RESEARCH ARTICLE

Dual adaptation to opposing visuomotor rotations with similar hand movement trajectories

Ravindra Baldeo · Denise Henriques

Abstract This research explored specific contextual cues that might facilitate human motor learning. Using a dual adaptation task, humans performed manual reaches to visual targets while experiencing a 30° clockwise or counterclockwise rotation, which randomly alternated between trials, of a seen cursor representing their unseen hand. Groups had different cues to distinguish between rotations: 'Cue' (colours and shapes), 'Workspace' (target locations) and 'Workspace with Cue' (combination of cues). Importantly, the workspace groups required similar hand movement trajectories to accurately acquire pairs of targets. Our data show that only the 'Workspace' and 'Workspace with Cue' groups, but not 'Cue' group, adapted to both rotations concurrently (dual adaption). These findings suggest that colour and shape cues, even when integrated with the end-effector and targets, do not facilitate dual adaptation. However, target separation is sufficient to facilitate dual adaptation, even when hand movement trajectories are similar. Interestingly, adaptation was less complete when required hand trajectories were completely overlapping for pairs of targets (versus being similar), suggesting an important role for the motor system as well. Nonetheless, the location of targets and consequent differences in motor planning may play a larger role in facilitating adaptation than previously thought.

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

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Introduction

Humans possess diverse motor skills and can perform actions in a wide variety of environments. Importantly, we can learn to behave in novel environments. This ability explains how humans can maintain accurate behaviour during growth, after experiencing injury, or interacting with novel tools, as examples (Gauthier et al. 2007). Since each environment or context has unique properties, each could be associated with a specific mapping between motor commands and sensory states within our bodies, and these mappings are known as 'internal models'. The brain is thought to have multiple internal models, and the 'Modular Selection and Identification for Control' (MOSAIC) theory might explain how they are recalled and switched depending on the context (Haruno et al. 2001). Our study examines how subjects reach to targets in novel environments that theoretically require switching of internal models for accurate performance, providing more insight into the mechanisms and sources of information that are associated with motor learning.

Visual perturbations have been used to create novel environments in which subjects perform motor tasks. Humans can typically learn to compensate for a single visual or force perturbation and show robust after-effects, which indicate adaptation. However, when multiple perturbations are present (e.g. clockwise (CW) and counterclockwise (CCW) visuomotor rotations), adaptation can be variable. For example, concurrent adaptation to variable environments has been shown to occur (Gandolfo et al. 1996; Ghahramani and Wolpert 1997; Osu et al. 2004; Bock et al. 2005; Woolley et al. 2007), occur with extensive training (Krouchev and Kalaska 2003; Wada et al. 2003) or not occur (Cunningham and Welch 1994; Gandolfo et al. 1996; Karniel and Mussa-Ivaldi 2002; Gupta and Ashe 2007; Woolley et al.

2007; Cothros et al. 2008), depending on available cues. The variety of results suggests that not all sources of information are equal; some contextual cues are more effective in facilitating learning than others.

Contextual cues that have previously led to successful dual adaptation, or resistance to interference, include colour (Wada et al. 2003; Osu et al. 2004). However, simply having colour cues available does not guarantee adaptation, even when performance appears to improve (Cunningham and Welch 1994; Gandolfo et al. 1996; Dumontheil et al. 2006; Woolley et al. 2007; Hinder et al. 2008b; Hegele and Heuer 2010). While these studies suggest that colour cues do not facilitate adaptation, there might be other conditions where they do, perhaps when integrated with the task. Correspondingly, we explored the use of colour and shape cues which were integrated with cursors and targets. Colour or shape cues, or a combination of them, might be useful in providing sufficient information for the control system to select appropriate motor commands for action, and this could be represented by dual adaptation in our experiment.

In addition to these cues, other types of information are available in reach tasks, such as: target locations, hand postures, movement trajectories, among others, and these factors have been shown to affect learning as well. For example, Woolley et al. (2007) showed that coupling opposing visuomotor rotations with separate visual target sets could facilitate dual adaptation. Their target sets were visually separated by 180° and inherently required separation of hand torque directions by an average of 120°. It was thought that the differences in torque direction caused distinct muscles and muscle synergies to be associated with each opposing rotation, primarily facilitating dual adaptation (Woolley et al. 2007).

Indeed, having distinct muscles or muscle synergies associated with separate perturbations could facilitate adaptation where there might otherwise be interference (Gandolfo et al. 1996; Ghahramani and Wolpert 1997; Bock et al. 2005). However, it is not always sufficient (Gandolfo et al. 1996; Krakauer et al. 2006). Since this hypothesis does not always apply, the previous dual adaptation could have primarily been due to another factor, such as differences in target locations. Indeed, Woolley et al. (2011) recently followed up on this possibility and found that subjects could dually adapt when visual targets were separated but associated torque production was similar for pairs of targets. Our study also follows up by exploring the contribution of target locations necessitating either similar or overlapping reach trajectories for pairs of targets in an unconstrained reach task.

Our first objective is to determine whether subjects dually adapt to opposing visuomotor rotations when only cued by the colour and shape of cursors and targets. Our second objective is to assess whether subjects dually adapt when targets are separated but required hand movement

trajectories are either similar or overlapping for pairs of targets. Lastly, we explored whether a combination of all cues facilitate dual adaptation above what would otherwise be established with a single cue. We hypothesize that both colour-related or movement-direction cues would be sufficient to allow for at least partial adaptation to the two opposing rotations, with the amount of adaptation being lower than that produced when adapting to only a single rotation. We also hypothesize that combining both sources of information could lead to relatively higher adaptation levels, closer to that of single adaptation. Whether dual adaptation is observed in these conditions will provide insight into sources of information that are relevant for motor learning.

Methods

Participants

Eighty-seven subjects (33 males, 54 females, average age = 22.49, SD ± 6.32) participated in this study and were assigned to only one subgroup or main group depending on whether they experienced a single or dual rotation, respectively (Table 1). All were right handed, had normal or corrected vision and were naïve to the purpose of the experiment. Subjects provided written consent in accordance with York University's Human Participants Review Committee and were granted bonus course credit in an undergraduate psychology course.

