b). During training, participants in the single distortion group experienced only one 30° rotation (either CW or CCW), whereas those in the dual distortion group experienced both opposing rotations. In the hand posture experiment, we refer to the single distortion training as SINGLE, the dual distortion group with DUAL1 for the first training set and DUAL2 for the additional second training set. Because we did not examine extended training in the body posture experiment, the two training sets were simply SINGLE and DUAL training. Participants assigned to the single distortion training finished the task in approximately 1 h, whereas those assigned to the dual distortion training finished within approximately 2 h.

Hand posture experiment

Pre-training (baseline measures)

Thirty-seven participants completed the hand posture experiment, with 14 assigned to the DUAL training set, nine to the SINGLE CW training set, and 13 to the SINGLE CCW training set. During pre-training, participants in both groups were asked to perform arm reaches towards the targets with an aligned cursor. The purpose of pre-training was to capture baseline performance in addition to familiarizing participants with the task. Participants in both groups completed 50 reaches with an aligned cursor during closed-loop pre-training trials (first box in Fig. 2a, b) followed by 30 open-loop trials to record baseline after-effects (second box). Prior to every trial, participants were

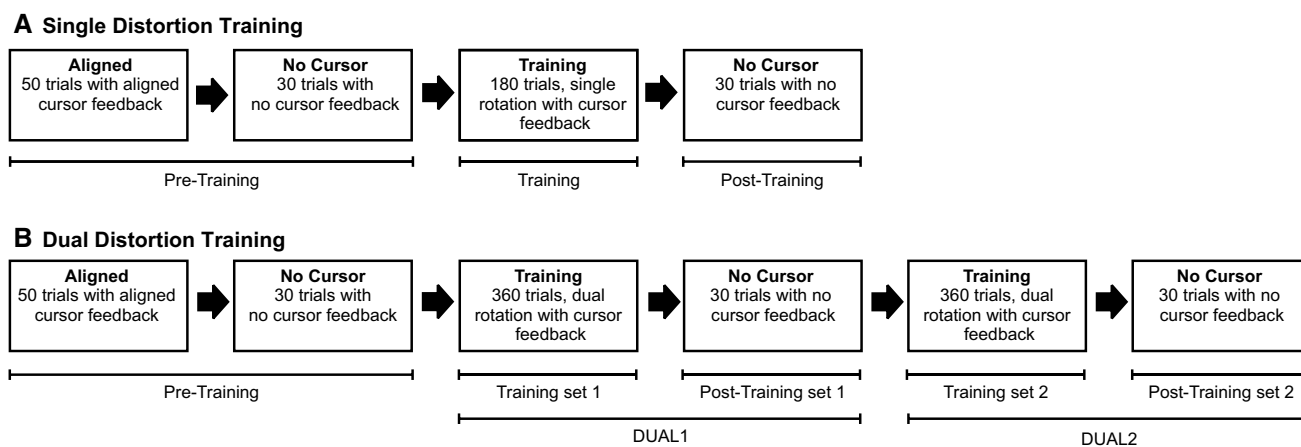


Fig. 2 Sequence of sessions for **a** single distortion training and **b** dual distortion training. In both experiments, the single distortion group (SINGLE) only completed trials under either a 30° clockwise (CW) or counterclockwise (CCW) rotation, but not both. In the hand posture experiment only, the dual distortion group completed a total of 720 interleaved training trials (DUAL1 and DUAL2) under both

30° CW (360 trials) and CCW (360 trials) rotations. In the body posture experiment, the dual distortion group completed only the DUAL1 sequence (i.e. no extended training) with a total of 360 interleaved training trials under both 30° CW (180 trials) and CCW (180 trials)

presented with the word “TOP” when they had to hold the stylus by the foam square attached to the top of the stylus using a power grip (Fig. 1b) or “BOTTOM” to hold the stylus like a pen using a precision grip (Fig. 1c). After every trial, participants placed the stylus back on the penholder located approximately 10 cm from the home position. During pre-training, half of the trials prompted participants to hold the stylus in a TOP posture and the remaining half in a BOTTOM posture.

Training (adaptation measures)

SINGLE distortion group The objective of the training sessions was to expose the participants to a single visuomotor rotation so as to capture an “ideal” learning rate and resulting after-effects from which to compare our dual groups. The task was to make arm reaches towards the target while experiencing a 30° CW (when using a power grip) or CCW (when using a precision grip) visuomotor rotation of the hand cursor. Throughout the whole experiment, participants in the SINGLE distortion training were required to hold the stylus with only one hand posture depending on which rotation they were assigned participants completed 180 trials with their designated rotation (third box in Fig. 2a) followed by 30 open-loop trials (fourth box in Fig. 2a). The purpose of the open-loop trials was to assess after-effects as a result of training with a misaligned cursor. Besides warning the participants that the cursor would not be visible, we did not provide further information (i.e. that the perturbation was also off or what strategy to use) to maintain naivety. A recent study by van Werner et al. (2015) suggests that either instructing participant to use or not use a learned

strategy produce equivalent after-effects for those participants that were not initially told about the specifics of the rotation (“implicit” group). Thus, we believe that our minimal instruction for the no-cursor task in our experiment provides a valid measure of implicit learning.

