RESEARCH ARTICLE

# The efficacy of colour cues in facilitating adaptation to opposing visuomotor rotations

**Mark R. Hinder · Daniel G. Woolley ·
James R. Tresilian · Stephan Riek · Richard G. Carson**

**Abstract** We investigated visuomotor adaptation using an isometric, target-acquisition task. Following trials with no rotation, two participant groups were exposed to a random sequence of 30° clockwise (CW) and 60° counterclockwise (CCW) rotations, with (DUAL-CUE), or without (DUAL-NO CUE), colour cues that enabled each environment (non-rotated, 30° CW and 60° CCW) to be identified. A further three groups experienced only 30° CW trials or only 60° CCW trials (SINGLE rotation groups) in which each visuomotor mapping was again associated with a colour cue. During training, all SINGLE groups reduced angular deviations of the cursor path during the initial portion of the movements, indicating feedforward adaptation. Consistent with the view that the adaptation occurred automatically via recalibration of the visuomotor mapping (Krakauer et al. 1999), post-training aftereffects were observed, *despite* colour cues that indicated that no rotation was present. For the DUAL-CUE group, angular deviations decreased with training in the 60° trials, but were unchanged in the 30° trials, while for the DUAL-NO CUE group angular deviations decreased for the 60° CW trials but *increased* for the 30° CW trials. These results suggest that in a dual adaptation paradigm a colour cue can permit delineation of the two environments, with a subsequent change in behaviour resulting in improved performance in at least one of these environments. Increased reaction times within the training block, together with the absence of aftereffects in the post-training period for the DUAL-CUE group suggest an explicit cue-dependent strategy was used in an attempt to compensate for the rotations.

**Keywords** Visuomotor rotation · Adaptation · Internal model · Visuomotor mapping · Interference · Implicit and explicit learning · Dual adaptation

M. R. Hinder · D. G. Woolley · J. R. Tresilian ·
S. Riek · R. G. Carson
Perception and Motor Systems Laboratory,
School of Human Movement Studies, University of Queensland,
Brisbane 4072, Australia

M. R. Hinder (✉)
School of Psychology, University of Tasmania,
Sandy Bay Campus, Hobart, TAS 7000, Australia
e-mail: Mark.Hinder@Utas.edu.au

D. G. Woolley
Motor Control Laboratory,
Research Centre for Movement Control and Neuroplasticity,
Department of Biomedical Kinesiology,
Katholieke Universiteit Leuven, Leuven, Belgium

J. R. Tresilian
Department of Psychology,
University of Warwick, Coventry CV4 7AL, UK

R. G. Carson
School of Psychology, Queen's University of Belfast,
Belfast BT7 1NN, Northern Ireland, UK

## Introduction

Adaptation is a process which is crucial to enable accurate motor tasks to be executed when exposed to novel environmental conditions. When initially exposed to a novel environment, for example a strong wind, movements are perturbed and we will fail to execute the desired task. However, with time, movements resemble those observed in the natural, or non-perturbed, environment. It is conceivable that this behavioural adaptation—a reduction of the errors initial exhibited in the novel environment—may be mediated by a variety of different neural and cognitive mechanisms.

Recent evidence suggests that adaptation may involve the development of an internal model (Kawato 1999). When adapting to novel forces the model compensates for the environmental forces encountered such that the desired behaviour is achieved, while in the case of a visuomotor perturbation, the model takes the form of a visuomotor map that transforms visual information into motor commands (Cunningham 1989; Krakauer et al. 1999). Experimentally, the formation of internal models can be assessed by exposing participants to novel forces (Shadmehr and Mussa-Ivaldi 1994) or perturbations of the visuomotor relationship, e.g. non-linear transformations (Flanagan and Rao 1995; Wolpert et al. 1995; Ghahramani and Wolpert 1997) or visuomotor rotations (Cunningham 1989; Krakauer et al. 1999; Wigmore et al. 2002). The formation of an internal model is characterised by the observation of aftereffects (Shadmehr and Mussa-Ivaldi 1994)—movement errors in the opposite direction to those observed upon initial exposure to the novel environment—upon re-exposure to the un-perturbed, or null, environment.

In a recent study, Mazzoni and Krakauer (2006) addressed the issue of the mechanisms mediating visuomotor adaptation. Participants aimed at visual targets presented radially around a central start position while exposed to a visuomotor rotation. Certain participants were provided with a verbal instruction ("aim to the neighbouring target") to compensate for the rotation. Following training the performance of these participants was *worse* than for those participants who adapted *without* verbal instruction. For the 'instructed participants' the authors suggest that there was a conflict between automatic adaptation that was presumably mediated by the re-configuration of the visuomotor map (Cunningham 1989; Krakauer et al. 1999), and an explicit form of adaptation engaged in response to the verbal instruction.

While the explicit mechanism was not useful in the context of the Mazzoni and Krakauer experiment, it may be that such mechanisms *can* be used successfully when the task characteristics prohibit adaptation from occurring via the (normally preferred) automatic mechanism. Indeed, extant studies indicate that it is difficult for the motor system to concurrently form distinct internal models or visuomotor maps for two novel environments discriminable only via contextual (colour) cues, a concept known as 'dual adaptation'. Gandolfo et al. (1996) reported that dual adaptation was not possible when participants were exposed to alternating blocks of 48 trials in two conflicting force fields when the different fields were associated only with colour cues. Woolley et al. (2007) reported that dual adaptation to equal and opposite 30° visuomotor rotations in an isometric target acquisition task was not possible solely on the basis of colour cues. In contrast, Osu et al. (2004) reported that colour cues did permit simultaneous formation of two inter-

nal models for two opposing force fields when the opposing fields were presented in a random, but not in a predictable (alternating), order.

The contrasting conclusions that have been drawn on the basis of existing dual adaptation literature suggest that apparently subtle differences in the available discriminative cues, as well as the specific adaptation task employed, can have a significant effect on the ability to concurrently adapt to multiple novel environments. In addition, although most human studies indicate that colour cues alone are not sufficient to allow dual adaptation, Krouchev and Kalaska (2003) found that monkeys could issue distinct feedforward commands to compensate for resistive or assistive forces solely on the basis of these cues. Given all the available data, it appears that under certain conditions colour cues can be sufficient to permit dual adaptation to novel visuomotor environments—the problem then is to determine exactly what these conditions might be. Furthermore, extant studies have not been designed to investigate the specific nature of any adaptation that may occur on the basis of the available colour cues.

In the present study, we studied visuomotor adaptation to two conflicting rotations (i.e., dual adaptation) of opposite polarity and unequal magnitude when each rotation was differentiated via a colour cue. We specifically compared the nature of any observable adaptation in the dual-rotation paradigm to the nature of the adaptation observed for participants who were only exposed to a single novel rotation.

Participants were required to move a cursor to target locations by exerting isometric torques about the two axes of rotation of the forearm (the flexion–extension and prona-tion–supination axes). The isometric task allowed us to focus on participants' ability to compensate for the external (imposed) perturbations (rotations) without the potential influence of the anisotropic visco-elastic properties of the effector system (Pellegrini and Flanders 1996). Previous work in our laboratory (Hinder et al. 2007, 2008) has indicated that in this isometric task context, adaptation to a single rotation occurs in a manner that is consistent with an automatic reconfiguration of a visuomotor map (Cunningham 1989; Krakauer et al. 1999) and displays attributes such as consolidation and interference. Following non-rotated or veridical trials, separate groups of participants were exposed to a 30° clockwise (CW) rotation of the visual (performance) feedback; a 60° counter clockwise (CCW) rotation, or a randomised presentation of both rotations. The participants were thus required to alter the patterns of muscle activation needed to acquire the various targets, with respect to those generated in the veridical feedback condition. The novel rotation(s) encountered in the training period could be differentiated from one another, and from the non-rotated task, by way of colour cues. The participants' ability to use colour cues to accurately select

motor commands for the specific environment in each trial, together with reaction times between target presentation and movement onset, were used to infer the nature of the mechanisms mediating any observable adaptation. Our results indicate that, consistent with previous work, adaptation to the single rotations occurred automatically, via a recalibration of the visuomotor map. In the dual-adaptation task, our data indicate that automatic adaptation was not possible. In the absence of such an automatic adaptation, an explicit, cue-specific, strategy was employed that was sufficient to reduce performance errors to some degree.

