

CONTEXT-DEPENDENT DUAL ADAPTATION TO OPPOSING VISUOMOTOR
ROTATIONS

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ABSTRACT

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

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INTRODUCTION

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

When visuomotor adaptation occurs, the brain forms distinct “internal models” in order to reliably predict the outcome of specific motor commands in that context and the sensory consequences of executing those commands (Wolpert & Ghahramani, 2000). We can probe the ability of the Central Nervous System (CNS) to maintain and recall multiple internal models simultaneously by introducing variants of the same environment serially (i.e. ABA paradigm) or concurrently. While ABA designs typically investigate whether the learning of one internal model will be affected by the subsequent learning of another, concurrent designs allow us to see simultaneous learning, acquisition, and switching between two or more internal models (also known as “dual adaptation”). A typical example of a concurrent paradigm is a task in which participants make out-and-back reaches in alternating trials of clockwise-perturbed and counter clockwise-perturbed hand-cursors, within the same experimental block. Often, adaptation to both visuomotor variants does not proceed when there is a lack of predictability regarding the impending perturbation from trial to trial. Indeed, this has been found in several studies

that examine the successive adaptation to two or more perturbations in which the adaptation to one perturbation fully interferes with the acquisition of another (Brashers-Krug, Shadmehr, & Bizzi, 1996; Caithness et al., 2004; Donchin, Francis, & Shadmehr, 2003; Karniel & Mussa-Ivaldi, 2002; Krakauer, Ghilardi, & Ghez, 1999).

One theoretical model, the Modular Selection and Identification for Control (MOSAIC) theory, suggests that a contextual switching mechanism must exist in order to change between internal models of specific motor commands and sensory states. Thus, in order for dual adaptation to proceed, a specific contextual cue must be associated to each of the visuomotor variants experienced. This predictive cue provides information about the impending sensorimotor mapping via responsibility predictors that add greater weighting on the probability of encountering one of the perturbed environments over the others (Haruno, Wolpert, & Kawato, 2001; Kawato, 1999). Interestingly, not every cue is a sufficient facilitator of dual adaptation. For instance, there has been mixed findings regarding the efficacy of colour and shape cues (Baldeo & Henriques, 2013; Hinder, Woolley, Tresilian, Riek, & Carson, 2008; Osu, Hirai, Yoshioka, & Kawato, 2004; Woolley, Tresilian, Carson, & Riek, 2007). When contextual cues are insufficient or unavailable, the CNS is unable to predict the sensorimotor consequences of the impending visuomotor perturbation. While these models provide us with a mechanism for understanding how humans are able to dually adapt, they do not inform us on what qualifies as an effective contextual cue or the actual cues themselves. Here, we examine whether contextual cues that tend to be motor-based (e.g. hand and body posture) are sufficient for facilitating dual adaptation despite

identical desired cursor trajectories (i.e. using identical target sets), as well as the role of extended training.

What qualifies a contextual cue to be an effective facilitator of dual adaptation? One possible property might be the visual features of the target or hand cursor. Extrinsic contextual cues refer to cues that are not motor-based, such as target or background colour. Dual adaptation as facilitated by extrinsic cues has been found to occur (Krouchev & Kalaska, 2003; Osu et al., 2004), or not occur (Baldeo & Henriques, 2013; Gupta & Ashe, 2007; Hegele & Heuer, 2010; Hinder, Woolley, et al., 2008; Hirashima & Nozaki, 2012; Woolley et al., 2007). One study by Gupta and Ashe (2007) had participants concurrently adapt to two opposing, velocity-dependent force fields with each perturbation associated with a colour cue, an external, non-motor based property of a context, with the same set of visual targets and found no evidence for dual adaptation. Likewise, Woolley and colleagues used background colour as a predictive cue but found no evidence for dual adaptation while training with opposing visuomotor rotations when there is an overlap in the visual workspace (Hinder, Tresilian, Riek, & Carson, 2008; Woolley et al., 2007). Baldeo & Henriques (2013) integrated target and cursor colour as predictive visual cues and found that it still does not facilitate dual adaptation. Using a more explicit approach with colour cues Osu and colleagues provided a coloured windmill-like diagram that showed the magnitude and direction of the impending force field prior to every trial. They found that participants were able to dual adapt to opposing force-field perturbations after distributed training over two consecutive days although these results may have been influenced by enhanced consolidation (Osu et al., 2004). Thus, while dual adaptation is difficult to achieve with

extrinsic cues on shorter timescales, Osu and colleagues suggest that perhaps extended practice may allow for significant learning.

In contrast to extrinsic cues, intrinsic or motor-based cues involving distinct muscle recruitment patterns, change in the end-effector, or previous behavioural context have shown to be more promising in facilitating dual adaptation (Baldeo & Henriques, 2013; Galea & Miall, 2006; Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; L. Wang & Musseler, 2014; Woolley, de Rugy, Carson, & Riek, 2011). This may be due to the idea that the generalization of motor learning depends on context, which is determined based on the history of the prior movement of that end-effector (Baraduc & Wolpert, 2002; Krakauer, Mazzoni, Ghazizadeh, Ravindran, & Shadmehr, 2006). Indeed, Krakauer et al (2000) initially demonstrated that when adapting to visuomotor rotations, the extent by which this adaptation generalizes depends on the proximity of the novel target direction compared to the trained direction. Baraduc and Wolpert (2002) further showed that even when the target or hand path direction is identical, reach aftereffects (and thus, generalization) become smaller when reaches are made with increasingly different arm postures than the one used during training with a visuomotor rotation (i.e. as the upper arm becomes more adducted relative to the arm posture used during training). Likewise, Krakauer and colleagues (2006) suggested that using different effectors can function as intrinsic contextual cues for retrieving specific internal models. In this ABA study (serial adaptation blocks to opposing perturbations), participants made pointing movements with a rotated cursor using either their arm (shoulder and elbow) or wrists. When both body parts were serially exposed to opposite cursor-rotations, there was no interference between the effectors, but when exposed to the same rotation, the wrist benefitted from

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

Not surprisingly, when hand trajectories overlap, dual adaptation may proceed at a slower rate and require more training than adaptation to a single perturbation. This is evidenced by a less steep learning curve for adaptation to reaches that required

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

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

experiment using hand posture as a cue, we gave participants double the amount of training to increase practice with learned associations between context and visuomotor mapping.

LITERATURE REVIEW

Motor adaptation to a single visuomotor distortion (single adaptation)

The remarkable ability of the nervous system to adapt to visuomotor distortions has been demonstrated in many studies examining motor adaptation of reaching movements in response to altered visual feedback of the hand by manipulating the hand-cursor relationship in a virtual reality environment (Baldeo & Henriques, 2013; Dumontheil, Panagiotaki, & Berthoz, 2006; Krakauer et al., 1999), force-field perturbations (Gandolfo et al., 1996; Osu et al., 2004), prism translation (Martin, Keating, Goodkin, Bastian, & Thach, 1996; Miall, Jenkinson, & Kulkarni, 2004), and prism-like visuomotor translations (Ghahramani & Wolpert, 1997). Whenever a visual perturbation is introduced, initial reaching errors are large, indicating a prediction error made by the central nervous system (CNS). As trials of training proceeds, the CNS learns to adapt to the perturbation as evidenced by a systematic decrease in reaching errors to the target. In particular, visuomotor (or hand-cursor) rotations have been used as a model for motor learning as it has been widely established that the CNS plans reaching movements as a vector in extrinsic space which has a hand-centered reference axis relative to an egocentric reference frame (Gordon, Ghilardi, & Ghez, 1994; Vindras & Viviani, 1998). In order to adapt to a visuomotor rotation, we must have adaptive control over a scaling factor that relates the target distance in extrinsic space relative to the peak velocity and a reference axis centered about the hand relative to the self (Graziano, Yap, & Gross, 1994).