Apparatus

Subjects sat on an adjustable chair facing a digitizing tablet and screen. The digitizing tablet (Wacom Intuos3, 12″ × 12″ surface, resolution of 5,080 lines/inch) was located at waist level, permitting hand movements in the horizontal plane. The screen was positioned vertically, approximately 60 cm from the tablet work surface. A projector (Epson 3LCD) rear projected an image that participants were able to view in front of them. A shield positioned in front of the subject prevented observation of their reaching arm [Cf. (Dionne and Henriques 2008; Balitsky Thompson and Henriques 2010)]. Subjects reached to targets (1.5 cm in diameter) by moving a hand-held stylus pen across the surface of the tablet, which moved a cursor (1 cm in diameter) on the screen. The hand–cursor relationship was similar to using a desktop computer and movements were made with a 1:1 ratio.

Procedure

All subjects completed pre-training, training and post-training sessions, within 1 h (Fig. 2). Starting at the home

Table 1 Subject allocation and group features

Main group (collapsed)	Subgroup	N	Training rotation direction (°)	Training target set	Novel target set
Single CCW	Single-Top CCW	9	30 CCW	Top	Right and Middle
	Single-Middle CCW	9	30 CCW	Middle	Right and Top
Single CW	Single-Right CW	9	30 CW	Right	Middle and Top
	Single-Middle CW	9	30 CW	Middle	Right and Top
Dual Cue	Dual Cue-Top	9	30 CCW and 30 CW	Top	Right and Middle
	Dual Cue-Middle	9	30 CCW and 30 CW	Middle	Right and Top
Dual workspace		12	30 CCW and 30 CW	Right for CW & Top for CCW	Middle
Dual workspace with cue		9	30 CCW and 30 CW	Right for CW & Top for CCW	Middle
Dual workspace 45°		12	45 CCW and 45 CW	Right for CW & Top for CCW	Middle

position, subjects made smooth and direct reaches to targets (located 10 cm away), which were presented individually and in a pseudo-randomized order (each target location appeared once before appearing again). During trials with cursor feedback (closed loop), subjects acquired targets. During trials with no cursor feedback (open loop), subjects estimated the location of the target by moving towards it and then remaining stationary for 500 ms. Within open loop trials, cursor feedback was only available in a small window (2 cm radius) around the home position, providing a brief contextual cue.

Pre-training (baseline measures)

Single and dual distortion groups The objective of the pre-training session was to familiarize subjects with the task and capture baseline performance. In the aligned session (Fig. 2, first boxes), subjects reached 10 times to each of the 9 targets with concurrent feedback of the aligned cursor (90 trials). The targets were presented at either: 345°, 0°, 15°, 30°, 45°, 60°, 75°, 90° or 105° (Fig. 1). In the no cursor session (Fig. 2, every second box), subjects reached 5 times to each of the 9 targets (45 trials).

Training (adaptation) and post-training (after-effects)

Single distortion groups The purpose of training (Fig. 2a, third box) was to expose subjects to the visuomotor rotation. 'Single distortion' groups had the cursor consistently rotated either 30°CW or CCW, but not both (Fig. 3a). For example, the 'Single-Top CCW' group had the cursor rotated 30°CCW while subjects made 30 reaches to a set of 3 targets (90 trials) located at 90° ± 15° (Fig. 3a, top portion). To assess after-effects, subjects performed no cursor reaches 5 times to each of the same nine targets as in pre-training (45 trials) (Fig. 2a, fourth box). Subjects then
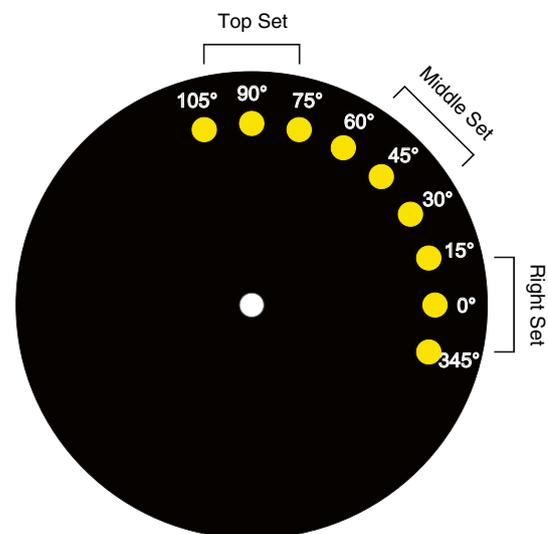

Fig. 1 Visual targets. All visual target locations are shown and are referred to by their angular position or target set. Targets (*yellow circles*) were located 10 cm away from the home position (*white circle*) and spanned 120° in 15° intervals. When the cursor was aligned with the stylus, subjects could reach directly to the target positions. However, when visuomotor rotations were present, subjects could have adapted by reaching 30°CW or CCW relative to the visual target to counter the perturbation (moving the cursor directly towards the target). Angular error represented any cursor (*closed loop trials*) or hand movement (*open loop trials*) deviations from a direct reach path towards the visual targets. Figure not drawn to scale

repeated training for a total of 180 rotated trials (Fig. 2a, fifth box), followed again by no cursor trials totalling 90 (Fig. 2a, last box). Since 'no cursor' trials consisted of all target locations and 'training' only consisted of three targets, common targets were considered 'trained'; otherwise, they were 'novel'.