## Methods

### Participants

Thirty-six self-reported right-handed participants (22 males, 14 females, 19–44 years) participated in this study. All participants gave informed consent to the procedures, which were approved by the Medical Ethics Committee of the University of Queensland, and conformed to the Declaration of Helsinki.

### Apparatus

Participants sat in a height-adjustable chair 65 cm from a computer display, positioned at eye level. The right arm was placed in a custom made restraint, which was positioned such that when the participant grasped the manipulandum (Fig. 1), the elbow was flexed at 90°, the forearm was in a neutral position, half way between pronation and supination, and the participant's palm vertical. Participants grasped an instrumented vertical cylindrical handle, with pads positioned above and below in order to minimise movement of the hand.

Forces and torques exerted on the isometric manipulandum were recorded using a six degree of freedom force/torque transducer (Delta ATI, Industrial Automation, USA). Force (flexion/extension) and torque (pronation/supination) were sampled at 2 kHz at an analogue to digital interface (AT-mio-16E-10, National Instruments, Texas) and saved to a personal computer for subsequent off-line analysis. LabVIEW (vers 5.0, National Instruments, Texas) was used to write in-house experimental control and data acquisition routines. Further analysis routines were implemented using Matlab.

### Procedure

Visual feedback of the torques along the pronation/supination (*x*-axis) and flexion/extension (*y*-axis) degrees of freedom was provided in real-time via movement of a cursor on
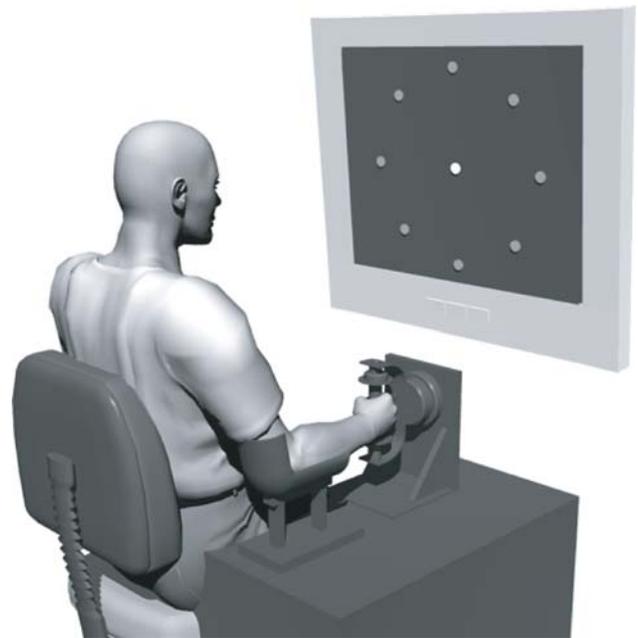


**Fig. 1** Experimental set-up. Participants held the manipulandum and controlled cursor movement via flexion–extension (vertical cursor movement) and pronation–supination (horizontal cursor movement) torques of the elbow–forearm complex. Torques were measured by the force/torque transducer positioned behind the handle. Movement of the cursor was scaled equally for all target directions and all participants, such that a fixed torque would result in a specific cursor displacement. When participants relaxed their arm in the restraint, zero torque was registered, and the cursor appeared at the start position in the centre of the screen (depicted as a *white dot*). One of eight visual targets (represented as *grey dots*), equally spaced around the start position, was presented on each trial

the computer display. The magnitude of the cursor displacement from the start position was directly proportional to the level of torque generation. Elbow flexion and extension torques resulted in a vertically upward, and downward, cursor movement, respectively. Pronation and supination torques resulted in cursor movement to the left, and right, respectively.

A yellow dot at the centre of the screen, corresponding to zero torque, was presented at the beginning of each trial and represented the start zone. Each trial began with a random period of 1–3 s, during which participants were instructed to stay within the start zone. One of the eight targets, equally spaced at 45° intervals around, and at a constant distance of 5.4 cm from the start zone was then presented as a yellow dot. Presentation of the target was accompanied by an auditory tone. Participants were instructed to move the cursor to the target as quickly as possible by producing isometric torque in one or both of the two degrees of freedom of the elbow–forearm complex (flexion–extension; pronation–supination). When the cursor was within the target zone, defined as a region ±5% with respect to the specific target torque requirements (see the

target torque computation section below), the target turned red. Once the participants had held their torque within the target zone for a period of 100 ms a second tone was generated (indicating a successful trial), at which point participants relaxed, and the cursor returned to the start zone. Each trial lasted 10 s. During trials in which the participant failed to acquire the target within this period, there was no second tone (unsuccessful trials) and the target disappeared. The trial was not repeated, and the next trial began as normal.

Participants were randomly assigned to one of five groups (eight participants per group SINGLE rotation groups and DUAL-CUE group; four participants in the DUAL-NO CUE group, see below). Each group was exposed to three separate blocks of trials. In each block there was a specific relationship between the direction of torque production and direction of the ensuing cursor movement. The visual feedback was either veridical (the cursor moved in the intuitive direction) or perturbed, whereby the cursor movement was rotated with respect to the torque direction. The background colour of the computer display indicated the operative relationship between the direction of torque production and the direction of ensuing cursor movement (i.e., the visuomotor relationship) for all but the DUAL-NO CUE group (see below).

The PRE block consisted of ten trials to each target, during which the cursor moved in the intuitive direction, i.e., flexion torque moved the cursor up, extension moved the cursor down, etc. The purpose of this block was to provide familiarisation with the general relationship between torque production and movement of the cursor. Within each 16-trial cycle, two trials to each target were undertaken; the order of target presentation within the cycle was randomised. The PRE block consisted of five such cycles, resulting in a total of 80 trials. All PRE trials were conducted with a black background on the visual display.

Following the PRE block, three groups were exposed to a block of trials consisting of a single visuomotor rotation (SINGLE rotation groups). One of these groups (R30) was exposed to a condition in which visual feedback of the cursor position was rotated 30° clockwise (CW), with respect to the direction of torque production. A second group (R60) was exposed to a condition consisting of a 60° counter-clockwise (CCW) rotation. These training, or rotation (ROT), blocks consisted of 40 trials to each target (20 cycles), i.e., 320 trials. 30° CW trials were performed with a red background, while 60° CCW trials were performed with a blue background. A third group of participants undertook a substantially shorter ROT block, consisting of three trials to each target (24 trials in total) in the presence of a 60° counter-clockwise (CCW) rotation (R60short), again accompanied by a blue background.

The fourth group of participants undertook 40 trials to each target under *both* the 30° CW and 60° CCW rotations (40 cycles, 640 trials; 320 trials in each rotation condition). For this group, each cycle consisted of one trial to each target under each rotation. Both the target location and rotation type were randomised within each cycle. There was a brief break after 20 cycles in order to prevent fatigue. Again, a red background indicated 30° CW rotation, while a blue screen accompanied 60° CCW trials. The screen colour was refreshed at the start of each trial, such that the participant was provided with information during the trial foreperiod (prior to target presentation) that indicated the rotation that would be applied. In this group, we assessed the ability of participants to adapt to two rotations (i.e., the ability to *dual adapt*), when each rotation could be identified by a colour cue. This group will be referred to as the DUAL-CUE group.