Krakauer and colleagues (2000) have shown that the decrease in reaching errors towards single targets saturate at about 20 trials following a 30° single visuomotor rotation. That is, as training proceeds, the cursor trajectory towards the target show a significant reduction in directional angular errors as the CNS learns to adapt to the perturbation. Additionally, this demonstrates the rapid ability of the motor system to compensate for a discrepancy between the visual feedback of the hand and actual reaching movements (Krakauer, Pine, Ghilardi, & Ghez, 2000). In order to produce corrective movements, this adaptation process requires a re-mapping of the hand-cursor relationship which can be referred to as a new internal model (Wolpert & Ghahramani, 2000). In summary, single adaptation studies have demonstrated that humans are able to produce controlled movements that tend to remain stable over time as a result of motor learning following a single visual perturbation of the hand. This is evidenced by an initially large directional reaching error following exposure to a visual perturbation and a subsequent decrease to asymptotic baseline performance (i.e. performance prior to the visual perturbation).

Adapting reach movements in response to visuomotor rotations is believed to be implicit because it often proceeds automatically and without awareness (Krakauer, 2009). It is generally accepted that implicit adaptation is accompanied by feed-forward control in which movements are planned prior to onset (Mazzoni & Krakauer, 2006). Thus, in the execution of a motor command, the discrepancy between the desired and executed trajectory are reduced over time, allowing for more accurate movements (Mazzoni & Krakauer, 2006). This can explain why initial motor errors are large at the onset of a visual perturbation; as adaptation proceeds, the discrepancy between the

desired and resultant trajectory becomes smaller. These large motor errors at the initial phase of movement are ideal measures of performance because they reflect the initial prediction errors prior to on-line correction with visual feedback (Hinder, Tresilian, et al., 2008; Krakauer, Ghez, & Ghilardi, 2005). For example, at the onset of a visuomotor rotation, the feed-forward model assumes that the estimated hand trajectory is congruent with the visual feedback. Because a rotation has been introduced, the prediction error will be large and the trajectory towards a target will be indirect. The incongruous relationship between expected hand trajectory and actual hand trajectory is reduced through adaptation, making the initial error an ideal measure of implicit adaptation.

We can further probe the implicit adaptation process by employing open loop trials. These refer to “catch” trials wherein visual feedback of the hand is withheld (or in the case of force-field perturbations, the force-field is withheld). Typically, participants will continue to compensate for the learned rotation, implying that the adaptation that occurred is an implicit process (Krakauer, 2009). The presence of these direction-dependent errors implies that a feed-forward process occurs wherein movements are planned prior to its onset without integrating visual feedback for correction (Reza Shadmehr, Smith, & Krakauer, 2010). These residual motor effects following a perturbation are called “after-effects” (Harris, 1963), and they signify the ability of the CNS to learn and maintain an adapted state even after the removal of visual feedback. Furthermore, the presence of after-effects further supports the notion that adaptation is an implicit process. When large rotation-dependent errors are present in the absence of visual feedback, we are assured that participants are not simply using a cognitive

strategy to counter the effect of a visual perturbation to the motor system (Mazzoni & Krakauer, 2006). Thus, the manifestation of after-effects demonstrates the ability of the motor system to adapt to changes in the visual feedback.

Generalization and Interference

After adapting movements under a single visual perturbation, we may need to expand this adaptive state towards a different context, perhaps outside the workspace it was learned, under the same perturbation. For example, adapting to a single perturbation reaching task might be followed by training in another reaching task with different targets. When adapting in a new context, generalization from what was learned from the previous adaptive state can be beneficial if it is transferred under the same perturbation (e.g. (Krakauer et al., 2000; Woolley, Carson, Tresilian, & Riek, 2008)). Krakauer and colleagues showed that the generalization of learning in a single direction is localized such that novel targets that are closer to the trained target are reached more accurately and those further away from the trained target show reduced adaptation (Krakauer et al., 2000). Additionally, Wang and Sainburg demonstrated that generalization of a learned rotation was greatest when participants made movements towards targets in the same direction, even in unpractised workspaces where they reached in the trained direction but from a novel start location after having trained under the same visuomotor rotation (Wang & Sainburg, 2005). Thus, participants were able to transfer their adapted state to a visuomotor rotation from one context to another, provided that it was under the same perturbation.

If a different perturbation that is not associated with a predictive contextual cue is introduced, then the motor learning that has occurred in the previous task will likely interfere with the acquisition of a new adaptive state. For example, abruptly introducing a counter-rotation after the initial adaptation to a rotation will likely produce large errors because the CNS does not have the correct visuomotor mapping for that new environment (Wolpert & Flanagan, 2001). Secondly, there is no way to predict the conditions of the secondary adaptive state which can lead to interference in the concurrent learning of both states. When contextual cues are insufficient or unavailable, mutual interference between the concurrent adaptive states is likely to occur. Indeed, this has been found in several studies looking at the successive adaptation to two or more perturbations in which the adaptation to one perturbation fully interferes with the acquisition of a new adaptive state (Gupta & Ashe, 2007).

Interference is the process by which any one task affects learning of another or vice-versa. The basic paradigm used to study the effect of interference across varying time intervals is the ABA format in which an initial rotation is learned (task A) followed by a counter-rotation (task B) and a final re-exposure to task A. Using this format, we can examine how largely the adaptation to one rotation interferes with the transition to a different rotation. Interference can take the form of anterograde interference in which the adaptation to an initial rotation interferes with the adaptation of a second rotation or the re-adaptation to the initial rotation is interfered by the learning of the second rotation (Miall et al., 2004; Shadmehr & Brashers-Krug, 1997). Conversely, retrograde interference arises when the adaptation to the second rotation interferes with the recall of task A. Consistent with this definition are research findings suggesting no significant

difference in the rate of adaptation between the initial exposure and the re-exposure to rotation A (i.e. task A) following counter-rotation B (i.e. task B). Some authors argue that this return to a naïve state for task A is actually the result of the sum of the task A rotation and the task B counter-rotation and thus, represent savings (Miall et al., 2004). This notion was challenged by Krakauer and colleagues (2005) and found that the after-effect from Task A is carried over to Task B is carried over up until the 24 hour interval. Additionally, interference in Task A is just as robust even after one week (Krakauer et al., 2005). Although the rate of adaptation should increase, Krakauer (2005) hypothesized that this does not occur because the original rotation learning is no longer associated with the task after having completed several trials with a counter-rotation. Now, recall for both adaptive states (rotation A and B) compete in that current context and manifest itself in a robust interference. Using a concurrent adaptation paradigm, interference might be more prevalent if there are no differentiating cues between adaptive states. To this end, adaptive states can be associated with predictive contexts that serve as cues to facilitate their recall. If this is true, we should be able to see concurrent adaptation to two or more perturbations.

Concurrent adaptation to two or more visual distortions: Dual adaptation

An interesting ability of the CNS that has been studied over the past decade is the concurrent adaptation to two visuomotor rotations also known as the phenomenon of “dual adaptation.” Proposed in 1993 by Welch and his colleagues, dual adaptation refers to the ability to concurrently adapt to two or more visuomotor perturbations, suggesting the possibility of switching between adaptive states. Interestingly, dual

adaptation does not simply occur with the introduction of randomly alternating visual perturbations. Indeed, Donchin and colleagues first demonstrated that without distinct, predictive contextual cues between adaptive states, dual adaptation cannot occur (Donchin et al., 2003). Although Welch et al. showed that dual adaptation can occur between two different prism displacements, their paradigm was structured in a block-wise fashion that did not allow for concurrent learning (Welch, Bridgeman, Anand, & Browman, 1993). Thus, a more ideal method of studying dual adaptation is to introduce two distinct perturbations presented on a concurrent, trial-by-trial basis (i.e. alternating perturbations). Later studies have shown that dual adaptation can occur in a concurrent experimental design but only if the adaptive state can be associated with a specific contextual cue such as different limb effectors (Galea & Miall, 2006), and distinct muscle synergies within the same effector limb (Baldeo & Henriques, 2013; Gandolfo et al., 1996; Woolley et al., 2007). How would it then be possible for the motor system to differentiate states and effectively use these cues to facilitate learning of two or more adaptive states? One notable theoretical framework was proposed by Haruno, Wolpert and Kawato (2001) describing the role of predictive forward models and corrective inverse models in motor learning and adaptation.