DUAL distortion group First training set (adaptation measures) and post-training (after-effects): participants in the dual distortion group were exposed to both 30° CW and CCW rotations during two training sets. Half of the trials had a CCW-rotated cursor (required reaching with a precision grip) and the remaining half had a CW-rotated cursor (required reaching with a power grip) in pseudo-randomized order. In between trials, participants were prompted with a screen that said either “TOP” or “BOTTOM” to indicate which posture to take. Target locations appeared in a pseudo-randomized order per cursor rotation. Participants completed 360 dual distortion trials followed by 30 open-loop trials to test for after-effects (third and fourth boxes in Fig. 2b). Critically, participants were also prompted to hold the stylus in the “TOP” or “BOTTOM” position during open-loop trials in order to examine whether posture-specific after-effects manifest, although again, they were not explicitly told that the rotation had been removed.

Second training set (extended adaptation) and post-training (after-effects): the purpose of the second training set was to determine whether extended DUAL training with misaligned cursor rotations lead to greater adaptation and reduction in reach errors over time. Participants in the DUAL distortion group completed an additional 360 trials followed by an additional 30 open-loop trials to assess after-effects (fifth and sixth boxes in Fig. 2b).

Body posture experiment

Forty-one participants completed the body posture experiment, with 17 assigned to the DUAL training set, 14 to the SINGLE CW training set, and 10 to the SINGLE CCW training set. The task and experimental procedures were identical to that of the hand posture experiment except for the cue implemented. Here, participants turned the seat to the left or right position with their legs, while always keeping their head facing forward. The body rotations were cued on the screen by a leftward or rightward arrow, indicating a leftward- and rightward-rotated body orientation, respectively. A metal stopper stopped the swiveling of the seat when the participant has fully turned 10° to the cued direction using their feet (either to the left or right) while keeping the head directed forward. The purpose of the second experiment was to examine whether the direction of a whole-body rotation, and thus the resulting change in the location of the shoulder and limb posture, is sufficient in facilitating dual adaptation. Like the hand posture experiment, distinct intrinsic cues (i.e. direction of body rotation) were associated with opposing visuomotor rotations. Like the hand posture experiment, participants completed pre-training followed by 30 open-loop trials and training followed by 30 open-loop trials. During pre-training, participants were prompted to turn their seat to the left in half of the trials and to turn right in the remaining half.

The magnitude of the visuomotor rotations and target locations were the same as in the hand posture experiment. The order of the tasks, as illustrated in Fig. 2a, b, also remained the same.

SINGLE distortion group During misaligned training, participants assigned to the SINGLE distortion group completed 180 trials with either a CW- or CCW-rotated cursor but not both, in the SINGLE body orientation associated with that cursor rotation followed by 30 open-loop trials in the same body orientation (third and fourth boxes, Fig. 2a). Again, results of the SINGLE group served as a baseline for the results for the DUAL group.

DUAL distortion group As in the DUAL distortion groups in the hand posture experiment, participants in the DUAL distortion group in the body posture experiment were exposed to both 30° CW and CCW rotations during training. Half of the trials had a CCW-rotated cursor, when the body was turned right (indicated by a rightward arrow), and the remaining half had a CW-rotated cursor, when the body was turned left (indicated by the leftward arrow), again in pseudo-random order (third box in Fig. 2b). Again, training was followed by 30 open-loop trials in which participants were prompted with a leftward or rightward arrow so as to examine context-specific after-effects (fourth box).

Data analysis

The hand cursor data were digitally smoothed using a first-order, low-pass Butterworth filter with a frequency cut-off of 2.5 Hz. Movement onset was set as the time at which 10 % of peak velocity was reached. Reach adaptation to a visuomotor rotation can be examined using several dependent measures that reflect hand path deviation. In the following experiments, we used ‘angular error at maximum velocity’ as the target measure of hand path deviation. ‘Angular error at maximum velocity’ refers to the angular difference between the target and the cursor relative to home position at peak velocity and represents feed-forward movement planning, making it unlikely that participants are actively making corrections in this phase. As participants adapt to the visuomotor rotation, we expect the angular deviation of the cursor at peak velocity to decrease such that cursor-to-target reach trajectories straighten over time. Angle at peak velocity was acquired at approximately one-third of the movement duration across all groups and rotations (Fig. 3). Angular reach errors were separated by rotation and blocked into groups of five trials to allow for a full cycle presentation of the five different target locations.

Hand posture experiment

To rule out whether the direction of cursor rotation (and the accompanying hand posture) affected the results, we flipped the sign of the angular reach errors for the CCW rotation and compared these normalized errors along with the two other factors, TRAINING SESSION (SINGLE, DUAL1, and DUAL2) and BLOCK (initial and final). We found no significant effect of or interaction with ROTATION as a factor (two-way ANOVAs; all $p > 0.05$). Hence, for further analysis, we collapsed the normalized errors across the two rotations and performed a 3 (training session) \times 2 (block) way mixed analysis of variance (ANOVA). One participant was excluded as their angular deviations during training were >2 standard deviations from the mean. Adaptation was assessed by comparing the initial and final blocks of training using a paired t test for each group (Bonferroni-corrected). Additionally, we compared the angular errors for the final block of trials across the three training sets (SINGLE, DUAL1 and DUAL2) using a one-way ANOVA followed by independent t tests to assess differences between groups (Bonferroni-corrected).