The final group of participants were exposed to the same random presentation protocol as that described for the DUAL-CUE group, with one important difference: this group *did not* receive colour cues to enable each task variant (or rotation) to be identified. Instead of red and blue screens, participants saw the same black screen which had been used in the PRE block. Thus, because the presentation of the 30° CW and 60° CCW trials was again randomised, this group had no means to determine which task they would encounter on any particular trial within the training (ROT) block. This DUAL-NO CUE group therefore provides a direct 'control' for the DUAL-CUE group which enables us to assess the capacity of colour cues to permit dual adaptation. We note that for the DUAL groups, exposure to two rotations of *unequal* magnitudes would enable us to discriminate between a scenario where participants compensated for the mean of the two rotations and that situation where participants simply did not attempt to adapt to either rotation. With equal and opposite rotations, this differentiation would not be possible.

Finally, all groups repeated the protocol used in the initial block (POST). A black screen was presented in this non-rotated block, as was the case in the PRE block. Thus, we provided those participants who had received colour cues within the ROT (or training) block sufficient information to enable them to be aware that the initial condition was being replicated. The purpose of the POST block was to assess potential aftereffects that may have occurred as a result of exposure to the rotations. There was a short break between the PRE and ROT and ROT and POST blocks of ~1 min. During this period, participants remained seated with their arm relaxed in the manipulandum. The computer screen remained blank during this short period. In total, the experimental protocol lasted approximately 90 mins for the R30 and R60 groups, 35 mins for the R60short and 135 mins for the DUAL group.

All participants were instructed to acquire the target as quickly as possible in each trial. Those participants who received colour cues were informed that the colour of the computer screen indicated the relationship between the direction of the forces they produced, and the direction in which the cursor would move. They were told that each screen colour represented a different relationship, and that each relationship may be repeated within the experiment. These instructions were re-stated at the commencement of each block. The DUAL-NO CUE group were simply reminded at the commencement of each trial block to acquire the target as quickly as possible on each trial.

The R30, R60 and both DUAL groups were all exposed to the same number of trials in the respective rotated environments (320 trials). While this controlled for the level of exposure to the rotated environment, re-exposure to the non-rotated environment may have been affected by the degree of performance improvement apparent in the training (ROT) block, which, initial analysis revealed, was greater for R30 and R60 groups than for the DUAL groups (see "Results"). Thus, the R60short group was included to assess re-exposure to the non-rotated environment in circumstances in which smaller performance improvements had occurred during exposure to the rotated environment. The number of trials in this block was determined in a post hoc manner. We fitted a power function of the form $y = ax^b$ to the participant average data in the ROT block for the R60 and DUAL-CUE groups. Using the time constants of these power functions, we estimated that performance following three trials to each target in a block of only 60° CCW trials would be similar to that observed in 60° CCW trials following completion of the ROT block for the DUAL-CUE group. Thus, the R60short group enabled us to control for the degree of adaptation within the ROT block, rather than only controlling exposure level (number of trials).

The torque magnitude required to attain each target was identical across all targets and experimental blocks, was well within the capabilities of all participants (10–20% of participants' maximum torque capacity), and was small enough to minimise possible fatigue effects. For targets representing combinations of torques in two degrees of freedom, the vertical (flexion/extension) and horizontal (pronation/supination) torque components were determined as the cosine of the subtended angle between the target direction and the single degree of freedom target, multiplied by the single degree of freedom torque. In the ROT block, the vertical and horizontal torque components were re-calculated according to the imposed rotation (30° CW or 60° CCW).

For all trials, the angular mapping between force/torque production and cursor displacement was unitary, i.e., $x°$ error in the direction of torque production relative to the required torque direction (which, due to the rotation of the visual feedback, may not be in the same direction as the visual target) resulted in an angular error of $x°$ in visual co-ordinates.

Data reduction and analysis

Torque time series, representing cursor position in the two degrees of freedom, were digitally low-pass filtered at 15 Hz with a second-order, dual pass Butterworth filter. Movement onset was determined using an algorithm based on cursor speed (Teasdale et al. 1993), with an initial threshold of 15% of the maximum tangential speed. Movement offset was determined as the time 100 ms prior to the second tone, i.e., the start of the first period of at least 100 ms duration in each trial in which participants remained in the target zone.

Angular error, $\theta$, was calculated as the average angle between the vector defined by the start and target positions, and the vector defined by the start position and actual cursor position, in a 10 ms window centred at 100 ms after movement onset. On the basis of the assumption that no modifications based on visual feedback would occur prior to 100 ms, this measure assessed *feedforward* performance.

Reaction time (RT), was also calculated as the interval from target presentation to movement onset and was used as a measure of length of the pre-movement planning period. One might anticipate that adaptations to rotation(s) via mechanisms that automatically modify the visuomotor map (i.e., implicit adaptation, Krakauer et al. 1999; Mazzoni and Krakauer 2006) would not impact upon reaction times. In contrast, if adaptations are mediated by the application of explicit response strategies (Mazzoni and Krakauer 2006), pre- planning, and thus reaction times, may increase.

Previous work in our laboratory has indicated that in this particular isometric task, participants' initial performance did not vary as a function of target location nor did the ability to improve performance with training vary as a function of target position (Hinder et al. 2007, 2008). As such, we characterised performance by computing cycle averages for both dependent variables (i.e., angular error and reaction time)—see "Procedure" for the specific definition of cycle. This method of characterising performance has been used extensively in the motor learning literature (e.g., Krakauer et al. 1999; Caithness et al. 2004; Hinder et al. 2007) Note that for the DUAL groups, cycle averages for the ROT (training) block were computed for each rotation (30°CW and 60°CCW) *separately*. The first (initial) and last (final) cycle of each experiment block (PRE, ROT and POST), i.e., PREintial, PREfinal, ROTinitial, ROTfinal, POSTinitial and POSTfinal were used for subsequent statistical analyses.

A two-way (three blocks {PRE, ROT, POST} × two cycles {initial, final}), repeated measures ANOVA was

performed for the three single rotation groups (R30, R60, R60short), while for the DUAL groups (i.e., DUAL_CUE and DUAL-NO CUE) we conducted a three-way (two rotations {30° CW, 60° CCW} × three blocks {PRE, ROT, POST} × two cycles {initial, final}) repeated measures ANOVA. These ANOVAs provided a framework for a set of theoretically meaningful *planned comparisons* where the ANOVA sum of squares value could be used to determine effect size associated with each of the comparisons. All comparisons were conducted at the a priori alpha level of 0.05. We note that planned comparisons *are not contingent upon the presence of statistically reliable main effect or interaction terms* (c.f. post hoc tests, where main or interaction effects *must* be significant to allow post hoc analyses to be conducted–see Keppel 1982).

For angular error, two planned comparisons were conducted for each SINGLE group, and for each rotation within the DUAL groups. To determine if any adaptive responses occurred in response to the imposed rotation (within the training period), we compared angular error in the ROTinitial cycle to that in the ROTfinal cycle. We also compared POSTinitial with PREfinal to determine if aftereffects were manifested as a result of exposure to the rotated environment(s)—i.e., did exposure to the rotated environment(s) have any affect on performance in the non-rotated task environment?