'Single-Right CW', 'Single-Middle CCW' and 'Single-Middle CW' followed the same procedure and their features
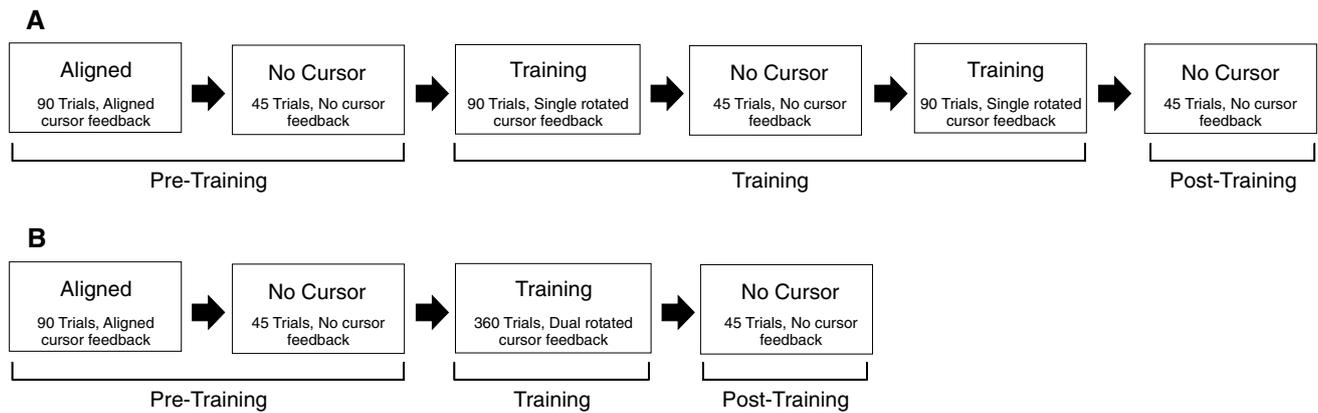
Fig. 2 Sequence of sessions for **a** Single distortion groups and **b** Dual distortion groups. Single distortion groups served as a control for adaptation to visuomotor rotations, having a total of 180 trials under either a 30°CW or CCW rotation, but never both. Dual distortion groups had a total of 360 trials under both CW (180 trials) and CCW (180 trials) rotations, which were randomly interleaved between trials. Pre-training measures were subtracted from 'training' and 'post-training' measures to remove movement biases
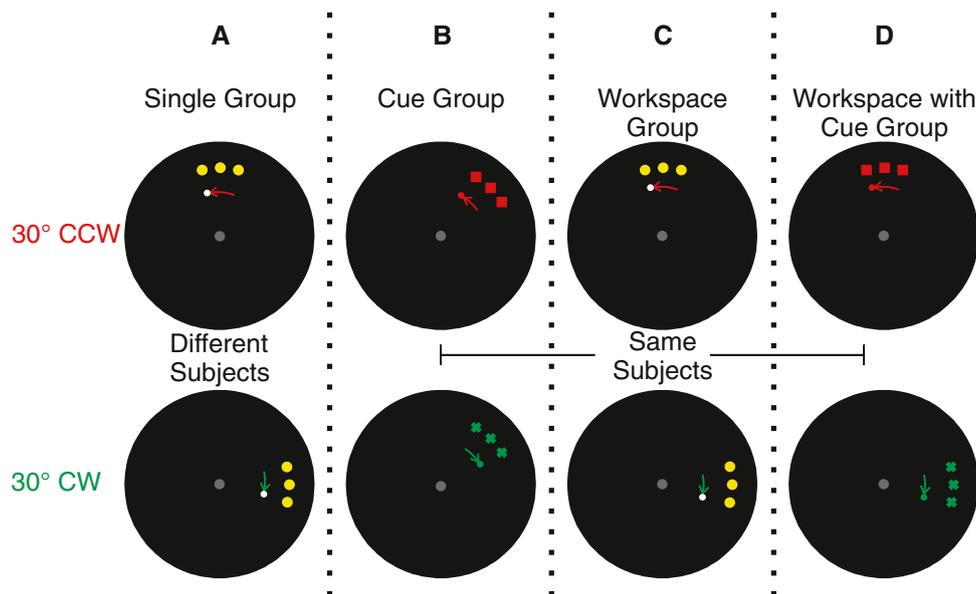

Fig. 3 Sample target locations and associated cues for each main group. Single distortion groups (column **a**) did not have cues. Dual distortion groups (columns **b–d**) had colour and shape cues (**b**), target location cues (**c**), or a combination of both (**d**), coupled with visuomotor rotations. Specifically, top targets or *red squares* were coupled with CCW rotations (*top row*), and right targets or green crosses were coupled with CW rotations (*bottom row*). Importantly, if adaptation occurred in **b** or **d**, the required hand reaches would have been increasingly similar for pairs of targets (converging between the visual target sets shown above). While multiple targets are shown here for illustration, only a single target appeared on any trial during the experiment

are summarized in Table 1. Testing different groups allowed us to rule out performance differences based on target location and rotation combinations.

Dual distortion groups The 'Dual distortion' groups had the cursor rotated 30°CW and CCW during training (Fig. 2b). For example, 'Dual Cue-Middle' subjects made 120 reaches to each of three targets (360 trials) located at 45° ± 15° (Fig. 1, Middle Set). Half of the reaches (180 trials) were made under CW rotations and half under CCW rotations (Fig. 2b, 3rd box). A green cursor and green cross-target were coupled with CW trials, while a red cursor and red square target were coupled with CCW trials (Fig. 3b). 'Dual Cue-Top' training was similar; however, the three targets were located at 90° ± 15° (Fig. 1, Top Set), allowing us to investigate target-dependent differences in learning.

'Dual Workspace' subjects followed the same procedure, but without any colour and shape cues. Instead, rotations were coupled with separate regions of workspace (Fig. 3c). For example, one target set located at $0° \pm 15°$ (Fig. 1, Right set) was coupled with 30°CW rotations, while the second target set located at $90° \pm 15°$ (Fig. 1, Top set) was coupled with 30°CCW rotations. An additional 'Dual Workspace' group was also added to the experiment with the only difference being that it contained 45°CW and CCW rotations. These groups allowed us to assess adaptation when required hand movement trajectories are similar (Dual Workspace 30°) versus when they are overlapping (Dual Workspace 45°) for pairs of targets.