To assess improvement across the initial and final blocks between groups, we quantified a measure called “per cent improvement” which was defined as the difference between the mean angular errors during the initial block and final blocks, divided by the mean angular error for the initial block per participant (c.f. Baldeo and Henriques 2013). We used a one-way ANOVA model to compare the mean

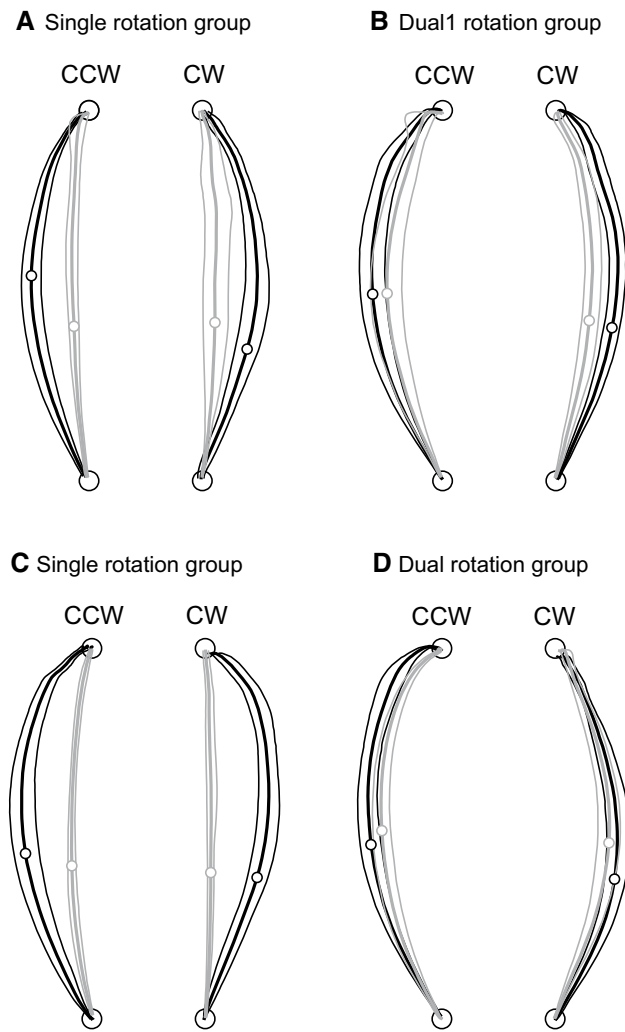


Fig. 3 Average hand trajectories between the SINGLE and DUAL1 groups and rotations collapsed across all target locations. Mean hand paths for the **a** SINGLE and **b** DUAL groups of the hand posture experiment. Mean hand paths for the **c** SINGLE and **d** DUAL groups of the body posture experiment. Mean paths for the first five trials are depicted in *black* and last five trials in *grey*. The *top black discs* represent the target while the lower black disc represents the home position. The mean (*central solid line*), 95 % confidence limits (*two thin bordering lines*), and point at peak velocity (*black disc*) are plotted across all participants for each group and rotation. For the hand posture experiment, as a proportion of movement duration, angle at peak velocity occurs on average at 0.28 for the SINGLE groups and 0.29 for the DUAL group during the first block, and 0.34 for the SINGLE group and 0.32 for the DUAL group during the final block. For the body posture experiment, as a proportion of movement duration, angle at peak velocity occurs on average at 0.26 for the SINGLE groups and 0.25 for the DUAL group during the first block, and 0.37 for the SINGLE group and 0.35 for the DUAL group during the final block (colour figure online)

per cent improvement collapsed across the rotations for all three training sets (SINGLE, DUAL1 and DUAL2) followed by multiple post hoc comparisons with Bonferroni correction. In order to test whether a second

training session (DUAL2) with the opposing distortions lead to greater reduction in errors (greater learning) for the DUAL2 training session, we assessed percentage improvement relative to the initial block of errors in the first training set (DUAL1).

We assessed after-effects during post-training by comparing the mean angular reach errors of the first block of five trials relative to performance on open-loop trials during pre-training to examine context-dependent errors. We did not collapse the after-effects across rotations because we found that they are significantly different and instead performed separate one-way mixed ANOVA for the two hand postures to compare after-effects following SINGLE, DUAL1 and DUAL2 training. Follow-up, paired *t* tests with Bonferroni correction revealed which groups had significant after-effects.