For RT, three planned comparisons were undertaken: first, we compared POSTfinal and ROTinitial to determine if the initial exposure to the rotation resulted in a change in the reaction time. We then conducted the same two planned comparisons as those described for angular error: ROTinitial versus ROTfinal determined whether reaction time in the novel environment changed within the course of training, while the PREfinal versus POSTinitial comparison was used to assess whether the reaction time in the non-rotated task was affected by exposure to the novel rotation(s).

The modified Bonferroni adjustment for multiple comparisons was used to adjust the alpha value for each comparison, such that the a priori criterion for statistical

significance was maintained. In order to further assist in the interpretation of the tests of significance, measures of effect size were calculated following Cohen (1969). The effect size index, *f*, for planned comparisons within an ANOVA is a dimensionless index, which describes the degree of departure from no effect, in other words, the degree to which the phenomenon is manifested.

## Results

Figure 2 shows cursor paths in the first and last trial of each of the three blocks for one participant in the R60 group. Paths are only shown for four of the eight target directions for purposes of clarity, but are representative of all target directions. Qualitatively, paths within the PRE block are relatively straight. Initial exposure to the rotation(s) lead to angular deviations in the direction of the imposed rotation, which was reduced with training. Aftereffects—angular deviations in the opposite direction to the deviations exhibited upon initial exposure to the rotation—are clearly manifested upon re-exposure to the non-rotated environment (POST block) in this instance.

### Angular error

Figure 3a–e shows target-average angular errors in the three experimental blocks for each participant group. For all groups, and consistent with our previous work (Hinder et al. 2007, 2008; Woolley et al. 2007), angular errors within the pre-training (PRE) block were small, and no changes in angular error within the PRE period were observed. This suggests that the directional control of the cursor was fairly intuitive, i.e., participants understood the mapping between motor commands and cursor movements in the non-rotated task environment. As expected, for all groups, introduction of the rotation(s) led to an increase in angular error, the magnitude and direction of which was related to the magnitude and direction of the imposed



**Fig. 2** Example of cursor paths. Paths are shown for the first (*thin line*) and last trial (*thick line*) to four different targets in each movement block (PRE *left*; ROT *centre*; POST *right*) for an individual participant in the R60 group
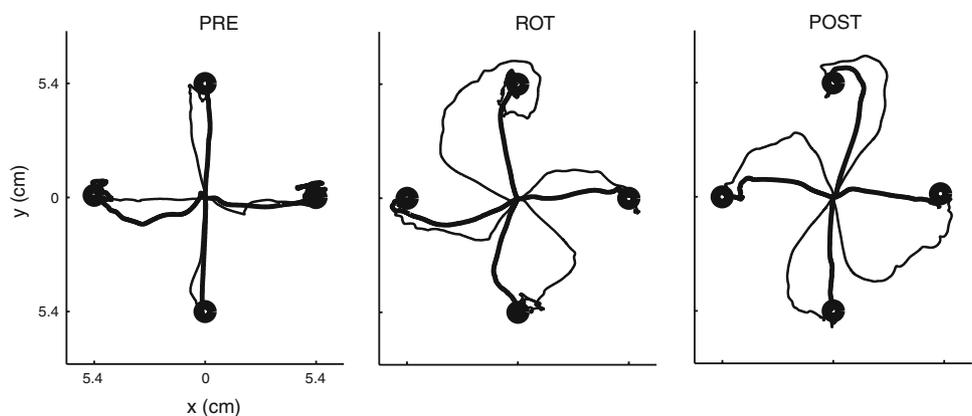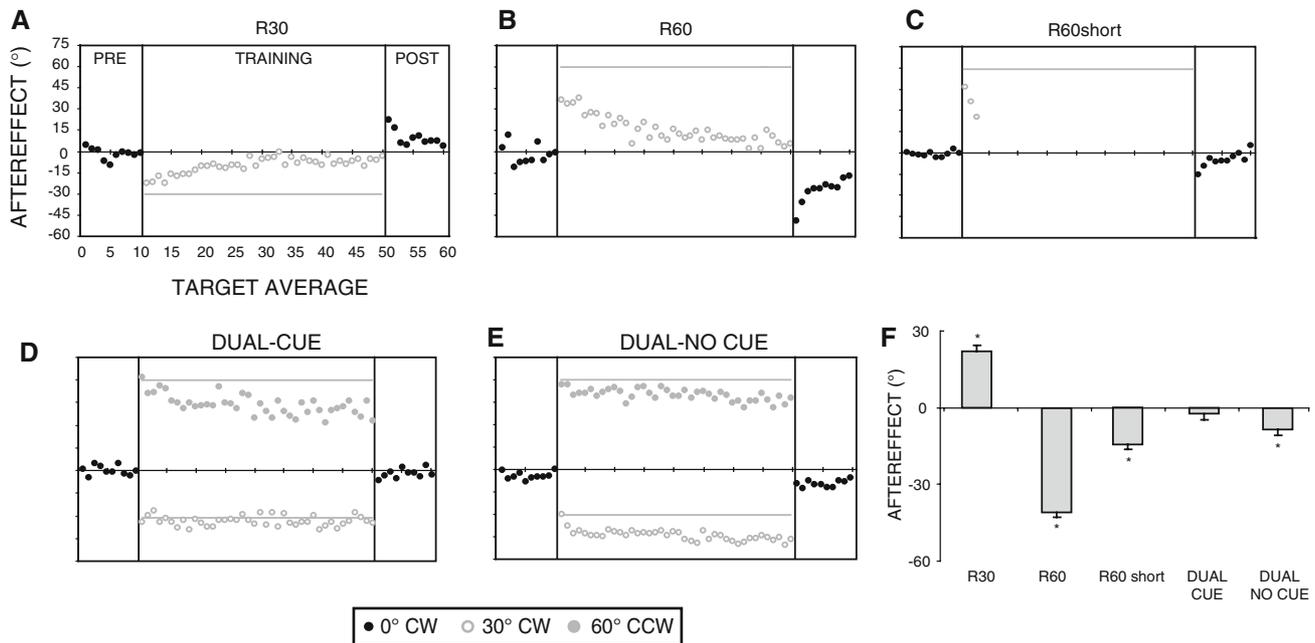
**Fig. 3** Performance indicated by angular error over the course of the experiment for each group. **a–e** Group mean (averaged across targets) angular errors for the five participant groups. *Horizontal lines* show the magnitude of the imposed rotation in each ROT block. Note that the data are shown relative to the PREfinal cycle, i.e. any small offsets relative to a straight-line cursor path have been removed to allow better inter-group visual comparisons. The horizontal and vertical scale are identical for plots **a–e** (see **a** for scale) **f** Aftereffects in the POSTinitial trial, relative to that in the PREfinal trial (error bars show 95% confidence intervals) for each group. * Denotes a significant aftereffect ($P < 0.05$)

rotation. To assess the extent to which angular error could be reduced with training in the novel rotated environment, we compared the angular error in the initial training trials (ROTinitial) to that error in the trials following completion of the training (ROTfinal). For all SINGLE rotation groups, angular error was significantly reduced within the training period ($P < 0.05$, $f = 0.57$, $0.55$ and $0.46$ for R30, R60 and R60short groups, respectively). For the DUAL-CUE group, angular error for the 60° CCW trials was significantly reduced over the course of training ($P < 0.05$, $f = 1.22$), while no significant change occurred on the 30° CW trials ($P = 0.78$, $f = 0.05$). For the DUAL-NO CUE group there was a significant decrease in the angular error for the 60° CCW trials within the training period ($P < 0.05$, $f = 0.74$), together with a significant *increase* in the angular error of the 30° CW trials ($P < 0.05$, $f = 1.32$). Following completion of the training period, the magnitude of the error in the 60° CCW rotation was 47.0°, and in the 30° CW rotation the error was 44.4°, i.e., following training, the magnitude of the error in each rotation was similar. This is consistent with participants compensating for the mean of the two rotations on each trial.