Internal Models

The Modular Selection and Identification for Control (MOSAIC) Model

The MOSAIC model is a proposed modular architecture for how the brains uses motor predictions prior to movement and sensory input to appropriately select a module

for any given situation. Previous models were unable to explain the acquisition of inverse models (Narendra & Mukhopadhyay, 1997), and how multiple inverse models can be used efficiently (Gomi & Kawato, 1993). In sum, the main goals for the MOSAIC model was to show generalization, primary learning of modules, and the ability to switch between the learned models based on prediction errors and sensory cues (Haruno et al., 2001). In the MOSAIC model, a module is any combination of a forward (predictor) and inverse (controller) model. Over training, forward models learn to predict the consequences of a motor command in any given context based on past experienced contexts. In dual adaptation, when a rotation associated with a sensory cue is introduced, initial movements will have large errors based on the predictions made by forward models but as feedback is integrated by the inverse models, the appropriate dynamics will be learned. When this is followed by a counter-rotation which is associated with a different sensory cue, the same learning process occurs. Over concurrent training of the two rotations, motor errors are reduced if the appropriate internal models are recalled based on sensory cues. Furthermore, if internal models can be robustly associated with predictive contexts in order to produce appropriate movements within a specific environment, perhaps this association can be strengthened through extended practice. One major criticism of the MOSAIC model is that it fails to account for the timescale for learning and forgetting, the increase of large errors in the beginning of blocks in serial dual adaptation experiments, and spontaneous recovery of initial adaptation following reverse adaptation (Lee & Schweighofer, 2009; Smith, Ghazizadeh, & Shadmehr, 2006).

Serial vs. Parallel Architecture of Motor Adaptation

Smith and colleagues proposed a model that accounts for the multi-timescale aspect of adaptation including savings, anterograde interference, and spontaneous recovery (Lee & Schweighofer, 2009; Smith et al., 2006). In this linear, two-state model, there is thought to be a fast process which accounts for the initial phase of learning that tends to forget quickly, and a slow process that is retained in the long-term but learns slowly. However, it is unknown how these fast and slow neural processes are organized. For instance, if these processes are organized in parallel to one another, both the fast and slow processes might update their states based on movement errors but if they are organized serially, the fast learning process might provide the slow processes with online information (with each process updating their states in a serial manner). Critically, this model also cannot account for dual adaptation because adaptation to one visuomotor variant would then have to override the learning of the other variant. Lee and Schweighofer (2009) ameliorated this architecture by proposing a revised model that accounts for the organization of the fast and slow states. In this simulation, it was found that human dual adaptation data most corresponded with a parallel architecture with one fast and n slow states with multiple inner states (Lee & Schweighofer, 2009). While these computational models show how certain cues aid in the retrieval of internal models and the timescale in which these processes occur, it does not inform on what specific cues are sufficient facilitators of dual adaptation. Despite its downfalls, it nevertheless provides researchers with a theoretical platform for prediction and hypotheses construction regarding adaptation. To this end, the present

experiments explore the possible intrinsic cues that can facilitate dual adaptation and its extent following prolonged training.

Intrinsic vs. Extrinsic Cues

In an attempt to find predictive cues that effectively facilitate dual adaptation, Gupta and Ashe (2007) subjected participants to an opposing velocity-dependent force-field concurrent adaptation task with each perturbation associated with a colour cue, an external property of a context, with the same set of visual targets and found no evidence for dual adaptation. Likewise, Woolley and colleagues used background colour as a predictive cue but found no evidence for dual adaptation while training with opposing visuomotor rotations when there is an overlap in the visual workspace (Woolley et al. 2007). Likewise, Dumontheil and colleagues (2006) used a virtual reality navigation task and associated different visual gains with background colour and found only a subset of participants were able to adapt their whole body orientation. The remaining participants were not able to dually adapt their movements to both gains and this was attributed to differing perceptive styles (Dumontheil et al., 2006). Because background colour might not be a sufficient cue, Baldeo & Henriques (2013) integrated target colour as the predictive visual cue and found that it does not facilitate dual adaptation. These findings suggest that colour, an extrinsic contextual cue, is not likely to be a sufficient cue in retrieving internal models of previously learned adaptive states (Haruno et al. 2001). Interestingly, using a more explicit approach with colour cues to facilitate dual adaptation, Osu and colleagues found that participants were able to dually adapt to opposing visuomotor perturbation over a period of 48 hours which may have been

influenced by enhanced consolidation and duration of training (Osu et al. 2004).

Cothros, Wong and Gribble were also able to show successful dual adaptation to a velocity-dependent force-field perturbation and a null force-field by using a visual cue which represented the relationship of the hand to the end-effector (Cothros et al. 2009). In this study, participants grasped the manipulandum throughout the experiment but received a visual cue of grasping when the force-field was in effect. Evidently, research focusing on the ability of the CNS in using extrinsic cues has been highly variable.

In contrast, intrinsic cues, such as muscle recruitment patterns that are likely to be proprioceptively mediated, have shown to be more promising in facilitating dual adaptation (Gandolfo et al. 1996; Galea and Miall 2006; Woolley et al. 2011; Baldeo and Henriques 2013). A classic example of dual adaptation is achieved by associating opposing rotations with different limbs. Using a block-wise (ABA) paradigm, Bock and colleagues (2005) were able to demonstrate that two internal adaptive states can be created and function without mutual interference. In this study, participants were able to accurately adapt their reaching to their respective perturbations because the way in which sensory information was transformed into motor output was distinct between the two limbs (Bock, Worringham, & Thomas, 2005). Because block-wise designs do not necessarily show concurrent adaptation to two or more perturbations, it was still necessary to investigate the effect of using different limbs as a contextual cue with a concurrent design. Using a concurrent paradigm, Galea & Miall (2006) were able to show that participants are able to adapt to two different visual transformations at a similar rate when each limb was associated with opposing displacements. A related finding by Krakauer and colleagues (2006) suggested that using different end-effectors

can function as intrinsic contextual cues in retrieving specific internal models. In their study, participants were asked to make pointing movements with a rotated cursor using either their arm (shoulder and elbow) or wrists. After initially adapting wrist movements to a cursor-rotation, training the arm immediately afterwards to an opposing rotation did not interfere with the recall of the previous adaptation of the wrist a day later (Krakauer et al. 2006). When both body parts were exposed to the same rotation, the wrist benefitted from the previous adaptation of the arm, although not vice-versa (Krakauer et al. 2006). Thus, distinct intrinsic mapping of motor coordinates in internal models is necessary for a stronger association with the context and to reduce the likelihood of interference.

Not surprisingly, differing movement trajectories will produce distinct muscle recruitment patterns that can be used as intrinsic, contextual cues. Because generalization of learning of a single trained target is localized such that it does not transfer to targets further away, target location in the workspace can be associated with distinct visual perturbations. Indeed, Wang and Sainburg (2005) found that generalization is greatest in novel targets when the trained targets were along the same vector trajectory. More recent work by Baldeo and Henriques (2013) disentangled the issue of whether the integration of colour and target separation into the task context can facilitate concurrent adaptation in a reaching task. In this study, colour was integrated into the task to increase saliency but was insufficient in facilitating dual adaptation (Baldeo and Henriques 2013). When target colour and target separation were jointly used as contextual cues, participants were able to dually adapt. Lastly, target separation alone effectively functioned as an intrinsic cue to facilitate dual adaptation

suggesting that colour provided no additional benefit to the context distinction (Baldeo and Henriques 2013). Another possible contextual cue is target reach amplitude. Woolley et al. (2008) tested whether target reach amplitude was a sufficient contextual cue for dual adaptation given that shorter distances will produce different muscle synergies than that of longer distances. They found conflicting evidence such that complete interference occurs between the varying amplitudes. This was likely due to the generalization from one adaptive state to another (i.e. between the short and long amplitudes) (Woolley et al. 2008). Additionally, whole-body rotations which affects vestibular information, an intrinsic cue, was found to be sufficient in facilitating dual adaptation in a virtual reality navigation task in a group of participants who tended to place more weight on non-visual than visual information (Dumontheil et al., 2006; Lambrey & Berthoz, 2003). In this study, participants were asked to navigate around a virtual reality corridor where they alternated between altered visual gains of 0.5 and 1.5, such that the way they turn their bodies must correspond with the present visual feedback. Thus, dual adaptation is possible in a locomotion paradigm given a vestibular cue such as a whole-body rotation.