Body posture experiment

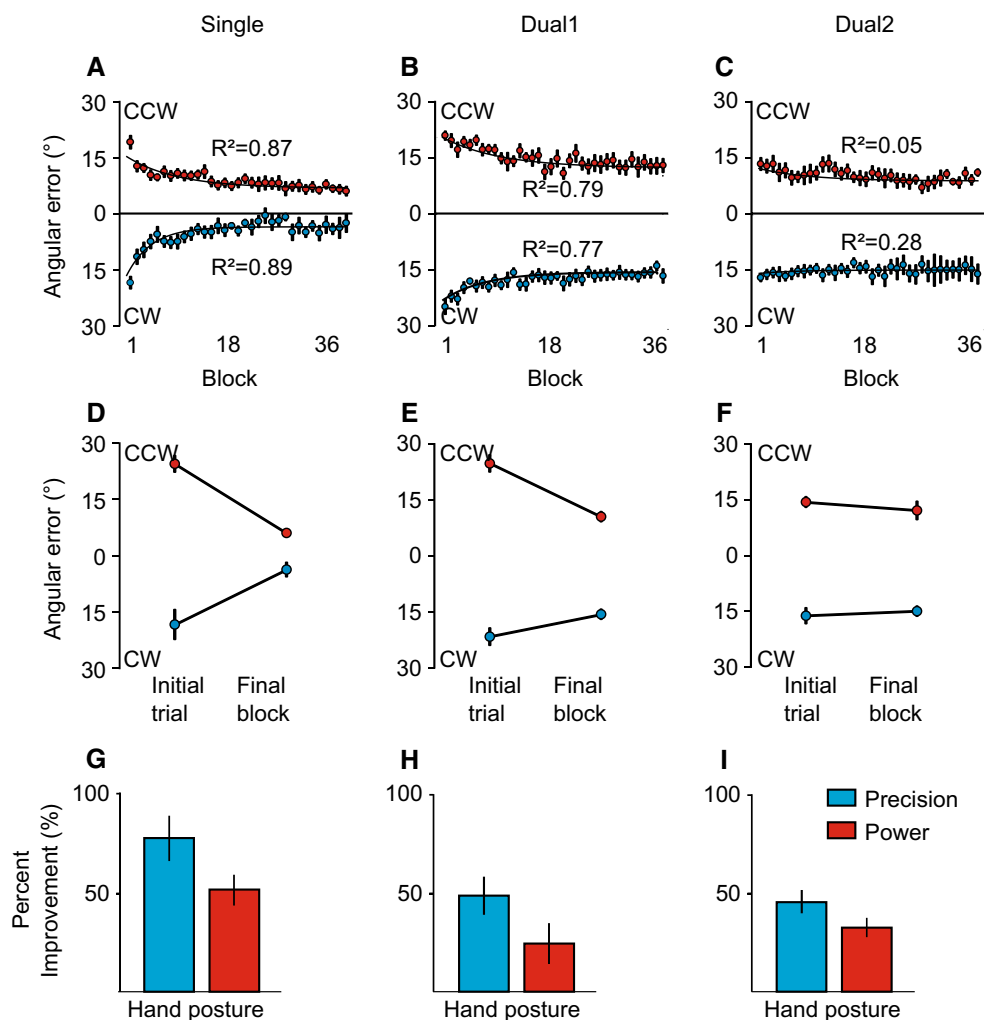
Like the hand posture experiment, we first explored whether body orientation significantly affected angular reach error during training. Since body orientation did not significantly interact with reach errors for either the SINGLE groups ($F(1,23) = 0.531, p = 0.474$) nor the dual group ($F(1,16) = 2.284, p = 0.150$), we collapsed the data across the two rotations (CW and CCW) for all groups. We compared angular reach errors between SINGLE and DUAL groups using a 2 (GROUP \times 2) (BLOCK) mixed ANOVA to determine the efficacy of body rotation direction as cues in facilitating dual adaptation. Additionally, we compared per cent improvement between SINGLE and DUAL groups using an independent samples *t* test. Lastly, to assess after-effects, we first examined whether the context (i.e. body rotation) elicited a rotation-dependent reach error. Again, since the direction of the body did not significantly affect adaptation for either the SINGLE groups ($t(23) = 0.331, p = 0.744$) nor dual group ($t(16) = 0.196, p = 0.847$), we collapsed these measures across the postures. Finally, we used an independent samples *t* test to compare after-effects between the SINGLE and DUAL groups.

To further quantify and illustrate the change in reaching errors across training, we fitted a single exponential function to both datasets across all blocks (of 5 trials) of training and averaged across participants, for each rotation and group using VEEL (<http://veel.sourceforge.net/>). The equation takes the form of $RD = be^{(-ax)} + c$ where x represents the block number, a the rate of learning, c the asymptotic level of performance, and b the scaling factor. The exponential fit changed in sign depending on the rotation (CW or CCW).

Finally, we analysed the efficacy of the cues between experiments by comparing per cent improvement in the

Fig. 4 Angular reach error across blocks during training for the hand posture experiment.

a–c The top row of plots depicts angular reach errors across blocks (of 5 trials) during training. Thin black lines represent fitted exponential curves for reach deviations for the entire training session with the equation $RD = be^{-ax} + c$. SINGLE CCW ($7.98e^{-0.20x} + 8.18$), SINGLE CW ($11.27e^{-0.61x} + 7.15$), DUAL CCW T1 ($7.50e^{-0.08x} + 15.43$), DUAL CW T1 ($8.32e^{-0.06x} + 13.36$), DUAL CCW T2 ($1.76e^{-0.11x} + 14.43$), and DUAL CW T2 ($3.53e^{-0.03x} + 9.73$). **d–f** The bottom row of plots depicts mean angular reach error across the initial trial and the final block for each group. Blue circles indicate reach errors during precision grip trials while red circles indicate reach errors during power grip trials. **g–i** Per cent improvement for the hand posture experiment for the SINGLE, DUAL1, and DUAL2 training sets. Blue bars represent percentage improvement for precision grip trials, while red bars represent percentage improvement for power grip trials. Error bars represent SEM (colour figure online)



DUAL groups using an independent samples *t* test. The assumed level of significance was $p < 0.05$ for all analyses.

