



Movements following force-field adaptation are aligned with altered sense of limb position

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Abstract

Previous work has shown that motor learning is associated with changes to both movements and to the somatosensory perception of limb position. In an earlier study that motivates the current work, it appeared that following washout trials, movements did not return to baseline but rather were aligned with associated changes to sensed limb position. Here, we provide a systematic test of this relationship, examining the idea that adaptation-related changes to sensed limb position and to the path of the limb are linked, not only after washout trials but at all stages of the adaptation process. We used a force-field adaptation paradigm followed by washout trials in which subjects performed movements without visual feedback of the limb. Tests of sensed limb position were conducted at each phase of adaptation, specifically before and after baseline movements in a null field, after force-field adaptation, and following washout trials in a null field. As in previous work, sensed limb position changed in association with force-field adaptation. At each stage of adaptation, we observed a correlation between the sensed limb position and associated path of the limb. At a group level, there were differences between the clockwise and counter-clockwise conditions. However, whenever there were changes in sensed limb position, movements following washout did not return to baseline. This suggests that adaptation in sensory and motor systems is not independent processes but rather sensorimotor adaptation is linked to sensory change. Sensory change and limb movement remain in alignment throughout adaptation such that the path of the limb is aligned with the altered sense of limb position.

Keywords Sensory plasticity · Motor learning · Force-field adaptation · Somatosensory perception

Introduction

There is accumulating evidence that motor learning involves changes to brain motor areas and movements as well as changes to perceptual systems and to sensory areas of the brain. Perceptual changes have been reported in studies involving visuomotor (Cressman and Henriques 2009), force-field (Haith et al. 2009; Ostry et al. 2010) and prism adaptation (Hatada et al. 2006b), in studies of reinforcement learning (Bernardi et al. 2015) and tasks involving skill acquisition without perturbations (Wong et al. 2011). They have also been reported for lower limb movements (Statton

et al. 2017) and for the perception of speech sounds in association with speech motor adaptation (Lametti et al. 2014; Nasir and Ostry 2009). In spite of these multiple indications of sensory and perceptual change in conjunction with motor learning, the nature of the relationship between sensory and motor adaptation is uncertain.

The uncertainty about the relationship between sensory and motor adaptation comes from contradictory findings in adaptation studies. There are reports that measures of perceptual change are correlated with the magnitude of learning (Mattar et al. 2013) suggesting that the two processes are linked. However, most studies to date have found that these changes are uncorrelated (Cressman and Henriques 2009, 2010; Lametti et al. 2014; Salomonczyk et al. 2011, 2012) and hence that the processes underlying perceptual and motor adaptation are independent.

The assessment of sensorimotor function at different stages of the adaptation may provide a window into the nature of the relationship between motor and somatosensory components. Measurements acquired before exposure to an

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unfamiliar perturbation reflect the previously acquired relationship between these two variables. Sensorimotor function after washout trials as well as that during the adaptation enables the assessment of how transient learning-related changes affect the relationship and the extent to which this changed relationship is maintained and may be incorporated into subsequent sensorimotor function. In the context of the present study, the primary focus is on washout trials rather than on performance during adaptation, since during washout, performance is not confounded by the ongoing presence of a perturbation.

There have been a number of reports in which movements in washout trials following force-field (Ostry et al. 2010), prism (Hatada et al. 2006a) and visuomotor adaptation (Haith et al. 2015) do not return to baseline values. In studies of speech motor adaptation, incomplete washout is routinely observed following the return of unaltered auditory feedback (Purcell and Munhall 2006). In addition, there is evidence that even when movements in washout trials reach baseline levels, washout does not erase motor memories (Krakauer et al. 2005). Consistent with this observation is the finding that following washout trials, motor-evoked potentials elicited by stimulation of primary motor cortex are increased relative to baseline levels (Orban de Xivry et al. 2013). It has been proposed that the savings observed following washout reflect intrinsic rather than more cognitive aspects of adaptation (Smith et al. 2006).