A final potential intrinsic cue that can be used to facilitate dual adaptation is the hand posture in which the end-effector is held. Gandolfo and colleagues (1996) were the first to show that associating a null and counter-rotation force-field with two distinct types of grip on a manipulandum aids in predicting the impending forces. The after-effects found were consistent with the type of grip and force-field. Additionally, when after-effects of the counter force-field were completely washed out, if the grip is changed to the other, after-effects consistent with the type of grip arise (Gandolfo et al.

1996). Interestingly, even an illusory grasp or a lack thereof of the end-effector can facilitate dual adaptation (Cothros et al., 2009). By associating a distinct hand posture as a predictive cue with each rotation, we can elicit distinct muscle recruitment patterns in reaching and intrinsically cue the retrieval of a learned internal model.

In sum, the use of contextual cues can yield variable results in facilitating switching between internal models. The contextual cues hypothesized to facilitate dual adaptation may be arbitrary external properties of the workspace such as colour (Hinder, Woolley, et al., 2008; Osu et al., 2004) or intrinsic to the CNS, such as a changes in the limb effector (Gandolfo et al. 1996; Galea and Miall 2006; Cothros et al. 2009) or sensory patterns (Dumontheil et al. 2006; Woolley et al. 2007; Baldeo and Henriques 2013). Recent research suggests that intrinsic cues, assumed to be mediated by proprioceptive mechanisms, are more accessible to the CNS and can thus be more readily integrated into internal models. Ideally, in order for dual adaptation to occur, there should be no interference in the adaptation to one rotation by the other (Donchin et al. 2003).

In the present experiments, we aim to investigate what intrinsic cues are sufficient in facilitating dual adaptation to opposing visuomotor rotations. The intrinsic cues we will explore include hand posture when gripping the end-effector and body rotation about the horizontal axis. By associating opposing visuomotor rotations with distinct intrinsic cues, we hope to show that dual adaptation is possible due to the successful retrieval of the appropriate internal models between rotations. Additionally, we know that the extent of learning for dual adaptation is not the same as that for single adaptation. Thus, it is possible that performance can reach baseline accuracy if

extended training with the intrinsic cues was prolonged. The second objective of the present studies is to determine if additional practice will lead to reduced interference between rotations and strengthening of the associations between cues and adaptive states.

HYPOTHESES

Hand Posture experiment

Hypothesis 1

We believe that participants will be able to concurrently adapt to two opposing visuomotor rotations given the intrinsic contextual cues in the form of hand postures. If participants are able to dual adapt, the presence of hand posture cues will reduce the amount of interference between rotations as evidenced by a significant reduction in angular deviation across rotations over time. This will suggest that intrinsic cues can be used by the CNS to plan movement based on the contextual cues provided to reduce reaching errors for both environments.

Hypothesis 2

We believe that participants will be able to dual adapt despite identical desired trajectories (i.e. identical target locations) across rotations if they are given hand posture cues. If participants are able to dual adapt, this suggests that hand posture can be used by the CNS to facilitate learning even when targets are identical for both rotations.

Hypothesis 3

We believe that participants in the DUAL condition will not be able to reduce their reaching errors to the same extent as those in the SINGLE conditions even if they are provided extended training. If this is true, reaching errors for both rotations would not show a significant reduction from the initial to the final blocks of the DUAL2 training set. If extended training does not provided additional benefits, this suggests that dual learning might require more than double the amount of training or that dual learning reaches a saturation point in which no additional benefits will be found regardless of the amount of training.

Body Posture experiment

Hypothesis 1

We believe that participants will be able to concurrently adapt to two opposing visuomotor rotations given the intrinsic contextual cues in the form of body postures (body left or right turn). If participants are able to dual adapt, the presence of a body posture cue will reduce the amount of interference between rotations as evidenced by a significant reduction in angular deviation across rotations over time. This will suggest that intrinsic cues can be used by the CNS to plan movement based on the contextual cues provided to reduce reaching errors for both environments.

Hypothesis 2

We believe that participants will be able to dual adapt despite identical desired trajectories (i.e. identical target locations) across rotations if they are given body posture cues. If participants are able to dual adapt, this suggests that body posture can be used by the CNS to facilitate learning even when targets are identical for both rotations.

METHODS

Participants

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

Apparatus

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

inset). Reaching movements were made to one of five radially-spaced targets (located at 60°, 75°, 90°, 105°, 120°), always starting at a common origin located 12 cm away.

The hand-cursor relationship was similar to using a desktop computer so that movements were made with a 1:1 ratio.

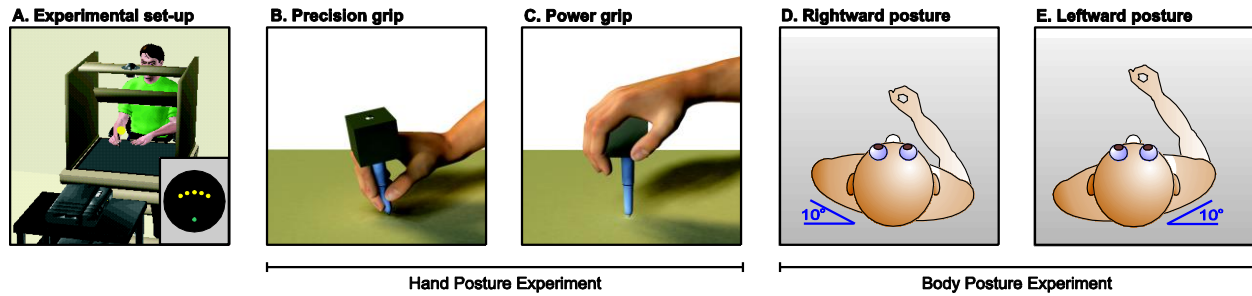


Figure 1. A: Experimental apparatus and target display. Stimuli were projected onto the vertical screen by a projector located approximately 60 cm behind the screen. Participants reached towards targets using a stylus on a digitizing tablet along the horizontal plane while viewing a projected image of the targets and visual feedback of their hand on a circular, vertical screen. An opaque chipboard occluded visual feedback of the participants' hands during the task. Inset: The home position was depicted as a green disc and the participant's hand was depicted as a white disc. The yellow discs depict all 5 possible locations of the target. The equipment was calibrated so that the hand-cursor ratio was approximately 1:1. B: Hand posture "BOTTOM" or "precision" grip, associated with a CCW rotation; C: Hand posture "TOP" or "power" grip, associated with a CW rotation. D: Body posture with a rightward 10° body rotation, associated with a CCW rotation; E: Body posture with a leftward 10° body rotation, associated with a CW rotation.

General procedure

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

For both experiments, participants completed pre-training, training, and post-training sessions (see Figure 2A and 2B). During training, participants in the single distortion group experienced only one 30° rotation (either CW or CCW) whereas those in the dual distortion group experienced both opposing rotations. In the Hand Posture

experiment, we refer to the single distortion training as SINGLE, the dual distortion group with DUAL1 for the first training set and DUAL2 for the additional second training set. Because we did not examine extended training in the Body Posture experiment, the two training sets were simply SINGLE and DUAL training. Participants assigned to the single distortion training finished the task in approximately one hour whereas those assigned to the dual distortion training finished within approximately two hours.