Results

Hand posture experiment

Mean hand path trajectories in Fig. 3 illustrate that both groups exhibited large rotation-dependent errors at the initial stage of training (black lines depicting the mean path of the first 5 trials), angular deviations reduced over time as evidenced by a rapid decline towards pre-training levels (grey lines depicting the mean path of the last 5 trials). Figure 4 shows hand posture-dependent reach errors for blocks of five trials per rotation for the SINGLE rotation groups, DUAL rotation training set 1, and DUAL rotation training set 2 across the training session. The exponential fits to the blocked mean reaching errors shown in green dashed lines resemble the exponential curve typically associated with motor learning although to a lesser extent for

the second set of training blocks for the DUAL groups (Krakauer et al. 2000). In general, exponential fits appear less steep in the DUAL groups with values ranging from -0.03 to -0.11 , compared to those of the SINGLE groups with values of 0.20 and -0.61 .

In order to assess adaptation for the DUAL and SINGLE groups, we compared the mean angular reach errors across the initial trial and final block (Fig. 4, second row). We found that the errors during the final block of trials were significantly less deviated than those of the initial ($F(1, 72) = 37.61, p < 0.001$), but this change varied between groups ($F(2, 72) = 5.87, p < 0.005$). Both SINGLE ($t(22) = 7.42, p = 0.000$, one-tailed, $\alpha = 0.016$) and DUAL1 ($t(25) = 2.492, p = 0.010$, one-tailed, $\alpha = 0.016$) show smaller errors in the final block compared to the initial block. Likewise, we found a significant drop in errors when comparing the initial block in DUAL1 with the final block in DUAL2 ($F(1, 12) = 15.528; p < 0.005$). However, since reaching errors were smaller at the start of DUAL2 as a result of training in DUAL1, we found no further significant change in errors at the final block for the second

set of training compared to initial trial in DUAL2, as can be seen Fig. 4f ($p > 0.05$). The reach errors in final block of training for both DUAL1 and DUAL2 were nonetheless significantly larger than that of the SINGLE groups suggesting that neither DUAL sets achieved the same extent of error reduction as the SINGLE group ($t(47) = -4.961$; $p < 0.001$; $t(47) = -4.337$; $p < 0.001$, respectively). Together, these results suggest that associating distinct postures with each opposing rotation is sufficient in facilitating concurrent adaptation although not by far to the same extent as learning under a single perturbation.

Per cent improvement To better compare adaptation levels across the groups, we calculated percentage improvement across the initial and final block relative to each participant's initial performance on the first block of training, as plotted in Fig. 4, third row. Per cent improvement in the dual distortion training set (DUAL2) was calculated relative to initial performance during training set 1. Thus, larger percentages indicate greater learning. Although Fig. 4g–i suggests that the percentage improvement was slightly smaller for precision grip trials (CCW-rotated cursors) compared to power grip trials (CW-rotated cursors), we found no significant difference between the two hand postures. More importantly, per cent improvement differed significantly between groups ($F(2,72) = 3.248$; $p < 0.05$). Follow-up analyses revealed that percentage improvement for the SINGLE training set was significantly larger than that of the DUAL1 training set ($t(47) = 2.417$; $p < 0.033$) but not DUAL2 ($t(47) = 2.107$; $p > 0.033$). The absence of a difference between SINGLE and DUAL2 training suggests that although there was not a significant reduction in reach errors within the second set of DUAL training, there was enough of a reduction that the overall percentage improvement across both DUAL1 and DUAL2 (i.e. double the training) approached that of the SINGLE group.

After-effects An additional measure for motor learning is to determine whether participants continue to make deviated movements when reaching without visual feedback of the hand cursor following context-dependent adaptation. Figure 5 shows the after-effects produced between the three training sets, with the SINGLE group showing model after-effects produced as a result of complete visuomotor adaptation. Indeed, we found significant after-effects in the direction of distortion depending on the hand posture, not only in the SINGLE group ($F(1, 21) = 123.23$, $p < 0.001$), but also for the DUAL group ($F(1,24) = 21.29$, $p < 0.001$) when comparing no-cursor reaches pre- and post-training. The after-effects also varied with direction of distortion for the SINGLE group, with the precision grip trials showing slightly larger deviations than that of power grip trials ($F(1,21) = 7.25$, $p = 0.014$). After-effects did not vary with the direction of distortion for the DUAL group ($F(1, 24) = 0.614$, $p > 0.05$). Furthermore, we found that

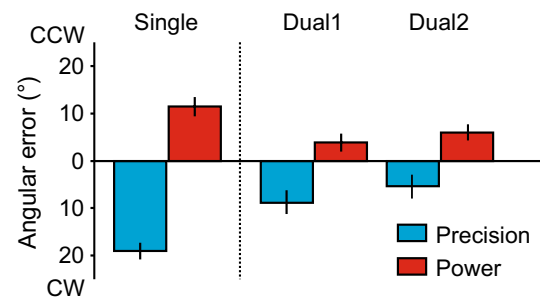


Fig. 5 After-effects for the hand posture experiment. *Blue bars* represent after-effects for precision grip trials while *red bars* represent after-effects for power grip trials. *Error bars* represent SEM (colour figure online)

the after-effects for both DUAL1 and DUAL2 were significantly smaller (and about half the size), than those of the SINGLE training set ($p < 0.01$), but not significantly different from each other ($p = 0.650$). Although we saw significant context-dependent after-effects in the DUAL training sets, they are not as large as that of the SINGLE group nor do they approach its magnitude despite extended training.