The 'Dual Workspace with Cue' group followed a similar procedure but were presented with a combination of visual cues from 'Dual Cue' along with workspace cues from 'Dual Workspace' to distinguish between the 30° rotations (Fig. 3d).

The 'no cursor' trials (Fig. 2b, fourth and last box) that followed training also included the visual cues, but the cursor was only visible around the home position within a small radius. This provided a brief contextual cue in trials where cursor feedback was not otherwise available.

Data analysis

Performance was assessed using 'angular error at maximum velocity', which was the angular difference between the target and cursor, relative to the home position, at peak velocity. Therefore, measurements were taken within the initial phase of movement and represented feed-forward movement planning. Angular errors from individual trials were separated by rotation and blocked into groups of three (three targets within each target set). Performance in the 'Single distortion' groups was not statistically different, and data were subsequently collapsed for each rotation, forming the main 'Single CW' and 'Single CCW' groups (Fig. 3a). Similarly, 'Dual Cue-Top' and 'Dual Cue-Middle' groups were collapsed into the main 'Dual Cue' group (Fig. 3b). The collapsed data were used in subsequent analyses.

To assess learning, we considered the changes in hand–cursor deviations across blocks in the 'training' and 'post-training' sessions. Specifically, adaptation was assessed by comparing the initial and final block of training using a 4(Group) × 2(Block) mixed ANOVA, for each rotation. Follow-up paired t tests revealed which groups improved over the course of training. Next, we quantified adaptation for each subject by calculating percent improvement, which was the difference between a subject's initial and final angular error, divided by their initial error. A one-way ANOVA was used to compare each dual group's performance to the single group which experienced the same rotation. Follow-up one-sample t tests revealed which groups had significant percent improvements. Similarly, we assessed after-effects using a one-way ANOVA to compare between groups within CCW and CW trials. Follow-up one-sample t tests revealed which groups had significant after-effects. The assumed level of significance was $p < 0.05$, and multiple post hoc comparisons had Bonferroni correction.

Lastly, we illustrated the changes in reach deviations over trials by fitting a single exponential function to the data within the first 30 blocks, averaged across subjects, for each rotation, for each group. The equation takes the form $RD = c - ae^{-bn}$ where n presents the block number, b the rate of learning and c the asymptotic performance level. The sign of the fit changed depending on whether the rotation was CW or CCW. However, given that some groups did not dual adapt, the fits for these curves were more linear than exponential (with $b < 0.02$) and thus we did not perform statistical comparisons.

Results

Adaptation to visuomotor rotation

Figure 4 shows reach errors for the (a) 'Single distortion', (b) 'Dual Cue', (c) 'Dual Workspace' and (d) 'Dual Workspace with Cue' groups across trials (by blocks of 3) throughout the training session. Red squares represent CCW trials and green circles represent CW trials. We can see that the 'Single distortion' (Fig. 4a), 'Dual Workspace' (Fig. 4c) and 'Dual Workspace with Cue' (Fig. 4d) groups initially had large rotation-dependent errors that quickly reduced to near pre-training levels of performance (ordinate at '0'). However, 'Dual Cue' performance (Fig. 4b) was less accurate throughout, especially for CCW trials. Correspondingly, the fits to these mean reach errors across the initial 30 blocks (*yellow dotted lines*) for the 'Single', 'Dual Workspace' and 'Dual Workspace with Cue' groups resemble the exponential curve usually associated with motor learning (Krakauer et al. 2000), but not the 'Dual Cue' group. However, exponential fits for the 'Dual Workspace' group appear less steep (b of the fits of the averaged data were -0.13 to -0.20 for the two rotations) compared to that of the 'Single' groups (b of -0.28 to -0.36).