In parallel with the incomplete washout of motor components, the perceptual adaptation that occurs in conjunction with motor learning persists following adaptation. Perceptual change following force-field learning does not return to baseline values after a short period of washout trials (Ostry et al. 2010). Changes to perceptual boundaries which are measured by having subjects identify the direction of passive limb displacement are present 24 h after learning, and are similar in magnitude to those which are recorded immediately following adaptation (Nourouzpour et al. 2015; Ostry et al. 2010).

The motor and associated somatosensory components following washout may thus provide a means to assess the nature of the relationship between perceptual and motor adaptation. In our previous work documenting changes in somatosensory function following force-field adaptation, we observed patterns in washout trials that suggested movements are aligned with the altered sense of limb position (Ostry et al. 2010). However, this observation was serendipitous, and because the number of washout trials in the earlier paper was limited it was uncertain whether or not asymptotic performance following washout was related to the magnitude of the perceptual shift. The goal of the present study was to examine this relationship in detail and, in particular, to assess whether or not perceptual and motor adaptation are independent. We hypothesized that if there is a relation

between perceptual and motor adaptation, when one variable is manipulated, the other should change as well. We found that both at a group level and at an individual subject level whenever perceptual change was observed following adaptation, it was tied to non-zero movement curvature after washout. At a group level when movements after washout were no different than baseline, there was no perceptual change either. The findings are consistent with the idea that motor learning is linked to perceptual change.