On re-exposure to the non-rotated environment, as indicated by the change in colour cue, all SINGLE groups exhibited significant aftereffects; the angular error in the initial POST block trials (POSTfinal) was signifi-

cantly larger than that in the final non-rotated trials prior to the training period i.e., PREfinal ($P < 0.05$, $f = 0.69$, $0.73$ and $0.30$ for the R30, R60 and R60short groups, respectively). As expected, this aftereffect was in the opposite direction to that error observed when these participants were initially challenged with the rotated environment. For the DUAL-CUE group, there was no significant difference between the non-rotated trials immediately prior to (PREfinal) and following (POSTinitial) the training period ($P = 0.50$, $f = 0.13$), indicating an absence of aftereffects. In contrast, for the DUAL-NO CUE group the angular error in the trials following training (POSTinitial) was of larger magnitude than that error in the PREfinal trials before training ($P < 0.05$, $f = 0.69$). The magnitude of this aftereffect was 8.3° and occurred in a clockwise direction. This is consistent with participants issuing motor commands that would compensate for the mean of the two rotations encountered in the training block. The fact that the magnitude of the aftereffect is somewhat less than 15° is accountable for by the not insignificant amount of relearning that occurred during the first cycle of trials within the POST block. Indeed, the value of the aftereffect on the first few trials of the first POST cycle was often greater than 15°. The magnitude of the aftereffect for each participant group is clearly depicted in Fig. 3f.

Comparison of motor commands in the 30° CW and 60° CCW trials of the DUAL groups following training

To aid in the interpretation of our results, we also wished to compare the direction of *torque production* in the ROT-final trials in the 30° CW and 60° CCW trials for the DUAL-CUE and DUAL-NO CUE groups (Fig. 4). Rather than compare the direction of the cursor 100 ms after movement onset (i.e., the angular error of the cursor) which is dependent, of course, on the visuomotor rotation, we compared the direction of the two-dimensional torque vector at 100 ms, as measured from the transducer mounted in the handle of the manipulandum. This measure assesses participants' actual motor commands (or actions) rather than the consequences of those actions in the various visual environments (rotations). Accordingly, this particular comparison enables us to determine if, following learning, participants were able to issue different motor commands in each task variant (i.e., the 30° CW and 60° CCW rotations). For the DUAL-CUE group, the initial direction of the torque vector, following training (POSTfinal) was significantly different in the two rotations ($P < 0.05$, $f = 0.86$; Fig. 4c). In the 60° CCW trials the torque vector had been rotated approximately 30° over the course of the training, while there was no trend for a change in the direction of the torque vector in the 30° CW trial training (Fig. 4a). We note that the $\sim -10°$ offset in the torque vector for the DUAL-CUE 30° CW trials throughout the training phase (see Fig. 4a) can be accounted for by the fact that similar-magnitude negative offsets ($-5$ to $-10°$) were apparent throughout the PRE block for this group, i.e., participants produced a similar torque in these 30° CW trials as they had done in the PRE (non-rotated) trials.

In contrast, for the DUAL-NO CUE group, there was no significant difference in the initial direction of the torque vector following training in the two rotations ($P = 0.61$, $f = 0.12$; Fig. 4c). For this group, the accumulated adaptation across both rotations resulted in a change in torque direction (for both rotations) of $-15°$ (i.e., 15° CCW) over the course of the training period (Fig. 4b, c). By completion of the training, participants were compensating for the mean of the two imposed rotations.

Due to the fact that the presentation of each rotation was randomised for both DUAL groups, these results suggest that the DUAL-CUE group *were* able to discriminate between the two rotations on the basis of the colour cue and issue different motor commands for each task variant. In contrast, the DUAL-NO CUE group were not able to discriminate between the two rotations and therefore issued similar motor commands (which compensated for the mean of the two environments), regardless of the (unknown) rotation on any particular trial.
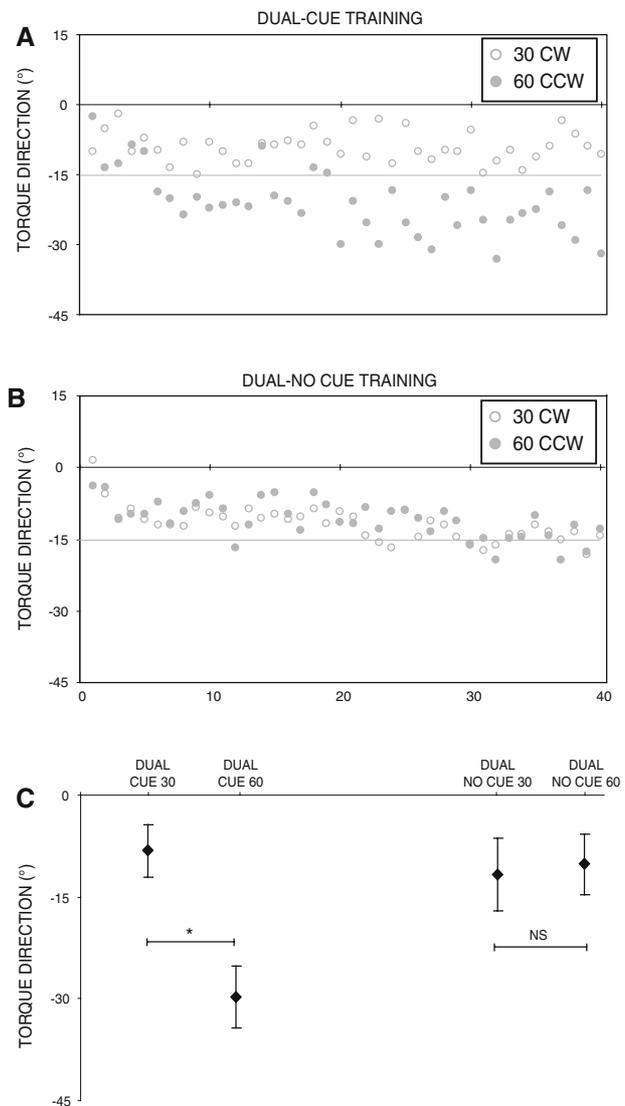


**Fig. 4** Initial direction of torque production (at 100 ms) during the ROT block for the DUAL-CUE (**a**) and DUAL-NO CUE (**b**) groups. The horizontal line at $-15°$ represents the average of the 30º CW and 60º CCW visuomotor rotations. **c** Initial direction of torque production for each rotational variant on the final cycle of the ROT (training) block. A significant difference was found between the directions of torque produced in each rotation in the DUAL-CUE group, suggesting colour cues enabled the planning of two different sets of motor commands. No significant difference was observed between the directions of torque produced in each rotational variant in the DUAL-NO CUE group, indicating that participants issued the same motor commands in each rotation on completion of the training period