Initial and final blocks (Fig. 4e–h) were compared and angular errors within CW trials reduced on average across all groups by the end of training ($F(1,53) = 132$, $p < 0.05$). However, for CCW trials, this reduction in errors between initial and final block varied as a function of group ($F(3,53) = 16.8$, $p < 0.05$). Follow-up analysis showed that under CCW rotations, all groups reduced their angular error by the end of training ($p < 0.05$), except for the 'Dual Cue'
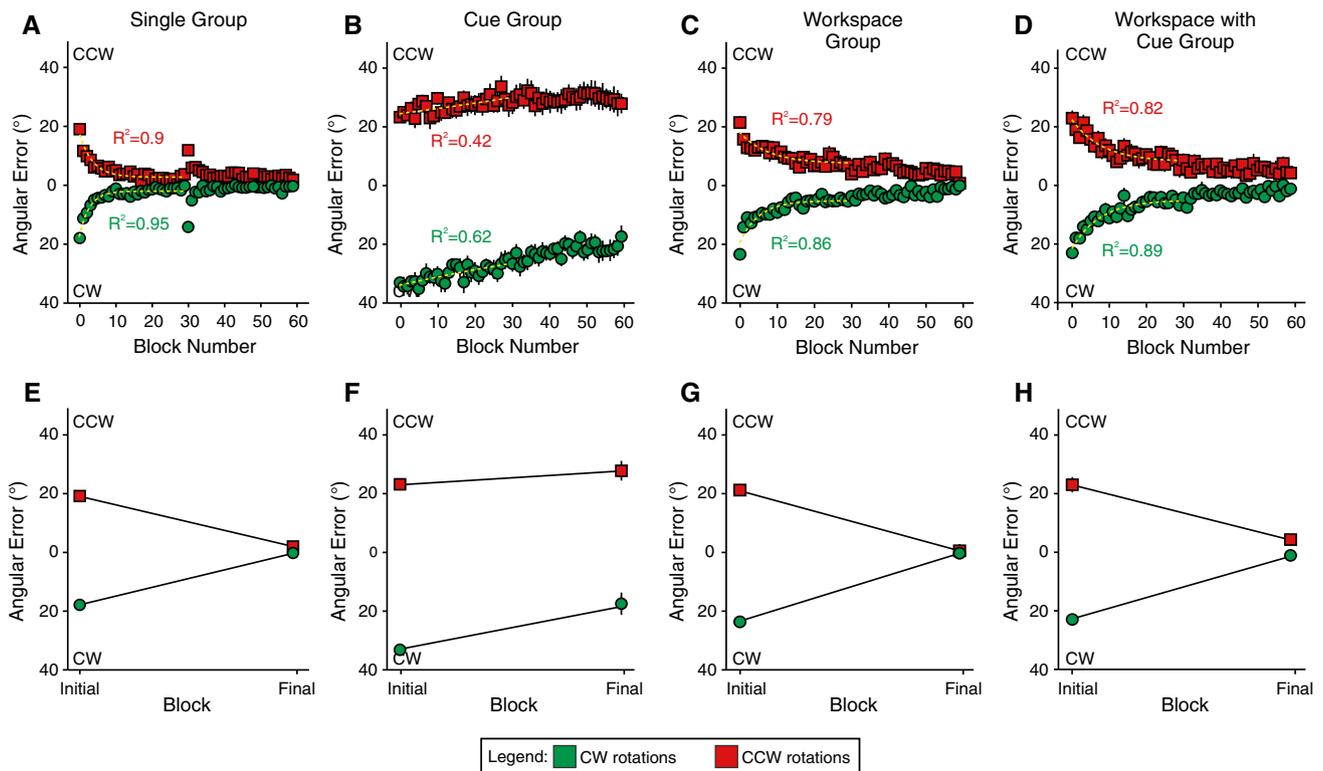
Fig. 4 Angular errors across blocks (of three trials) during training for single (**a**) and dual (**b**–**d**) distortion groups. Initial and final blocks (**e**–**h**) are shown for each group, respectively. Single distortion (**a**, **e**) is separated into CCW (*red squares*) and CW (*green circles*) groups. 'Dual Cue' (**b**, **f**), 'Dual Workspace' (**c**, **g**) and 'Dual Workspace with Cue' (**d**, **h**) are separated into CCW (*red squares*) and CW (*green circles*) trials. Large magnitudes of angular error in either direction are representative of non-direct reaches to targets (typical of initial exposure to rotations), and small errors indicate direct reaches (adaptation through practice). Only 'Dual Workspace' and 'Dual Workspace with Cue' groups have patterns resembling the 'Single' distortion controls, indicative of dual adaptation as they were exposed to both rotations concurrently. *Yellow dotted lines* represent fitted curves for the initial 30 blocks of reach deviations ($RD = c - ae^{(-bn)}$). Single CCW ($3.93 + 14.22e^{(-0.278n)}$), Single CW ($0.44 - 15.26e^{(-0.364n)}$), Dual Cue CCW ($-2.49 + 28.7e^{(0.006n)}$), Dual Cue CW ($-7.99 - 23.98e^{(-0.012n)}$), Dual Workspace CCW ($8.39 + 10.63e^{(-0.131n)}$), Dual Workspace CW ($-3.9 - 14.09e^{(-0.197n)}$), Dual Workspace with Cue CCW ($10.72 + 14.13e^{(-0.122n)}$), Dual Workspace with Cue CW ($-1.99 - 16.35e^{(-0.133n)}$). *Error bars* represent SEM

CCW group ($t(17) = -1.2$, $p = 0.24$). These results suggest that the 'Dual Workspace' and 'Dual Workspace with Cue' groups were able to concurrently adapt to the opposing visuomotor rotations (dually adapt), while the 'Dual Cue' group did not.

Percent improvement

Adaptation was quantified relative to each individual's initial performance by measuring percent improvement. This was the difference in angular error between a subject's initial and final block, divided by the error of their initial block. Correspondingly, higher percentages indicate greater improvement, relative to initial performance, within the training session.

Figure 5 shows the average percent improvement for each 'Single' and 'Dual' distortion group separated by CCW (red) and CW (green) trials. There was a significant difference in percent improvement between groups ($F(7,105) = 15.8$, $p < 0.05$). Follow-up analysis revealed a significant percent improvement for all groups ($p < 0.01$), except for 'Dual Cue CCW' trials ($t(17) = -1.2$, $p = 0.25$), which experienced a performance decrement. Even 'Dual Cue CW' trials showed only marginal improvement in that it was significantly less than the 'Single CW' group ($p < 0.05$, Bonferroni corrected post hoc comparisons). However, the 'Dual Workspace' ($p = 1.0$) and 'Dual Workspace with Cue' ($p = 1.0$) groups did not differ from the 'Single distortion' groups. This suggests that the 'Dual Workspace' and 'Dual Workspace with Cue' groups were able to dually adapt, while the 'Dual Cue' subjects did not.