Body posture experiment

Visuomotor adaptation and per cent improvement As expected, both SINGLE and DUAL groups initially made large reaching errors as a result of the visuomotor perturbation followed by a decrease in error over time as adaptation progressed (see Fig. 3c, d for mean hand path trajectories). As shown in Fig. 6a, b, participants from both the SINGLE and DUAL groups were able to significantly decrease their reaching errors between the initial block and final block ($F(1,40) = 89.70$, $p < 0.001$), but this change varied between groups ($F(1,40) = 31.306$, $p < 0.001$). A comparison of the final block of five trials between the SINGLE and DUAL groups showed that the SINGLE group had significantly lower mean angular deviations than that of the DUAL group by the end of training ($t(40) = 11.12$, $p < 0.001$). Additionally, per cent improvement from the initial trial to the final block was found to be significantly different between DUAL and SINGLE groups ($t(40) = -7.732$, $p < 0.001$) although both show significant improvement (see Fig. 6e, f). These findings suggest that body rotations, which produce distinct body postures and shoulder positions, can efficiently cue a previous adaptive state, such that two perturbations can be learned concurrently by the CNS but not to the same extent as learning under a single perturbation.

After-effects As with hand posture as a cue, after-effects appear in the direction depending on the cue (leftward or rightward body posture). Figure 7 illustrates the magnitude of after-effects produced between the two groups, with the SINGLE group showing model after-effects that

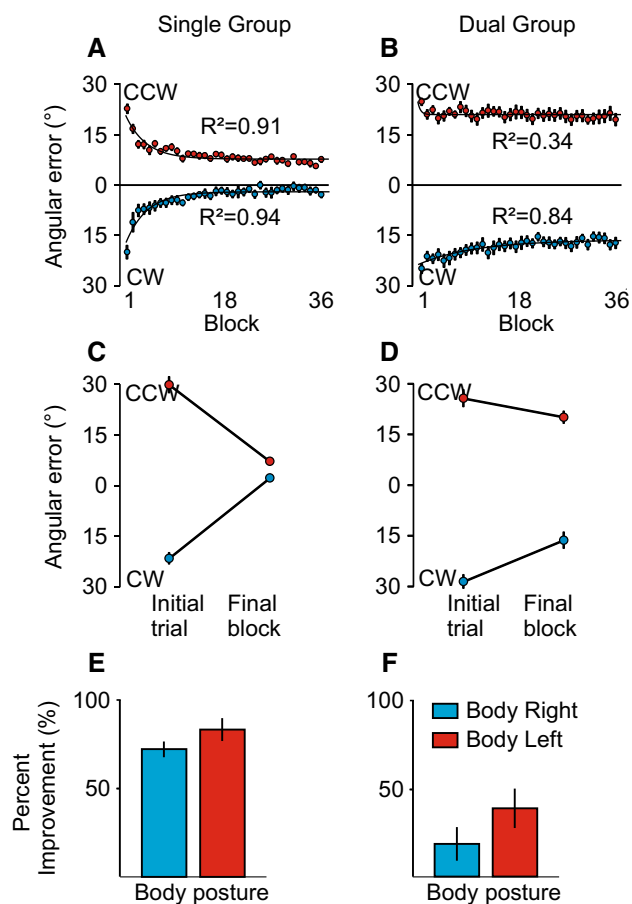


Fig. 6 Angular reach error across blocks during training for the body posture experiment. **a, b** The *top row* of plots depicts angular reach errors across blocks (of 5 trials) during training. *Thin black lines* represent fitted exponential curves for reach deviations for the entire training session with the equation $RD = be^{-ax} + c$. SINGLE CCW ($12.81e^{-0.33x} + 8.19$), SINGLE CW ($13.83e^{-0.56x} + 5.13$), DUAL CCW T1 ($2.78e^{-0.07x} + 20.55$), DUAL CW T1 ($7.72e^{-0.06x} + 16.04$). **c, d** The *bottom row* of plots depicts mean angular reach error across the initial trial and the final block for each group. *Blue circles* indicate reach errors during leftward body trials while *red circles* indicate reach errors during rightward body trials. **e, f** Per cent improvement for the body posture experiment for the SINGLE and DUAL training sets. *Blue bars* represent percentage improvement for leftward body trials, while *red bars* represent percentage improvement for rightward body trials. *Error bars* represent SEM (colour figure online)

were produced as a result of complete visuomotor adaptation. Again, after-effects differed between the two groups ($F(1,57) = 59.71, p < 0.001$). We then compared the after-effects from post-training with aligned cursors from that of post-training with misaligned cursors for each group, and found that these after-effects were significant for the SINGLE group ($t(24) = 14.15, p < 0.001$) but this was not true for the dual group ($t(16) = -0.96, p = 0.352$). In sum, although the DUAL group cued by distinct body postures significantly decreased their reach errors for both rotations