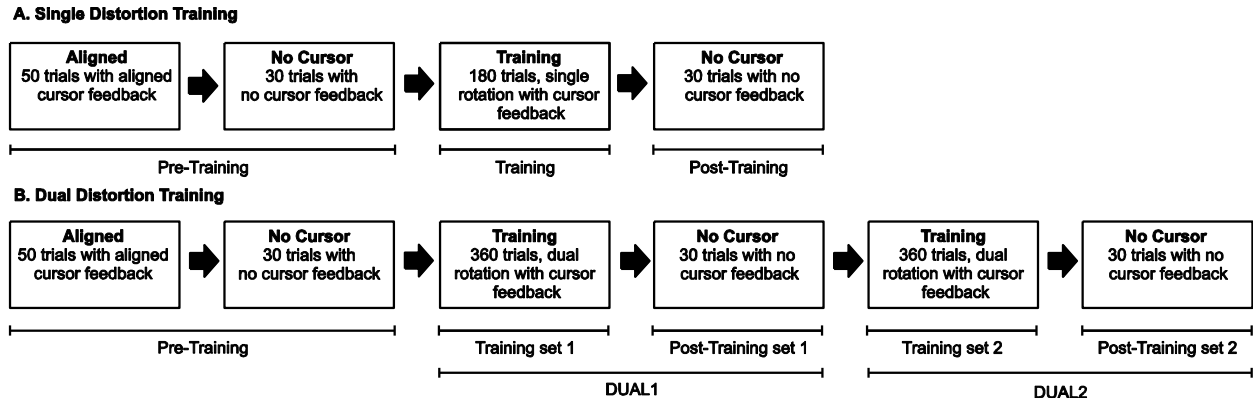


Figure 2. Sequence of sessions for A. Single Distortion Training and B. Dual Distortion Training. In both experiments, the single distortion group (SINGLE) only completed trials under either a 30° clockwise (CW) or counter-clockwise (CCW) rotation, but not both. In the Hand Posture experiment only, the dual distortion group completed a total of 720 interleaved training trials (DUAL1 and DUAL2) under both 30° CW (360 trials) and CCW (360 trials) rotations. In the Body Posture experiment, the dual distortion group completed only the DUAL1 sequence (i.e. no extended training) with a total of 360 interleaved training trials under both 30° CW (180 trials) and CCW (180 trials).

Hand Posture experiment

Pre-training (baseline measures)

Thirty-seven participants completed the Hand Posture experiment, with 14 assigned to the DUAL training set, 9 to the SINGLE CW training set, and 13 to the SINGLE CCW training set. During pre-training, participants in both groups were asked to perform arm reaches towards the targets with an aligned cursor. The purpose of pre-training was to capture baseline performance in addition to familiarizing participants with the task. Participants in both groups completed 50 reaches with an aligned cursor during closed-loop pre-training trials (first box in Figure 2A and 2B.) followed by 30 open-loop trials to record baseline aftereffects (second box). The purpose of the open loop trials was to assess aftereffects as a result of training with a misaligned cursor. Prior to every trial, participants were presented with the word “TOP” when they had to hold the stylus by the foam square attached to the top of the stylus using a power grip (Figure 1B) or “BOTTOM” to hold the stylus like a pen using a precision grip (Figure 1C). After every trial, participants placed the stylus back on the penholder located approximately 10 cm from the home position. During pre-training, half of the trials prompted participants to hold the stylus in a TOP posture and the remaining half in a BOTTOM posture.

Training (adaptation measures)

SINGLE distortion group

The objective of the training sessions was to expose the participants to a single visuomotor rotation so as to capture an “ideal” learning rate and resulting aftereffects from which to compare our dual groups. The task was to make arm reaches towards the target while experiencing a 30° CW (when using a power grip) or CCW (when using a precision grip) visuomotor rotation of the hand-cursor. Participants completed 180 trials with their designated rotation (third box in Fig 2A) followed by 30 open-loop trials (fourth box in Fig 2A). Throughout the whole experiment, participants in the SINGLE distortion training were required to hold the stylus with only one hand posture depending on which rotation they were assigned.

DUAL distortion group

First training set (adaptation measures) & post-training (aftereffects): Participants in the dual distortion group were exposed to both 30° CW and CCW rotations during two training sets. Half of the trials had a CCW rotated cursor (required reaching with a precision grip) and the remaining half had a CW rotated cursor (required reaching with a power grip) in pseudo randomized order. In between trials, participants were prompted with a screen that said either “TOP” or “BOTTOM” to indicate which posture to take. Target locations appeared in a pseudo-randomized order per cursor rotation. Participants completed 360 dual-distortion trials followed by 30 open-loop trials to test for aftereffects (third and fourth boxes in Figure 2B). Critically, participants were also prompted to hold the stylus in the “TOP” or “BOTTOM” position during open-loop trials in order to examine if posture-specific aftereffects manifest.

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

Body Posture Experiment

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

loop trials. During pre-training, participants were prompted to turn their seat to the left in half of the trials and to turn right in the remaining half.

The magnitude of the visuomotor rotations and target locations were the same as in the Hand Posture experiment. The order of the tasks, as illustrated in Figure 2A and 2B, also remained the same.

SINGLE distortion group

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

DUAL distortion group

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

DATA ANALYSIS

The hand cursor data were digitally smoothed using a first-order, low-pass Butterworth filter with a frequency cut-off of 2.5 Hz. Movement onset was set as the time at which 10% of peak velocity was reached. Reach adaptation to a visuomotor rotation can be examined using several dependent measures that reflect hand path deviation. In the following experiments, we used 'angular error at maximum velocity' as the target measure of hand path deviation. 'Angular error at maximum velocity' refers to the angular difference between the target and the cursor relative to home position at peak velocity and represents feed-forward movement planning, making it unlikely that participants are actively making corrections in this phase. As participants adapt to the visuomotor rotation, we expect the angular deviation of the cursor at peak velocity to decrease such that cursor-to-target reach trajectories straighten over time. Angular reach errors were separated by rotation and blocked into groups of 5 trials to allow for a full cycle presentation of the five different target locations.

Hand Posture experiment

To rule out whether the direction of cursor rotation (and the accompanying hand posture) affected the results, we flipped the sign of the angular reach errors for the CCW rotation and compared these normalized errors along with the two other factors, TRAINING SESSION (SINGLE, DUAL1, and DUAL2) and BLOCK (initial and final). We found no significant effect of or interaction with ROTATION as a factor (2-way ANOVAs; all $p > 0.05$). Hence, for further analysis, we collapsed the normalized errors across the

two rotations and performed a 3 (training session) x 2 (block) way mixed analysis of variance (ANOVA). One participant was excluded as their angular deviations during training were greater than 2 standard deviations from the mean. Adaptation was assessed by comparing the initial and final blocks of training using a paired t-test for each group (Bonferroni corrected). Additionally, we compared the angular errors for the final block of trials across the three training sets (SINGLE, DUAL1 and DUAL2) using a One-way ANOVA followed by independent t-tests to assess differences between groups (Bonferroni corrected).

To assess improvement across the initial and final blocks between groups, we quantified a measure called “percent improvement” which was defined as the difference between the mean angular errors during the initial block and final blocks, divided by the mean angular error for the initial block per participant (c.f. (Baldeo & Henriques, 2013)). We used a one-way ANOVA model to compare the mean percent improvement collapsed across the rotations for all three training sets (SINGLE, DUAL1 and DUAL2) followed by multiple post-hoc comparisons with Bonferroni correction. In order to test whether a second training session (DUAL2) with the opposing distortions lead to greater reduction in errors (greater learning) for the DUAL2 training session, we assessed percentage improvement relative to the initial block of errors in the first training set (DUAL1).

We assessed aftereffects during post-training by comparing the mean angular reach errors of the first block of 5 trials relative to performance on open-loop trials during pre-training to examine context-dependent errors. We did not collapse the aftereffects across rotations because we found that they are significantly different and

instead performed separate one-way mixed ANOVA for the two hand postures to compare aftereffects following SINGLE, DUAL1 and DUAL2 training. Follow-up, paired t-tests with Bonferroni correction revealed which groups had significant aftereffects.

Body Posture experiment

Like the Hand Posture experiment, we first explored whether body orientation significantly affected angular reach error during training. Since body orientation did not significantly interact with reach errors for either the SINGLE groups ($F(1,23)=.531$, $p=.474$) nor the dual group ($F(1,16)=2.284$, $p=.150$), we collapsed the data across the two rotations (CW and CCW) for all groups. We compared angular reach errors between SINGLE and DUAL groups using a 2 (GROUP) x 2 (BLOCK) mixed ANOVA to determine the efficacy of body rotation direction as cues in facilitating dual adaptation. Additionally, we compared percent improvement between SINGLE and DUAL groups using an independent samples t-test. Lastly, to assess aftereffects, we first examined whether the context (i.e. body rotation) elicited a rotation-dependent reach error. Again, since the direction of the body did not significantly affect adaptation for either the SINGLE groups ($t(23)=0.331$, $p=0.744$) nor dual group ($t(16)=0.196$, $p=0.847$), we collapsed these measures across the postures. Finally, we used an independent samples t-test to compare aftereffects between the SINGLE and DUAL groups.