After-effects

After-effects were angular deviations of *hand reaches* in 'post-training' as a result of being exposed to visuomotor
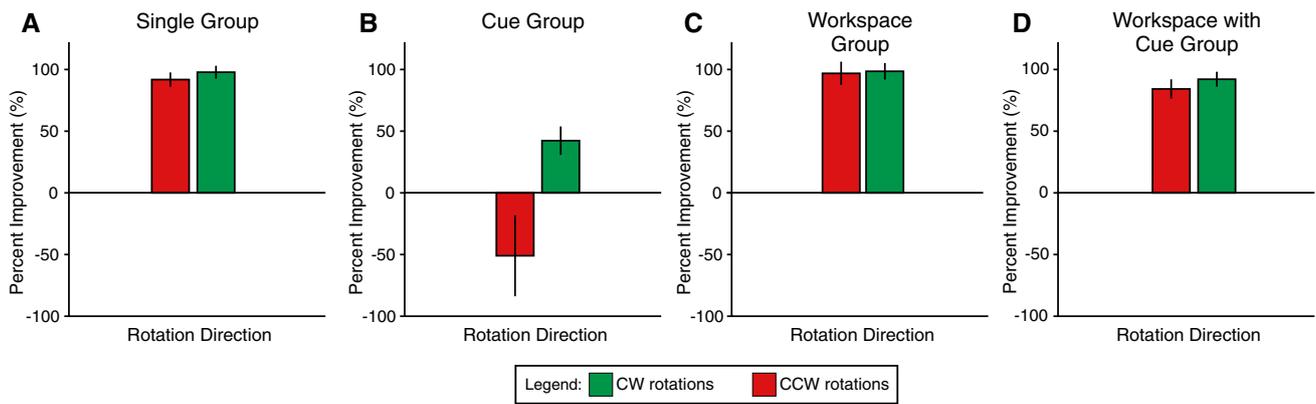
Fig. 5 Percent improvement during training for single (**a**) and dual (**b**–**d**) distortion groups. Single distortion (**a**) is separated into CCW (*red*) and CW (*green*) groups. 'Dual Cue' (**b**), 'Dual Workspace' (**c**) and 'Dual Workspace with Cue' (**d**) are separated into CCW (*red*) and CW (*green*) trials. Since percent improvement was computed as (initial block–final block)/(initial block), higher percentages indicate increasingly better performance (direct reaches) by the end of training, relative to initial. Similarly, negative percentages indicate a performance decrement by the end of training, relative to initial. Only 'Dual Workspace' and 'Dual Workspace with Cue' groups have patterns resembling the 'Single' distortion controls, indicative of dual adaptation as they were exposed to both rotations concurrently. *Error bars* represent SEM
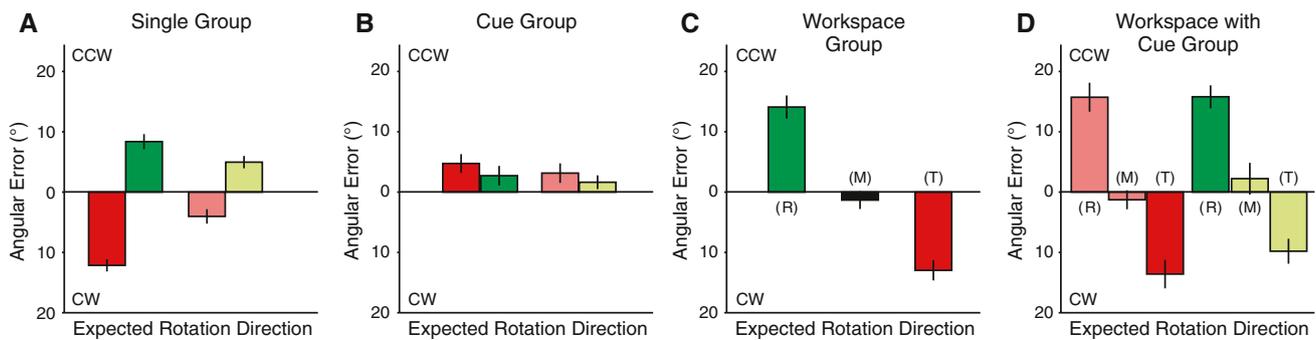

Fig. 6 After-effects during post-training for single (**a**) and dual (**b**–**d**) distortion groups. *Dark colours* indicate reaches to trained targets and light to novel. *R* Right target set, *M* Middle and *T* Top. *Red bars* represent when a CCW rotation should have been expected (thus having CW after-effects) based on the single distortion group the subjects were in (**a**), based on the colour and shape cues presented in 'Dual Cue' (**b**), based on the target locations presented in 'Dual Workspace' (**c**), and based on the combination of cues in 'Dual Workspace with Cue' (**d**). Similarly, *green bars* represent trials where CW rotations should have been expected (thus having CCW after-effects). 'Workspace' and 'Workspace with Cue' were the only dual distortion groups that had after-effects in accordance with cues presented, namely CCW when reaching to right targets (R) and CW when reaching to top targets (T), indicative of adaptation based on target location. Interestingly, 'Dual Workspace with Cue' expressed these after-effects even when colour and shape cues indicated the opposite rotation (**d** *light green* vs. *light red bars*), indicating that target location cues took precedence. *Error bars* represent SEM

rotations during 'training'. Specifically, continuing to produce reach movements that compensate for expected perturbations (opposite direction) in open loop trials, which is typically associated with adaptation. After-effects are illustrated in Fig. 6. Where CW rotations were present during 'training', CCW after-effects would be expected and this is represented in green; similarly, red represents CW after-effects. Dark colours represent 'trained' target locations and light colours represent 'novel' target locations.

After-effects for trained targets differed across groups within CCW ($F(3,53) = 36.9$, $p < 0.05$) and CW ($F(3,53) = 12.6$, $p < 0.05$) trials. These after-effects occurred in the expected

direction and were significant for 'Single distortion' (Fig. 6a), 'Dual Workspace' (Fig. 6c) and 'Dual Workspace with Cue' (Fig. 6d) groups ($p < 0.01$ one-tailed t tests), indicating that subjects continued to compensate for perturbations of which they were previously exposed, which is typical of adaptation. However, 'Dual Cue' subjects had small after-effects that were not in the expected directions based on 'training' (Fig. 6b), indicating that any compensation was not based on colour or shape cues. After-effects were also larger for trained targets (dark colours in Fig. 6a) than for novel targets (light colours) in the 'Single CCW' and 'Single CW' groups ($p < 0.05$), which is consistent with local generalization of

adaptation. 'Dual Workspace' ($t(11) = -0.9$, $p = 0.39$) and 'Dual Workspace with Cue' CCW ($t(8) = -0.81$, $p = 0.44$) and CW ($t(8) = 0.85$, $p = 0.42$) groups did not have significant after-effects for their novel targets (middle target set), which is not too surprising given they were located between two trained target sets.

'Dual Workspace with Cue' after-effects (Fig. 6d) were also divided into target sets and rotation angle cue since this particular group had both features represent rotations. Importantly, subjects had CCW after-effects when reaching to right target sets, whether CCW or CW cues were presented ($p < 0.01$), and similarly had CW after-effects when reaching to top targets, whether CCW or CW cues were presented ($p < 0.01$). This suggests that after-effects were based on target locations even when colour and shape cues were also available, indicating that movements were primarily based on target location cues.