*Reaction time*

Figure 5 displays the change in RT in the initial and final cycle of the training (ROT) block, as well as the initial cycle of the POST block, with respect to the RT in the final cycle of the PRE block. Initial exposure to the rotation (ROTinitial) led to an increase in RT for all SINGLE rotation groups,
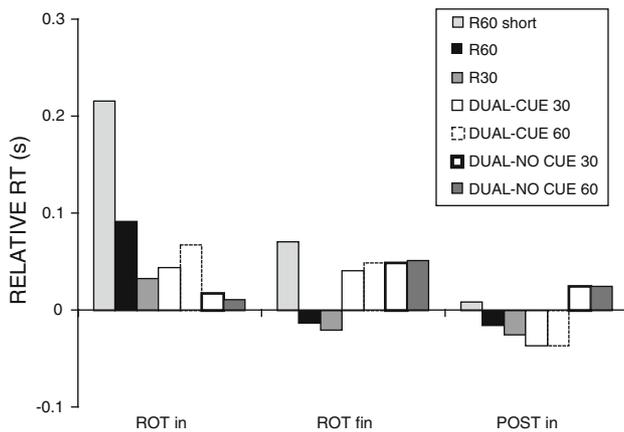
**Fig. 5** Reaction time (*RTs*) are shown in the ROTinitial, ROTfinal and POSTinitial cycles, relative to the PREfinal RT, for each of the five participant groups

relative to the RT in the final trials of the pre-training period (PREfinal). This increase was statistically significant for the R60 ($P < 0.05$, 0.81) and R60short groups ($P < 0.05$, $P = 0.98$), but was a marginal effect for the R30 group ($P = 0.12$, $f = 0.24$). An increase in RT was found for the DUAL-CUE group when participants initially encountered the 30° CW ($P < 0.05$, $f = 0.27$) and 60° CCW ($P < 0.05$, $f = 0.41$) rotations. In contrast, for the DUAL-NO CUE group, there was no significant difference between the RT in the pre-training trials and RT in the trials when participants were initially exposed to the 30° CW ($P = 0.20$, $f = 0.19$) or 60° CCW rotation ($P = 0.42$, $f = 0.12$). These results suggest that for all groups who received a colour cue to identify the novel rotation (SINGLE groups) or rotations (DUAL-CUE group), RT increased. However, when the change in environment could was not associated with a colour cue, RT was not affected.

For all SINGLE groups, RT fell substantially within the training period (ROTinitial versus ROTfinal: $P < 0.05$; $f = 0.38$, 0.93 and 0.66 for the R30, R60 and R60short groups, respectively). For the DUAL-CUE group, there was no significant difference between RT in the ROTfinal and ROTinitial trials for the 30° CW trials ($P = 0.68$, $f = 0.02$). RT fell with training in the 60° CCW trials for this DUAL-CUE group ($P = 0.03$, $f = 0.12$), although magnitude of this reduction (as indicated by the data in Fig. 5 and the effect sizes associated with the respective comparisons) was much lower than the reduction in RT for the SINGLE groups. For the DUAL-NO CUE group, RT actually *increased* within the training block for both the 30° CW ($P < 0.05$, $f = 0.32$) and 60° CCW trials ($P < 0.05$, $P = 0.43$). Finally, for *all* groups, RT was not significantly different upon initial re-exposure to the non-rotated task (POSTinitial) when compared to RT at the end of the PRE block, i.e., PREfinal ($P > 0.20$ range of $f = 0.04$–0.26).

## Discussion

### General overview

This study assessed the extent to which adaptation to two conflicting visuomotor rotations could be achieved when each rotation could be identified using colour cues. Participants moved a cursor to visual targets on a computer screen by producing isometric elbow flexion–extension and/or forearm pronation–supination torques. The performance of participants who were exposed to two visuomotor rotations (with or without colour cues) during the training phase was compared with other groups who were exposed to only one of the rotations. The data suggest colour cues did allow participants to issue distinct feedforward motor commands for each rotation in the dual-rotation context, although full dual-adaptation was not observed.

### Exposure to a single rotation

For the groups exposed to a single rotation (SINGLE groups), the data were consistent with previous work that has employed similar dynamic (Krakauer et al. 1999; Wigmore et al. 2002) or isometric (Hinder et al. 2007, 2008) paradigms, and suggest that adaptation occurred as a result of an automatic process involving iterative modifications to an intrinsic mapping between the visual input (target presentation) and resulting motor command. We used RT as a measure of the time required to plan the response in the period following target presentation. For the SINGLE groups RTs did not increase within the rotated environment. This result suggests that the process used to compensate for the rotation required a similar level of cognitive processing to that required to implement the motor commands utilised in the non-rotated (pre-training) period. We propose that in this instance participants did not need to make a decision on every trial as to how they should amend their feedforward commands in order to achieve accurate performance in the rotated environment.

The aftereffects for the SINGLE groups were consistent in character with the effects reported when a perturbing force is unexpectedly removed (catch trials) during an adaptation period (Shadmehr and Mussa-Ivaldi 1994), or when participants are re-exposed to the non-perturbed (null) field (e.g. Scheidt et al. 2001) or non-rotated visuomotor environment (Krakauer et al. 1999; Tong et al. 2002; Hinder et al. 2007, 2008) following completion of the training period. Although these SINGLE group participants *were* provided with the means to identify the change in task environment (via the colour cue), aftereffects were manifested nevertheless. This aspect of the results is consistent with previous work indicating that colour cues do not preclude the expression of aftereffects when participants adapt

in a reaching task (Miall et al. 2004) or an isometric target acquisition task when full visual feedbdback is provided (Hinder et al. 2008) The aftereffects obtained in the present study are consistent with the view that participants issue motor commands based on the newly acquired visuomotor mapping, or internal model of the input–output relationship, that characterises the *rotated* environment (Krakauer et al. 1999). The presence of aftereffects even when contextual cues were provided adds weight to the proposition that the original (non-rotated) visuomotor mapping for the non-rotated task environment had been modified during adaptation to the rotated task, and was no longer available. Re-adaptation to the non-rotated condition occurred over the course of the post training trials, apparent as incremental straightening of cursor paths. This is consistent with relearning of the visuomotor mapping for the non-rotated task environment.

Aftereffects associated with reduced adaptation to a single rotation

To preclude the possibility that the presence of aftereffects in the R30 and R60 groups, and the absence of aftereffects in the DUAL-CUE group (see "Discussion"), was simply due to variations in the levels of adaptation, a further group of participants (R60short) was exposed to a much shorter training phase (i.e., short ROT block). On the basis of the rates of reduction of angular error observed in trials conducted during the ROT block for the R60 and DUAL-CUE groups, we estimated that three trials to each target (24 trials in total) in a block solely consisting of 60° rotations would result in a reduction of angular error to a level similar to that seen following completion of the ROT block by the DUAL group (who performed 40 trials to each target). As expected, R60short participants showed reduced adaptation to the rotation compared to the R60 group (Fig. 3b, c). Despite this reduced adaptation, when R60short participants were re-exposed to the non-rotated environment, cursor paths were significantly less straight than those exhibited in trials that preceded the training block. The magnitude of the aftereffect was smaller than that exhibited by the R30 and R60 groups, but nonetheless reliable, and commensurate with the degree of adaptation that occurred during training. This finding suggests that the absence of the aftereffects for the DUAL-CUE group (discussed below) was not merely due to the fact that this group adapted less, but rather points to inherent differences in the nature of the adaptive processes that were engaged.

Exposure to two rotations identifiable by colour cues

Two groups of participants were exposed to two rotations (30° CW and 60° CCW) during the training period. The DUAL-CUE group were provided with colour cues to enable the rotations to be identified, while the DUAL-NO CUE group did not receive any cues. It is conceivable that, for the DUAL-CUE group, the colour cue could be used in one of two ways. It could simply allow separation of error processing for each rotation such that participants could subsequently adapt to the two rotations automatically, i.e., recalibrating the original visuomotor map into two new, distinct, maps. In this case, the colour cue would be used explicitly, but only insofar as separating error processing for each rotation such that the automatic (or implicit, see Mazzoni and Krakauer 2006) recalibration could occur for each rotation separately. Alternatively, it is possible that the performance error in each, or just one, of the novel rotations could be reduced using a wholly explicit strategy, Such a strategy may involve utilisation of the original visuomotor map but with participants planning cursor movements towards a 'virtual target', at a rotational offset (determined by the specific colour cue in any one trial) to the presented target.