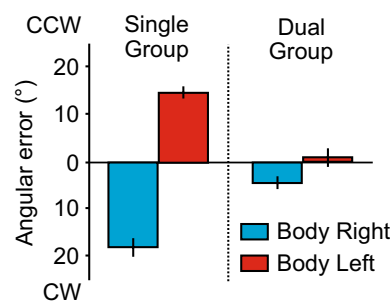


Fig. 7 After-effects for the body posture experiment. *Blue bars* represent after-effects for *rightward* body posture trials while *red bars* represent after-effects for *leftward* body posture trials. *Error bars* represent SEM (colour figure online)

across time, they showed negligible after-effects during post-training.

Hand posture versus body posture cue efficacy

Finally, to assess whether one contextual cue was more effective than the other, we compared percentage improvement between the DUAL groups of the two experiments. We found no significant difference in per cent improvement between these groups ($t(29) = 0.472, p = 0.640$) suggesting that hand and body posture have comparable efficacy in facilitating dual adaptation. However, since our contextual cues differ in their magnitude of distinction (and thus, there is no clear way to normalize this distinction across different cues), these between-experiment comparisons should be interpreted with care.

Discussion

The present studies assessed whether small changes in hand and body (and thus, limb) postures could provide sufficient contextual information to allow for the adaptation to two different and opposing visuomotor mappings for identical desired cursor paths when these were presented in a concurrent, pseudo-randomized manner. In addition, we investigated the extent of dual adaptation by providing extended practice to the DUAL group with hand posture cues. Our results show that angular deviations at peak velocity significantly decrease from the initial block to the final block of training for both rotations, indicating dual adaptation to opposing visuomotor rotations when specific hand or body posture contextual cues were associated with a distinct visuomotor mapping. As expected, the extent of dual adaptation was not as great as that of single adaptation. Indeed, dual adaptation did not reach the same baseline levels as single adaptation although angular errors significantly

decreased and eventually reached an asymptotic plateau for both opposing rotations.

Partial dual adaptation

Our present studies found that while dual adaptation is possible when target locations and desired cursor movements are identical across the two visuomotor conditions, reach error reduction did not reach baseline levels that rival that of adaptation to a single rotation. It is not surprising that our motor-based cues only elicited “partial” dual adaptation given previous findings regarding the pattern of generalization of motor learning. Complete dual adaptation occurs when there is greater motor distinction between visuomotor variants thereby preventing any interference across rotations. Indeed, dual adaptation tends to be complete for opposing perturbations that are associated with targets that are widely separated (Woolley et al. 2007) or involve the use of different limbs (Galea and Miall 2006). This is not surprising given that little generalization tends to occur for movements with very divergent directions, and across two arms. Thus, when opposing perturbations are associated with different target/movement directions, little interference is expected to occur and dual adaptation is more complete. The extent of dual adaptation in our studies, where targets were the same for the two rotations, was around a third to a half of that found in the SINGLE group. This allowed us to measure the extent of learning relative to adapting to only a single perturbation. Our findings were not surprising given that interference would have been high, and any adaptation would have been completely dependent on the effectiveness of the subtle change in intrinsic context. In other words, because adaptation is guided by motor generalization and the desired hand paths are identical across opposing rotations, we expected complete interference yet found that implementing cues reduced this significantly. Our present findings add to the current literature, which is currently dominated by studies looking at visual cues and segregated movement directions, to show that even for movements with identical desired paths, adaptation to two perturbations at the same time is possible when given motor-based cues.

Our study also addressed whether the reduction in reaching errors when adapting to two opposing rotations can eventually rival that of single rotation adaptation through extended training. That is, dual adaptation in other studies has only been partial because it is possible that it proceeds at a slower rate and hence simply requires more extensive training. To this end, we doubled the amount of trials in the DUAL training group in the hand posture experiment in order to determine whether extending practice can further strengthen the associations between the intrinsic context and visuomotor mapping. It is possible that contextual

cues in our experiments sufficiently facilitate dual adaptation to the same extent as single adaptation, but requires more training to saturate to the same baseline levels. However, extended training across days when accompanied by another cue such as colour can sometimes allow for partial (Gupta and Ashe 2007) or even complete dual adaptation (Osu et al. 2004), at least when adapting to opposing force fields by similar magnitude of force perturbations. It is possible that greater dual adaptation (i.e. equivalent to that of single adaptation) requires even more training than the two sessions that we offered; however, we found that errors appear to saturate in the second session with no further significant reduction for the additional 360 trials (additional 36 trials per target, per rotation). Thus, based on our findings, it seems unlikely that further training would lead to any substantial reduction in errors equivalent to that shown during one session of training with a single perturbation.