Additional dual workspace 45° group

While the previous 'Dual Workspace' group required *similar* hand movement trajectories for pairs of targets, the additional 'Dual Workspace 45' group required *overlapping* reach trajectories, eliminating small motor differences which could have contributed to dual adaptation. Figure 7 shows the various measurements from the 'Dual Workspace 45°' group. Figure 7a shows that, like the 'Dual Workspace' group, performance improved for both rotations by the end of training. Comparing initial and final blocks (Fig. 7b), these improvements were significant within both CW ($t(10) = -5.9$, $p < 0.05$) and CCW ($t(10) = 2.9$, $p < 0.05$) trials, suggesting dual adaptation.

The 'Dual Workspace 45°' group also had significant percent improvements (Fig. 7c) under both CW ($t(10) = 5.6$,

$p < 0.05$) and CCW ($t(10) = 2.8$, $p < 0.05$) trials. Interestingly, while improvements were made under both rotations, the percent improvement was larger for CW trials compared to CCW trials ($t(10) = 2.9$, $p < 0.05$). Correspondingly, further inspection showed that the percent improvement for CW trials was not statistically different from the 'Single CW' and 'Dual Workspace 30° CW' rotations ($F(2,38) = 1.9$, $p = 0.16$). However, there was a difference within CCW trials ($F(2,38) = 13.96$, $p < 0.05$), as the percent improvement was lower in 'Dual Workspace 45°' compared to both 'Single' and 'Dual Workspace 30°' ($p < 0.05$). This suggests that there was some decrement in performance when reach movements overlapped for pairs of targets.

Post-training revealed that subjects had CCW after-effects ($t(10) = 7.4$, $p < 0.05$) when reaching to the rightward targets and CW after-effects ($t(10) = -3.5$, $p < 0.05$) when reaching to top targets (Fig. 7d). Not surprisingly, subjects did not have significant after-effects in either the CW or CCW direction ($t(10) = -0.5$, $p = 0.64$) when reaching to middle targets. These results suggest that dual adaptation can occur when reach trajectories are similar or overlapping for pairs of targets, although there might be more interference in the latter, which suggests that visual separation of targets is sufficient to facilitate dual adaptation.

Discussion

Using visuomotor rotations, we explored whether specific contextual cues facilitate dual adaptation. Our results show that colour and shape cues were not sufficient to facilitate dual adaptation (Dual Cue). However, target locations did facilitate dual adaptation, even when reach trajectories were similar or overlapping, although adaptation was more
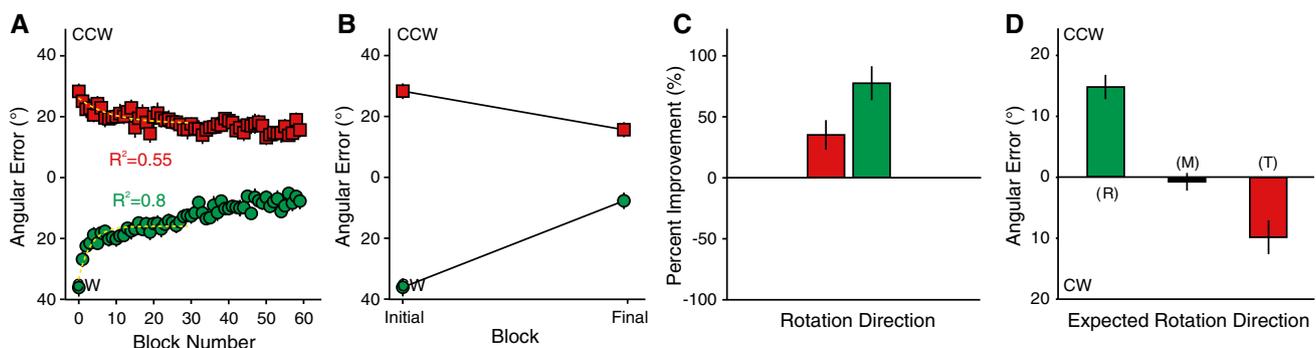

Fig. 7 Dual workspace 45° angular errors across blocks (of three trials) during training (**a**), initial versus final training block comparisons (**b**), percent improvement (**c**), and after-effects (**d**). Since this group was the same as 'Dual Workspace' with the only difference being that the rotations were 45°CW and CCW, the descriptions for these figures follow from the 'Dual Workspace' descriptions in Figs. 4, 5 and 6. While these data show that subjects were

able to dual adapt, the extent of adaptation was less than that of the 'Dual Workspace' group, suggesting that there are implications for adaptation when hand movement trajectories are similar versus overlapping. *Yellow dotted lines* represent fitted curves for the initial 30 blocks of reach deviations (RD = $c - ae^{(-bn)}$). Dual workspace 45 CCW ($17.74 + 8.24e^{(-0.116n)}$), dual workspace 45 CW ($-15.9 - 17.26e^{(-0.314n)}$)

complete in the former (Dual Workspace 30 vs. Dual Workspace 45). Also, combining visual with workspace cues did not provide additional benefits (Dual Workspace vs. Dual Workspace with Cue).

Colour and shape cues

Results from the 'Dual Cue' group did not suggest dual adaptation and is similar to other studies where colour was used as a contextual cue. Whereas these studies generally incorporated colour cues in a more abstract manner, such as with the background colour of a monitor (red CW and blue CCW rotations) (Woolley et al. 2007; Hinder et al. 2008b), frame around the workspace (blue rightward and red leftward forces) (Gupta and Ashe 2007) or colour of an illuminated room (green CW and red CCW force fields) (Gandolfo et al. 1996), we provided cues that were more integrated with components of the task. However, this did not facilitate dual adaptation.