While the performance characteristics within the rotated environments would be predicted to be similar under both these hypothesised mechanisms, only the first scenario would be expected to result in aftereffects in the post-training period, since the adaptation is sub-served by an implicit process. In contrast, post-training aftereffects would not be predicted if the second mechanism were utilised: since the original visuomotor map had not been overwritten or modified, the cue on any trial could be used to indicate that a rotation was not present and the 'offset' would not be required. However, if this second alternative were used an increase in reaction times may be predicted during the training phase (i.e., during exposure to the novel environments), relative to the pre-training (or baseline) trials, reflecting longer pre-movement processing times associated with implementing the explicit/cognitive response.

For the DUAL-CUE group, we observed improved performance in the 60° CCW trials, but no significant change in the 30° CW trials (Fig. 3d). The distinct torque directions observed for this group in the 30º CW and 60º CCW trials following completion of the training (Fig. 4c) indicate that participants learned to produce *different* motor commands to a particular target when exposed to the different rotations, i.e., they did not compensate for the mean of the two rotations on every trial. In contrast, the DUAL-NO CUE group were unable to produce different motor commands in the two rotations. As the rotation order was randomised within the training (ROT) block, colour cues were the *only* source of information available to the participants that indicated which rotation was present on a specific trial. Thus, for the DUAL-CUE group, the differentiation in motor commands *must* have been mediated by colour cues.

For the DUAL-CUE group, reactions times in the ROT block that were significantly longer than those in the PRE (non-rotated trials). On commencement of the POST block, we noted an absence of aftereffects in relation to angular error: post-training cursor paths were as straight as those generated in the pre-training trials (Fig. 4d). Furthermore, the reaction times in the POST training block were similar to those prior to training. These data are consistent with the fact that DUAL-CUE participants were able to use the colour cue to identify the return to a non-rotated task environment and therefore, that the cognitive process of determining an offset to the presented target was no longer required. Accordingly, the appropriate feedforward motor commands for the non-rotated environment could be selected. We suggest that the overall data for the DUAL-CUE group suggest that colour cues being utilised to evoke a wholly cognitive strategy to improve task performance (i.e., consistent with the latter of the two possible scenarios described above).

The presence during the training block of a small number of individual trials in the 30° CW condition in which the angular error approached 90° suggests that, on some occasions, participants generated commands appropriate for the 60° CCW rotation (i.e. as the red cue), when in fact the blue screen was present. This behaviour is consistent with our posited explicit, strategic, approach to learning. While we neglected to formally question all our participants as to how they attempted to compensate for the rotations, anecdotal conversations with them following the experiment indicated that the DUAL-CUE task was "mentally challenging", and they had to "remember which side of the target to aim for each screen colour".

We should note at this point that the data for the DUAL-CUE group should not be mistaken as evidence for dual adaptation: indeed, no performance improvement occurred for the 30° CW trials, and the extent of the adaptation in the 60° CCW trials did not approach that which was observed for those participants exposed to a similar number of solely 60° CW trials (R60 group, see Fig. 4).

The improvements in performance in the 60° CCW trials for the DUAL-CUE group (mediated by the posited cognitive, or explicit, strategy) occurred *incrementally*, as was the case in all the SINGLE groups (who adapted automatically). An approach where the DUAL-CUE participants attempted to compensate for the rotation by imposing one large rotational offset would have the potential to cause extremely large performance errors, if the offset was miscalculated (in either direction or magnitude). Accordingly, incremental, rather than gross, adjustments to motor commands under the putative cognitive strategy may be expected as they provide a more conservative approach which minimises the possibility for extremely large performance errors.

While some adaptation was possible under the posited explicit strategy, it clearly did not allow complete adaptation to both environments. We cannot determine categorically whether the lesser degree of adaptation to the rotated environments exhibited by the DUAL-CUE group, compared with that seen in the SINGLE rotation groups, was due to the fact that they appeared to implement an explicit strategy (and simply did not learn to impose a large enough offset) rather than automatic adaptation, or simply a result of attempting to concurrently adapt to more than one new task. However, recent work in our laboratory (Hinder et al. 2008), indicates that automatic (or implicit, see Mazzoni and Krakauer 2006) adaptation and (explicit) compensation strategies in response to a single rotation *can* occur at similar rates and result in similar levels of performance improvements in this isometric task. We do note, however, that the data obtained for the DUAL-CUE group in the present study are consistent with the slower rate of learning that has been reported in several previous dual adaptation studies (e.g. Wada et al. 2003; Wainscott et al. 2005; Osu et al. 2004).

The fact that we only saw significant decreases in angular error of paths in the 60° CCW trials for the DUAL-CUE group may have been due to the larger trajectory errors associated with 60° CCW trials, which may in turn have served as a more salient impetus for feedforward adaptation than those errors manifested in the 30° CW trials. Given the obvious cognitive demand associated with this particular form of adaptation, improving performance in the 30° CW trials may have been neglected, at least until errors in initial heading the 60° CCW trials had been reduced such that they were perceived as being more 'acceptable'. Further training may have resulted in improved feedforward performance in both the 30° CW and 60° CCW rotations, i.e., participants may have learned to implement offsets (i.e., explicit compensation strategies) that were appropriate for both rotations. Alternatively, it is possible that participants simply have the capacity to compensate for only one of the rotations on the basis of this form of adaptation, with the result that performance in the other rotation will necessarily remain unchanged.

Woolley et al. (2007) reported that adaptation to equal and opposite rotations of 30° did not occur in a paradigm similar to that used in the present study for the DUAL-CUE group, i.e., a random presentation of the two task variants, identifiable by way of colour cues. In the present study it is evident that the reduction of angular error in the 60° CCW rotation condition for the DUAL-CUE group was around 30°. Thus, following this partial-adaptation, participants faced a situation in which they encountered errors of 30° magnitude in both the 60° CCW and 30° CW trials. It is conceivable that further learning did not occur because adaptation to equal and opposite rotations is not possible in

this particular task, a suggestion consistent with Woolley et al.'s (2007) finding. Further work is warranted to investigate in what conditions dual-adaptation to equal and opposite rotations, and complete adaptation to rotations of unequal magnitude and polarity, may be possible.

Mazzoni and Krakauer (2006) reported that a verbal instruction to adapt explicitly (i.e., to aim away from the target to compensate for the imposed rotation) could not override the central nervous system's natural, or preferred, adaptation mechanism of automatically recalibrating the visuomotor map (Cunningham 1989; Krakauer et al. 1999). In their study participants were instructed to implement an explicit strategy of aiming away from the presented target (towards a virtual target) to compensate for an imposed rotation. For the initial few trials this strategy resulted in accurate performance. However, very quickly implicit adaptation also occurred such that the visuomotor rotation was accommodated within the intrinsic representation (internal model/visuomotor map) of the task environment. Ultimately, the explicit strategy actually served to increase, rather than decrease performance errors. Nevertheless, the possibility exists that an explicit process *may* successfully mediate performance improvements in a situation where the usual preferred implicit adaptation (Mazzoni and Krakauer 2006), i.e., automatic recalibration of the visuomotor map (i.e., the preferred mechanism of adaptation, see Mazzoni and Krakauer 2006) does not, or cannot, occur. It is conceivable that implicit adaptation to either rotation in the present study was prevented as a result of interference between the two conflicting rotations. Furthermore, in the present paradigm, participants *were not* instructed *how* to adapt. Accordingly, there was no conflict between the preferred mechanism of adaptation and any mechanism implied through verbal instruction. For these reasons, we do not view the results of the present study as being incompatible with those reported by Mazzoni and Krakauer (2006).