To further quantify and illustrate the change in reaching errors across training, we fitted a single exponential function to both datasets across all blocks (of 5 trials) of training and averaged across participants, for each rotation and group using VEEL (<http://veel.sourceforge.net/>). The equation takes the form of $RD=be^{(-ax)}+c$ where x

represents the block number, a the rate of learning, c the asymptotic level of performance, and b is a scaling factor. The exponential fit changed in sign depending on the rotation (CW or CCW).

Between-cue efficacy

Finally, we analyzed the efficacy of the cues between experiments by comparing percent improvement in the DUAL groups using an independent samples t-test. The assumed level of significance was $p < .05$ for all analyses.

RESULTS

Hand Posture experiment

Visuomotor adaptation

Mean hand trajectories in Figure 3 illustrate that both groups exhibited large rotation-dependent errors at the initial stage of training (black lines depicting the mean path of the first 5 trials), angular deviations reduced over time as evidenced by a rapid decline towards pre-training levels (grey lines depicting the mean path of the last 5 trials). Figure 4 shows hand posture-dependent reach errors for blocks of 5 trials per rotation for the SINGLE rotation groups, DUAL rotation training set 1, and DUAL rotation training set 2 across the training session. The exponential fits to the blocked mean reaching errors shown in green dashed lines resemble the exponential curve typically associated with motor learning although to a lesser extent for the second set of training blocks for the DUAL groups (Krakauer et al., 2000). In general, exponential fits appear less steep in the DUAL groups with values ranging from -0.03 to -0.11, compared to those of the SINGLE groups with values of 0.20 and -0.61.

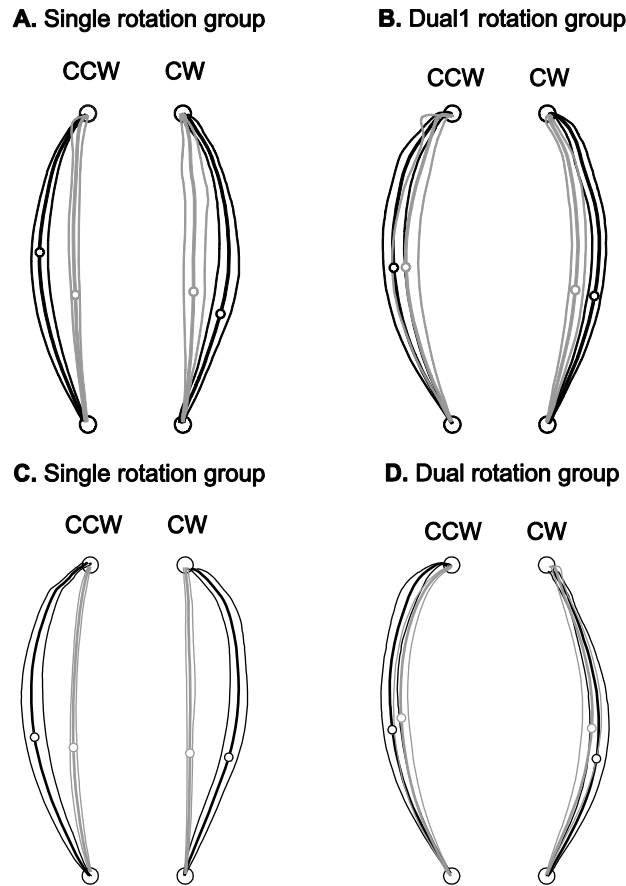


Figure 3. Average hand trajectories between the SINGLE and DUAL1 groups and rotations collapsed across all target locations. Mean hand paths for the A: SINGLE and B: DUAL groups of the Hand Posture experiment. Mean hand paths for the C: SINGLE and D: DUAL groups of the Body Posture experiment. Mean paths for the first five trials are depicted in black and last five trials in grey. The top black discs represent the target while the lower black disc represents the home position. The mean (central solid line), 95% confidence limits (two thin bordering lines), and point at peak velocity are plotted across all participants for each group and rotation.

In order to assess adaptation for the DUAL and SINGLE groups, we compared the mean angular reach errors across the initial trial and final block (Figure 4, second row). We found that the errors during the final block of trials were significantly less deviated than those of the initial ($F(1, 72)=37.61, p<0.001$), but this change varied between groups ($F(2, 72) = 5.87, p<0.005$). Both SINGLE ($t(22) =7.42, p=0.000$, one-tailed, $\alpha=0.016$) and DUAL1 ($t(25)=2.492, p=0.010$, one-tailed, $\alpha=0.016$) show smaller errors in the final block compared to the initial block. Likewise, we found a significant drop in errors when comparing the initial block in DUAL1 with the final block in DUAL2 ($F(1, 12)=15.528; p<.005$). However, since reaching errors were smaller at the start of DUAL2 as a result of training in DUAL1, we found no further significant change in errors at the final block for the second set of training compared to initial trial in DUAL2, as can be seen Figure 4F ($p>0.05$). The reach errors in final block of training for both DUAL1 and DUAL2 were nonetheless significantly larger than that of the SINGLE groups suggesting that neither DUAL sets achieved the same extent of error reduction as the SINGLE group ($t(47)=-4.961; p<0.001; t(47)=-4.337; p<0.001$, respectively). Together, these results suggest that associating distinct postures with each opposing rotation is sufficient in facilitating concurrent adaptation although not by far to the same extent as learning under a single perturbation.