This is in contrast to Osu et al. (2004), where they demonstrated dual adaptation in a dynamics task (velocity-dependent force field) using only background colour cues (red CW and blue CCW). To reconcile these findings, we considered the critical differences between studies. For example, whereas we provided subjects with concurrent feedback of the cursor during training, trajectory information in Osu et al. (2004) was provided after the trial, which could be associated with strategic learning (Hinder et al. 2008a). Also, whereas our experiment consisted of 360 rotated trials contained within a single training session, Osu et al. (2004) had almost 700 perturbation trials spread over 2 days, providing more training and time for consolidation. Lastly, whereas our task was kinematic in nature, theirs was dynamic and these systems are mediated by different mechanisms (Krakauer et al. 1999; Caithness et al. 2004; Diedrichsen et al. 2005; Shadmehr et al. 2010). Given these possibilities, further research will have to be conducted to confirm the relevant differences.

Although we did not observe dual adaptation, there seemed to be some improvement in our 'Dual Cue CW' group and this improvement (for only one rotation) is similar to what was reported in Hinder et al. (2008b). While colour and shape cues might appear to be effective in these circumstances, it may not actually be facilitating genuine adaptation. This is because the initial error for 'Dual Cue CW' trials was actually greater than the rotation applied, and even larger than the initial trials of 'Dual Cue CCW', so while the final block of the 'Dual Cue CW' was better relative to its initial, this was likely due to performance simply approaching the magnitude of rotation which is not indicative of genuine improvement. The lack of after-effects also supports this explanation. For these reasons, we do not believe that our colour and shape cues facilitate learning in a

dual rotation paradigm, even for a single rotation. Although we are uncertain as to why reach errors within 'Dual Cue' CW trials were higher than expected, it could have been an artefact of the targets for this group being along the diagonal (Fig. 3). Subjects may have initially reached more along the cardinal direction, consistent with the motor oblique effect (Mantas et al. 2008). Specifically, subjects may have begun by reaching a bit more rightward to these diagonal targets, which may have introduced the CW bias.

Target separation and hand movement similarities

Exploring the role of target locations and associated hand movement trajectories were important aspects to consider as either component could have contributed substantially to the outcome of dual adaptation. Previously, Woolley et al. (2007) had a condition where opposing visuomotor rotations were coupled with two target sets, separated by an average of 180°, and required compensatory hand torques separated by an average of 120° to achieve accurate performance. Under these conditions, both substantial target separation and distinct hand torques existed, and while subjects were able to dually adapt, it is not clear whether target locations or distinctive hand torques primarily contributed to dual adaptation. Indeed, Woolley et al. (2011) recently followed up on this question and showed that dual adaptation occurred when visuomotor rotations were coupled with targets located in separate regions of workspace and required similar hand torques for pairs of targets (Woolley et al. 2011).

Our study also addressed the question by exploring conditions where compensatory reach trajectories would have been similar and overlapping to accurately acquire pairs of targets in an unconstrained reach task. Specifically, target sets in our 'Dual Workspace' condition were separated by an average of 90°, forcing accurate compensatory reach movements to fall between them, separated by an average of only 30° (similar movements). Our results show that subjects were able to adapt under these conditions, which was surprising given that adaptation to one target set could have negatively influenced reaching towards to the other target set due to generalization of learning (Krakauer et al. 2000; Wang and Sainburg 2005). More importantly, however, it demonstrates that movement distinction was not necessary for dual adaptation and suggests that learning was primarily driven by differences in target location, similar to Woolley et al. (2011). While reach movements were considered to be similar under these conditions, there was some motor distinction as reaches were separated by an average of 30°. To eliminate this distinction, we added an additional group to the study.

The additional 'Dual Workspace 45' group experienced 45° rotations allowing us to assess performance when

movement trajectories overlapped between pairs of targets (no movement distinction). Our results show that subjects were able to dually adapt under these conditions, again suggesting that target locations rather than muscle distinction facilitated dual adaptation. Interestingly, however, our results showed that the dual adaptation under this group was not as complete as the 'Dual Workspace 30°' group, that is, adaptation was more complete when there was visual target separation in conjunction with some motor separation (Dual Workspace 30°), as compared to only target separation (Dual Workspace 45°).

These findings contribute to the understanding of dual adaptation by showing that target separation alone can facilitate dual adaptation (but not motor distinction alone as in the 'Dual Cue' group) and importantly, that interference can be further reduced by having an element of motor distinction as well. This is distinct from Woolley et al. (2011) where they varied the degree of visual separation. Here, we maintained target separation and varied the type of information that was available to subjects (motor and visual vs. visual), addressing the contribution of various sources of information. More complete adaptation in 'Dual Workspace 30' compared to 'Dual Workspace 45' was likely due to the additional motor distinction present in the former. This suggests that both sources of information play a role in the formation and selection of internal models and that there might be an optimal integration of both signals. Since both are relevant factors, future research can explore the combined nature of these signals rather than considering them in isolation, and this helps to explain why there is evidence of both types of information being capable of influencing adaptation.

Internal models

The Modular Selection and Identification for Control (MOSAIC) theory has been proposed to explain how humans might develop accurate compensatory movements and choose among them within a variable environment. Modules contain forward models, responsibility predictors and inverse models which allow for the appropriate selection of modules based on contextual cues (Kawato 1999; Haruno et al. 2001).

Since colour and shape cues or target location cues were consistently associated with each of our rotations, either could have provided adequate information for the 'responsibility predictor' to add greater weight about the probability of encountering one of the rotated environments over the other. Target locations, rather than colour and shape cues, seemed to provide more useful information since subjects compensated for CW rotations when reaching to the right target set, and for CCW rotations when reaching to the top set, in an accurate feed-forward manner. Target locations as

a contextual cue likely allowed for the responsibility predictor to select appropriate compensatory responses, and this occurred even when hand movement trajectories were similar or overlapping.

Conclusion

Colour and shape cues do not facilitate learning when they are the only cues available to distinguish between rotations. However, target locations (directions relative to start positions) coupled with opposing rotations provide sufficient information to facilitate motor adaptation, even when similar or overlapping movement trajectories are required.

Conflict of interest The authors declare no conflict of interest.

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