The results of our DUAL-CUE group are consistent with a recent study by Gupta and Ashe (2007). They reported a limited amount of improvement during training when opposing velocity dependent force-fields were presented in a randomised manner and associated with colour cues. However (as with our DUAL-CUE group) no aftereffects were present on catch trials (i.e. trials where colour cues were still presented but the associated force-fields were absent). This was interpreted by the authors as indicating that dual adaptation did not occur.

### Trial by trial adaptation, and accumulation of adaptation

A previous experiment by Scheidt et al. (2001) conducted a time series analysis of reaching movements in a velocity dependent force-field. The magnitude of the force-field was selected randomly on each trial from a pre-determined bimodal distribution. Participants adapted to the *mean* of the randomly varying environment, even though the bimodal distribution dictated that high and low magnitudes were experienced more frequently than the mean magnitude. A trial-by-trial modeling analysis of performance to concurrently presented opposing visuomotor rotations of equal and opposite magnitude (Diedrichsen et al. 2005) showed that the direction of movement on the current trial was influenced by the direction of error on the previous trial. It was found that systematic changes in the direction of movement which occurred from one trial to the next were consistent with *adaptation*. Although trial to trial adaptation was observed, no significant overall change to the direction of movement occurred over the course of the training period. This modeling indicates that complete interference observed between randomly switching novel environments that are opposite in direction and equal in magnitude is not due to an absence of adaptation, but is better described in terms of a "lack of accumulation" of adaptation.

The data for our DUAL-NO CUE group are therefore consistent with the work of Scheidt et al. (2001) and Diedrichsen et al. (2005). Because our rotations were not equal and opposite, but varied in both direction and magnitude, we were able to observe an accumulation of adaptation, i.e., incremental trial by trial adaptations accumulated throughout the training period. This accumulation resulted in the $-15°$ change in the direction of participants torque vector observed in the training period (Fig. 4c). Participants compensated for the mean of the two rotations (15° CCW) by rotating their torque by 15° in the opposite direction, i.e., $-15°$ or 15° CW.

For the DUAL-CUE group participants did not adapt to the mean of the two rotations. Rather the colour cue allowed participants to differentiate between the two rotations, and issue distinct motor commands for each rotation. However, this finding for the DUAL-CUE group does not preclude the possibility that trial-to-trial adaptation, adaptation to the mean of the two rotations, and accumulation of adaptation did not play a part in the manifested performance. Indeed, it is possible that there was competition between participants' cognitive strategy of issuing specific motor commands on the basis of the colour cues and trial-to-trial (automatic) adaptation.

### Summary

Compensation for single novel visuomotor environments occurred in a manner consistent with previous research (Krakauer et al. 1999; Tong et al. 2002). The patterns of adaptation indicated that this was likely the result of an automatic process, whereby a visuomotor map (or internal model) is modified to compensate for a rotation of the

visuomotor environment. In this context, aftereffects were observed despite the provision of contextual (colour) cues that indicated changes in the environment, consistent with the results of Miall et al. (2004) and Hinder et al. (2008). In contrast, the limited adaptation that occurred when participants were exposed simultaneously to two novel conflicting visuomotor rotations (when colour cues identified the rotations) appeared to be mediated by (explicit) compensation strategies. While modifications of the feedforward component of the response occurred in relation to only one of the rotations, it appears that in this instance the provision of a colour cue allowed the selection of alternative feedforward motor commands. Further research is warranted to determine the extent to which the provision of colour cues, as well as other forms contextual cues, impacts upon these two putative forms of learning.

## References

Caithness G, Osu R, Bays P, Chase H, Klassen J, Kawato M, Wolpert DM, Flanagan JR (2004) Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. J Neurosci 24:8662–8671

Cohen J (1969) Statistical power analysis for the behavioral sciences. Academic Press, New York

Cunningham HA (1989) Aiming error under transformed spatial mappings suggests a structure for visual-motor maps. J Exp Psychol Hum Percept Perform 15:493–506

Diedrichsen J, Hashambhoy Y, Rane T, Shadmehr R (2005) Neural correlates of reach errors. J Neurosci 25:9919–9931

Flanagan JR, Rao AK (1995) Trajectory adaptation to a nonlinear visuomotor transformation—evidence of motion planning in visually perceived space. J Neurophysiol 74:2174–2178

Gandolfo F, Mussa-Ivaldi FA, Bizzi E (1996) Motor learning by field approximation. Proc Natl Acad Sci USA 93:3843–3846

Ghahramani Z, Wolpert DM (1997) Modular decomposition in visuomotor learning. Nature 286:392–395

Gupta R, Ashe J (2007) Lack of adaptation to random conflicting force fields of variable magnitude. J Neurophysiol 97:738–745

Hinder MR, Walk L, Woolley DG, Riek S, Carson RG (2007) The interference effects of non-rotated versus counter-rotated trials in visuomotor adaptation. Exp Brain Res 180:629–640

Hinder MR, Tresilian JR, Riek S, Carson RG (2008) The contribution of visual feedback to visuomotor adaptation: How much and when? Brain Res 1197:123–134

Kawato M (1999) Internal models for motor control and trajectory planning. Curr Opin Neurobiol 9:718–727

Keppel G (1982) Design and analysis: a researcher's handbook, 2nd edn. Prentice-Hill, New Jersey

Krakauer JW, Ghilardi MF, Ghez C (1999) Independent learning of internal models for kinematic and dynamic control of reaching. Nat Neurosci 2:1026–1031

Krouchev N, Kalaska J (2003) Context-dependent anticipation of different task dynamics: rapid recall of appropriate motor skills using visual cues. J Neurophysiol 89:1165–1175

Mazzoni P, Krakauer JW (2006) An implicit plan overrides an explicit strategy during visuomotor adaptation. J Neurosci 26:3642–3645

Miall RC, Jenkinson N, Kulkarni K (2004) Adaptation to rotated visual feedback: a re-examination of motor interference. Exp Brain Res 154:201–210

Osu R, Hirai S, Yoshioka T, Kawato M (2004) Random presentation enables subjects to adapt to two opposing forces on the hand. Nat Neurosci 7:111–112

Pellegrini JJ, Flanders M (1996) Force path curvature and conserved features of muscle activation. Exp Brain Res 110:80–90

Scheidt RA, Dingwell JB, Mussa-Ivaldi FA (2001) Learning to move amid uncertainty. J Neurophysiol 86:971–985

Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. J Neurosci 14:3208–3224

Teasdale N, Bard C, Fleury M, Young DE, Proteau L (1993) Determining movement onsets from time series. J Motor Behav 25:97–106

Tong C, Wolpert DM, Flanagan JR (2002) Kinematics and dynamics are not represented independently in motor working memory: evidence from an interference study. J Neurosci 22:1108–1113

Wada Y, Kawabata Y, Kotosaka S, Yamamoto K, Kitazawa S, Kawato M (2003) Acquisition and contextual switching of multiple internal models for different viscous force fields. Neurosci Res 46:319–331

Wainscott SK, Donchin O, Shadmehr R (2005) Internal models and contextual cues: encoding serial order and direction of movement. J Neurophysiol 93:786–800

Wigmore V, Tong C, Flanagan JR (2002) Visuomotor rotations of varying size and direction compete for a single internal model in motor working memory. J Exp Psychol Hum Percept Perform 28:447–457

Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. Science 269:1880–1882

Woolley DG, Tresilian JR, Carson RG, Riek S (2007) Dual adaptation to two opposing visuomotor rotations when each is associated with different regions of workspace. Exp Brain Res 179:155–165