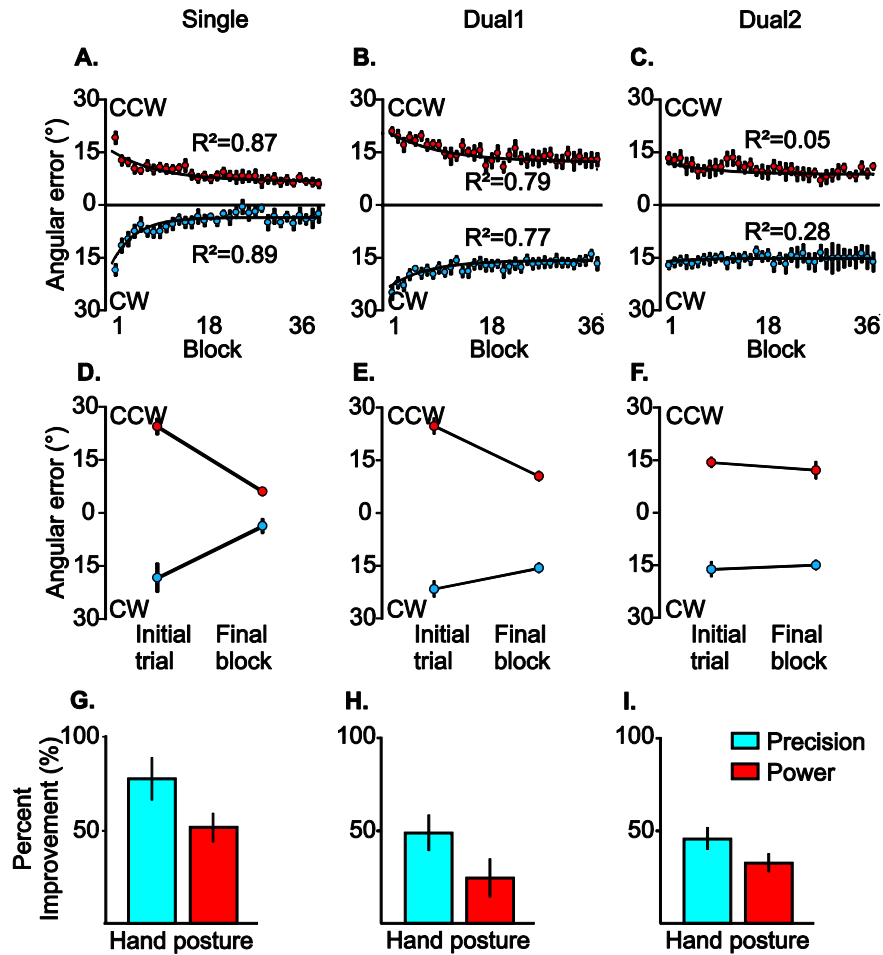


Figure 4. Angular reach error across blocks during training for the Hand Posture experiment. A - C: The top row of plots depicts angular reach errors across blocks (of 5 trials) during training. Thin black lines represent fitted exponential curves for reach deviations for the entire training session with the equation $RD = be^{-ax} + c$. SINGLE CCW ($7.98e^{-0.20x} + 8.18$), SINGLE CW ($11.27e^{-0.61x} + 7.15$), DUAL CCW T1 ($7.50e^{-0.08x} + 15.43$), DUAL CW T1 ($8.32e^{-0.06x} + 13.36$), DUAL CCW T2 ($1.76e^{-0.11x} + 14.43$), and DUAL CW T2 ($3.53e^{-0.03x} + 9.73$). D - F: The bottom row of plots depicts mean angular reach error across the initial trial and the final block for each group. Blue circles indicate reach errors during precision grip trials while red circles indicate reach errors during power grip trials. G - I: Percent improvement for the Hand Posture experiment for the SINGLE, DUAL1, and DUAL2 training sets. Blue bars represent percentage improvement for precision grip trials while red bars represent percentage improvement for power grip trials. Error bars represent SEM.

Percent improvement

To better compare adaptation levels across the groups, we calculated percentage improvement across the initial and final block relative to each participant's initial performance on the first block of training, as plotted in Figure 4, third row. Percent improvement in the dual distortion training set (DUAL2) was calculated relative to initial performance during training set 1. Thus, larger percentages indicate greater learning. Although Figure 4G-4I suggests that the percentage improvement was slightly smaller for precision grip trials (CCW-rotated cursors) compared to power grip trials (CW-rotated cursors), we found no significant difference between the two hand postures. More importantly, percent improvement differed significantly between groups ($F(2,72)=3.248$; $p<0.05$). Follow-up analyses revealed that percentage improvement for the SINGLE training set was significantly larger than that of the DUAL1 training set ($t(47)=2.417$; $p<.033$ but not DUAL2 ($t(47)=2.107$; $p>.033$). The absence of a difference between SINGLE and DUAL2 training suggests that although there was not a significant reduction in reach errors within the second set of DUAL Training, there was enough of a reduction that the overall percentage improvement across both DUAL1 and DUAL2 (i.e. double the training) approached that of the SINGLE group.

Aftereffects

An additional measure for motor learning is to determine whether participants continue to make deviated movements when reaching without visual feedback of the hand-cursor following context-dependent adaptation. Figure 5 shows the aftereffects

produced between the 3 training sets, with the SINGLE group showing model aftereffects produced as a result of complete visuomotor adaptation. Indeed, we found significant aftereffects in the direction of distortion depending on the hand posture, not only in the SINGLE group ($F(1, 21) = 123.23, p < 0.001$), but also for the DUAL group ($F(1, 24) = 21.29, p < 0.001$) when comparing no-cursor reaches pre- and post-training. The aftereffects also varied with direction of distortion for the SINGLE group, with the precision grip trials showing slightly larger deviations than that of power grip trials ($F(1, 21) = 7.25, p = 0.014$). Aftereffects did not vary with the direction of distortion for the DUAL group ($F(1, 24) = 0.614, p > 0.05$). Furthermore, we found that the aftereffects for both DUAL1 and DUAL2 were significantly smaller (and about half the size), than those of the SINGLE training set ($p < 0.01$), but not significantly different from each other ($p = 0.650$). Although we saw significant context-dependent aftereffects in the DUAL training sets, they are not as large as that of the SINGLE group nor do they approach its magnitude despite extended training.

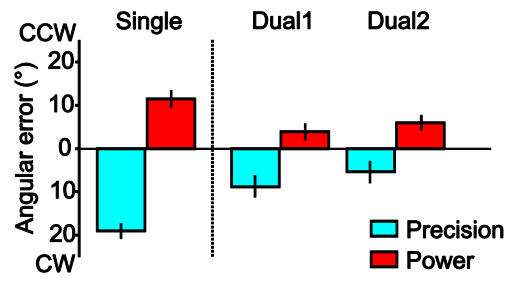


Figure 5. Aftereffects for the Hand Posture experiment. Blue bars represent aftereffects for precision grip trials while red bars represent aftereffects for power grip trials. *Error bars* represent SEM.

Body Posture Experiment

Visuomotor Adaptation and Percent Improvement

As expected, both SINGLE and DUAL groups initially made large reaching errors as a result of the visuomotor perturbation followed by a decrease in error over time as adaptation progressed (see Figure 3C-3D for mean hand trajectories). As shown in Figure 6A and 6B, participants from both the SINGLE and DUAL groups were able to significantly decrease their reaching errors between the initial block and final block ($F(1,40) = 89.70$, $p < 0.001$), but this change varied between groups ($F(1,40) = 31.306$, $p < 0.001$). A comparison of the final block of 5 trials between the SINGLE and DUAL groups showed that the SINGLE group had significantly lower mean angular deviations than that of the DUAL group by the end of training ($t(40) = 11.12$, $p < 0.001$). Additionally, percent improvement from the initial trial to the final block was found to be significantly different between DUAL and SINGLE groups ($t(40) = -7.732$, $p < 0.001$) although both show significant improvement (see Figure 6E-6F). These findings suggest that body rotations, which produce distinct body postures and shoulder positions, can efficiently cue a previous adaptive state, such that two perturbations can be learned concurrently by the CNS but not to the same extent as learning under a single perturbation.

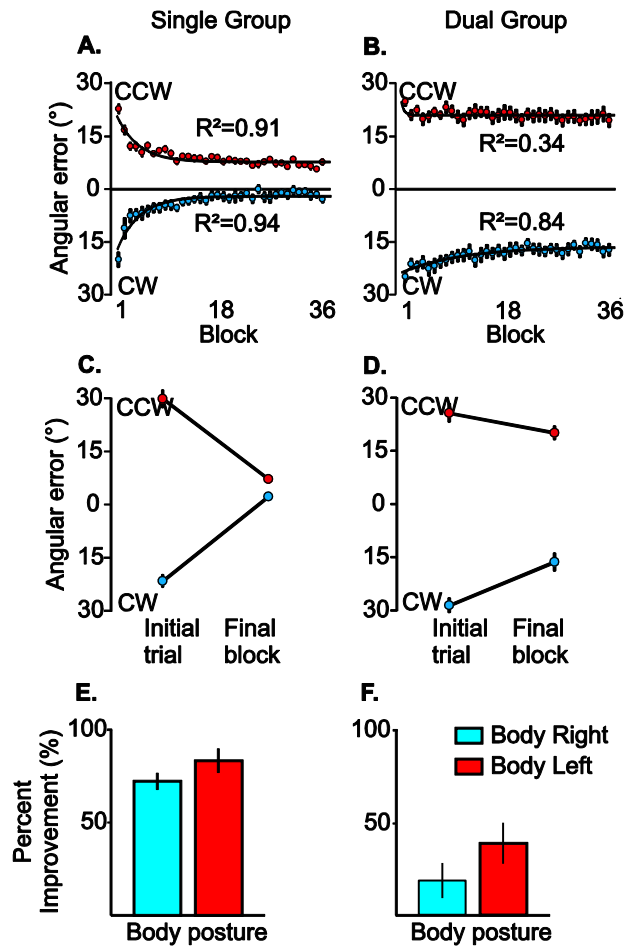


Figure 6. Angular reach error across blocks during training for the Body Posture experiment. **A - B:** The top row of plots depicts angular reach errors across blocks (of 5 trials) during training. Thin black lines represent fitted exponential curves for reach deviations for the entire training session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

Aftereffects

As with hand posture as a cue, aftereffects appear in the direction depending on the cue (leftward or rightward body posture). Figure 7 illustrates the magnitude of aftereffects produced between the 2 groups, with the SINGLE group showing model aftereffects that were produced as a result of complete visuomotor adaptation. Again, aftereffects differed between the two groups ($F(1,57)=59.71$, $p<0.001$). We then compared the aftereffects from post-training with aligned cursors from that of post-training with misaligned cursors for each group, and found that these aftereffects were significant for the SINGLE group ($t(24)=14.15$, $p<0.001$) but this was not true for the dual group ($t(16)= -0.96$, $p=0.352$). In sum, although the DUAL group cued by distinct body postures significantly decreased their reach errors for both rotations across time, they showed negligible aftereffects during post-training.