Intrinsic contextual cues

Exploring specifically what types of cues are able to facilitate dual adaptation was a key objective of the present studies. We began by testing whether an intrinsic cue like change in hand posture (and grip aperture) was sufficient. Baraduc and Wolpert (2002) showed that reach adaptation to a rotated cursor is posture-specific in that the transfer of adaptation was significant but smaller when the posture differed from that used during training. Given that the generalization across arm posture was limited, we hypothesized a similar change in hand posture, along with a grip aperture, may be sufficient for dual adaptation. One preliminary ABA (serial block adaptation) study associating different arm posture with opposing force fields have also shown serial adaptation when training with associated postures and perturbation (Gandolfo et al. 1996). Wang and Musseler (2014) showed significant but partial adaptation to opposing visuomotor rotations when reaching to the same forward central target but while moving their arm to the left or to the right of the tablet workspace thereby varying posture but not target location. Given these findings, we expected, and indeed found, that our participants would be able to partially dual adapt if opposing visual perturbations were coupled with different postures.

While hand path location or hand posture may be sufficient to allow for dual adaptation, grip aperture seems to be less promising. Cothros et al. (2008) found that changing the shape of the handle (e.g. stick vs. ball) participants used to reach, without changing the orientation or texture of the handle, was not sufficiently distinctive to allow for a reduction in interference between opposing force-field perturbations in an ABA task when each perturbation was associated with each grip shape. In fact, the extent of interference was just as large as that produced when the handle

remained the same. Likely, the change in tactile information did not cause an overall change in movement planning suggesting that haptic cues alone do not facilitate dual adaptation unless they are combined with other motor-based cues or if they allow for a sufficient change in movement planning. This suggests that not only the type but also the distinctiveness of the cue plays a role in reduced interference across the two adaptive states. The effect of context seems to be additive, such that more distinct cues allow for increased adaptation. In our hand posture experiment, we were not able to distinguish whether it was grip aperture or hand posture that provided the sufficient cue for partial dual adaptation. However, given the results above, it is unlikely that the change in grip or texture alone, apart from a change in posture is driving dual adaptation.

The second intrinsic cue we tested also involved changes in arm posture, but this time less directly, in that rotating the body changes the joint motions necessary to produce the same hand trajectory. By keeping the head facing straight, while the body turned beneath it, we avoided any potential vestibular cue (which is useful when adapting to altered visual feedback during locomotion; Dumontheil et al. 2006). Interestingly, although we found significant hand posture-specific after-effects in the DUAL group of the hand posture experiment, we did not find the same in the body posture experiment to complement our other visuomotor adaptation measures. While after-effects typically represent genuine implicit adaptation, it seems unlikely that participants employed explicit or cognitive strategies given that upon debriefing, most did not have a valid strategy or even noticed the rotations. Plus, recent findings by van Werner et al. (2015) show that the magnitude of after-effects was equivalent between trials where the participants were told to use or not use a learned strategy when reaching without a cursor, at least for participants in the implicit group.

Perhaps the lack of significant after-effects in our body posture experiment was likely due to the fact that the change in arm posture given the two body directions was not large enough to drive sufficient visuomotor learning to lead to substantial after-effects. Likely, the body posture cues were less distinctive than the hand posture cues (which also had additional haptic cues including grip texture and aperture) and other studies that manipulated arm posture such as those employed in Baraduc and Wolpert (2002). Since our set-up did not allow us to implement a large change in arm posture, we instead changed the body direction and thus the shoulder location and the linkages associated. Here, a body rotation of 10° CCW pushed the shoulder (and thus, centre of shoulder rotation) forward by roughly 3.2 cm based on the average woman's shoulder width (approximately 35 cm). Likewise, a body rotation of 10° CW pushed the shoulder back 3.2 cm resulting in sagittal difference of roughly 6 cm. If we looked at how much the shoulder has to rotate under

these two body postures in order to intersect a point from the body along the midline, the shoulder would have to rotate by 84° when forward (as in Fig. 1d), and by 64° when backward (as in Fig. 1e). If the difference in the joint angles between body postures had been larger, it is possible that dual adaptation would reach significant after-effects. Larger differences provide better context disambiguation for movement planning. Nevertheless, we show that even relatively subtle, motor-based cues in the body posture experiment are still able to elicit dual adaptation.

Finally, we provided participants with a visual cue (i.e. “TOP”, “BOTTOM”, “←”, “→”) to aid with posture switching prior to every trial. While it is possible that these visual cues prior to every trial may have aided with dual adaptation, it is highly unlikely given the results of other previously mentioned experiments in which more in-depth cues (e.g. colour cues) presented even during the trial were unable to elicit a reduction in error.

Our present findings suggest that hand and body postures which produce distinct joint angles associated with each sensorimotor context, provide adequate information for the CNS to allow for dual adaptation. Since there was no difference in percentage improvement between the DUAL groups of the hand posture and body posture experiments, this implies that either cue is able to provide useful information to the CNS even when the desired cursor movement trajectories are identical.

Conclusion

Motor-based cues such as hand and body posture facilitate dual adaptation when they are the only cues provided to dissociate between two opposing rotations when desired cursor trajectories are identical. Furthermore, while dual adaptation is possible given these contextual cues, the magnitude of learning is smaller than that of single adaptation, despite double the amount of reach training.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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