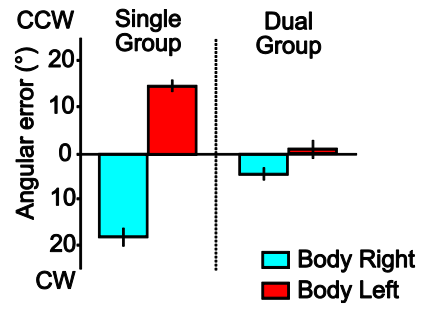


Figure 7. Aftereffects for the Body Posture experiment. Blue bars represent aftereffects for rightward body posture trials while red bars represent aftereffects for leftward body posture trials. *Error bars* represent SEM.

Between-cue comparison

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

DISCUSSION

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

Partial Dual Adaptation

Our present studies found that while dual adaptation is possible when target locations and desired cursor movements are identical across the two visuomotor conditions, reach error reduction did not reach baseline levels that rival that of adaptation to a single rotation. It is not surprising that our motor-based cues only elicited “partial” dual adaptation given previous findings regarding the pattern of generalization of motor learning. Complete dual adaptation occurs when there is greater motor

distinction between visuomotor variants thereby preventing any interference across rotations. Indeed, dual adaptation tends to be complete for opposing perturbations that are associated with targets that are widely separated (Woolley et al., 2007) or involve the use of different limbs (Galea & Miall, 2006). This is not surprising given that little generalization tends to occur for movements with very divergent directions, and across two arms. Thus, when opposing perturbations are associated with different target/movement directions, little interference is expected to occur and dual adaptation is more complete. The extent of dual adaptation in our studies, where targets were the same for the two rotations, was around a third to a half of that found in the SINGLE group. This is not surprising given that interference would have been high, and any adaptation would have been completely dependent on the effectiveness of the subtle change in intrinsic context. Hence, our results demonstrate that posture is a sufficient contextual cue for dual adaptation.

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

accompanied by another cue such as colour can sometimes allow for partial (Gupta & Ashe, 2007) or even complete dual adaptation (Osu et al., 2005), at least when adapting to opposing force fields by similar magnitude of force perturbations. It is possible that greater dual adaptation (i.e. equivalent to that of single adaptation) requires even more training than the two sessions that we offered, however we found that errors appear to saturate in the second session with no further significant reduction for the additional 360 trials (additional 36 trials per target, per rotation). Thus, based on our findings, it seems unlikely that further training would lead to any substantial reduction in errors equivalent to that shown during one session of training with a single perturbation.

Intrinsic contextual cues

Exploring specifically what types of cues are able to facilitate dual adaptation was a key objective of the present studies. We began by testing whether an intrinsic cue like change in hand posture (and grip aperture) was sufficient. Baraduc & Wolpert (2002) showed that reach adaptation to a rotated cursor is posture-specific in that the transfer of adaptation was significant but smaller when the posture differed from that used during training. Given that the generalization across arm posture was limited, we hypothesized a similar change in hand posture, along with a grip aperture, may be sufficient for dual adaptation. One preliminary ABA (serial block adaptation) study associating different arm posture with opposing force fields has also shown serial adaptation when training with associated postures and perturbation (Gandolfo et al., 1996). Wang and Mueseler (2014) showed significant but partial adaptation to

opposing visuomotor rotations when reaching to the same forward central target but while moving their arm to the left or to the right of the tablet workspace thereby varying posture but not target location. Given these findings, we expected, and indeed found, that our participants would be able to partially dual adapt if opposing visual perturbations were coupled with different postures.

While hand path location or hand posture may be sufficient to allow for dual adaptation, grip aperture seems to be less promising. Cothros et al. (2008) found that changing the shape of the handle (e.g. stick vs. ball) participants used to reach, without changing the orientation or texture of the handle, was not sufficiently distinctive to allow for a reduction in interference between opposing force-field perturbations in an ABA task when each perturbation was associated with each grip shape. In fact, the extent of interference was just as large as that produced when the handle remained the same. Likely, the change in tactile information did not cause an overall change in movement planning suggesting that haptic cues alone do not facilitate dual adaptation unless they are combined with other motor-based cues or if they allow for a sufficient change in movement planning. This suggests that not only the type but also the distinctiveness of the cue plays a role in reduced interference across the two adaptive states. The effect of context seems to be additive, such that more distinct cues allow for increased adaptation. In our Hand Posture experiment, we were not able to distinguish whether it was grip aperture or hand posture that provided the sufficient cue for partial dual adaptation. However, given the results above, it is unlikely that the change in grip or texture alone, apart from a change in posture is driving dual adaptation.

The second intrinsic cue we tested also involved changes in arm posture, but this time less directly, in that rotating the body changes the joint motions necessary to produce the same hand trajectory. By keeping the head facing straight, while the body turned beneath it, we avoided any potential vestibular cue (which is useful when adapting to altered visual feedback during locomotion; (Dumontheil et al., 2006)). Interestingly, although we found significant hand posture-specific aftereffects in the DUAL group of the Hand Posture experiment, we did not find the same in the Body Posture experiment to complement our other visuomotor adaptation measures. While aftereffects typically represent genuine implicit adaptation, it seems unlikely that participants employed explicit or cognitive strategies given that upon debriefing, most did not have a valid strategy or even noticed the rotations. Instead, the lack of significant aftereffects in the body posture experiment was likely due to the fact that the change in arm posture given the two body directions was not large enough to drive sufficient visuomotor learning to lead to substantial aftereffects. Likely, the body posture cues were less distinctive than the hand posture cues (which also had additional haptic cues including grip texture and aperture) and other studies that manipulated arm posture such as those employed in Baraduc & Wolpert (2002). Since our setup didn't allow us to implement a large change in arm posture, we instead changed the body direction and thus the shoulder location and the linkages associated. Here, a body rotation of 10° CCW pushed the shoulder (and thus, center of shoulder rotation) forward by roughly 3.2 cm based on the average woman's shoulder width (approximately 35 cm). Likewise, a body rotation of 10° CW pushed the shoulder back 3.2 cm resulting in sagittal difference of roughly 6 cm. If we looked at how much the shoulder has to rotate

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

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

Internal models

The present findings provide further support for the MOSAIC theory, which posits a contextual switching mechanism between multiple internal models that allows for accurate corrective movements within a variable environment (Haruno et al., 2001; Kawato, 1999). The MOSAIC model was able to show generalization, primary learning of modules, and the ability to switch between the learned models based on prediction errors and sensory cues (Haruno et al., 2001). In the MOSAIC model, a module is any combination of a forward (predictor) and inverse (controller) model. Over training, forward models learn to predict the consequences of a motor command in any given

context based on past experienced contexts. In dual adaptation, when a rotation associated with a sensory cue is introduced, initial movements will have large errors based on the predictions made by forward models, but as feedback is integrated by the inverse models, the appropriate dynamics will be learned. When this is followed by a counter-rotation, which is associated with a different sensory cue, the same learning process occurs. Over concurrent training of the two rotations, motor errors are reduced if the appropriate internal models are recalled based on sensory cues.

Although the previously discussed models show how certain cues aid in the retrieval of internal models as well as the timescale in which this occurs, they do not inform on what specific cues are sufficient facilitators of concurrent adaptation. Our present findings suggest that hand and body postures, when associated with an internal model that specifies the appropriate compensatory responses, provide adequate information to the CNS to allow for dual adaptation. Since there was no difference in percentage improvement between the DUAL groups of the Hand Posture and Body Posture experiments, this implies that either cue is able to provide useful information to the CNS even when cursor movement trajectories are identical.

CONCLUSION

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

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