Materials and methods

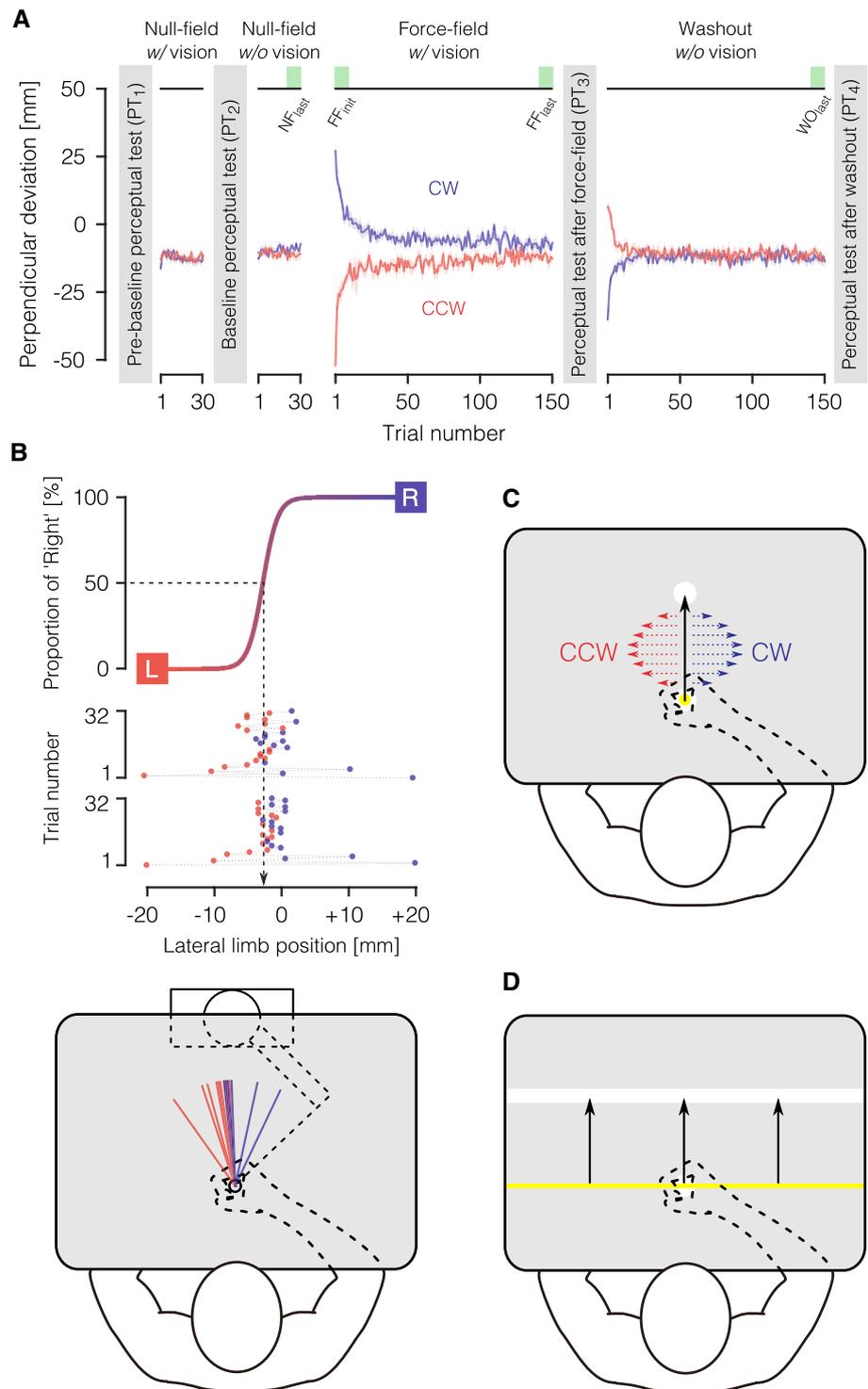
Subjects and procedure

Thirty-two healthy subjects participated in this study (15 males and 17 females, aged 18–30 years old). All subjects were right-handed and had not participated previously in studies involving force-field adaptation. The Human Investigation Committee of Yale University approved the experimental protocol.

Subjects were seated in front of a two degree of freedom robotic arms (InMotion2, Interactive Motion Technologies) and held the handle of the robot with their right hand. Two 16-bit optical encoders mounted on the motor shafts gave the position of the handle (Gurley Precision Instruments). Applied force was measured using a force–torque sensor (ATI Industrial Automation) mounted below the robot handle. Handle position and applied force were sampled at 200 Hz. Handle velocity was calculated numerically using the position data. The height of the seat was adjusted for each subject such that the upper arm was abducted approximately 70° from the trunk. Shoulder angle was approximately 45° relative to the frontal plane and the elbow was flexed at approximately 90°. An air sled supported the arm against gravity and the trunk was restrained. A semi-silvered mirror was horizontally mounted just below the subjects' eye level. A monitor projected visual information on the mirror. The room lights were turned off, and the subjects' vision of their arm and the robot handle were occluded by the mirror.

We tested for changes in motor and somatosensory function associated with force-field adaptation. Four perceptual tests that assessed sensed limb position were interleaved with different phases of a reaching task (Fig. 1a). The experiment began with an initial estimate of limb position (pre-baseline perceptual test, PT₁). Subjects then performed 30 baseline movements with vision of the hand in which the robot applied no force to the arm (null field with vision). This was followed by a second baseline estimate of the sensed limb position (baseline perceptual test, PT₂). Subjects then completed 30 movements in a null field with vision of the hand removed (null field without vision) which provided a reference against which subsequent washout trials

Fig. 1 Experimental design. **a** Perceptual tests were interleaved with four phases of a reaching task. Subjects were assigned to one of two conditions based on the direction of the force field during training. Mean perpendicular deviation (\pm SE) for each condition (blue: clockwise force field; red: counter-clockwise force field) is shown for each of stage of the experiment. **b** In the perceptual test, the robot moved the subject’s hand outward in a direction chosen from among a set of fan-shaped trajectories (bottom panel). The middle panel shows a sequence of two blocks with lateral displacement on the horizontal axis and the trial number on the vertical. Red and blue represent trials in which the subject answered ‘left’ and ‘right’, respectively. The top panel shows a logistic function fitted to the responses. **c** In trials with vision, a yellow cursor indicated the position of the handle and white circles indicated start and target positions. In force-field trials, a velocity-dependent force displaced the handle to the left (CCW) or right (CW). **d** In trials without vision, a yellow horizontal bar indicated the sagittal position of the handle and a white target stripe extended across the entire display screen



also without vision could be compared. This was followed by 150 movements in a velocity-dependent force field with vision of the hand enabled (force field with vision). A further estimate of sensed limb position was obtained following force-field training (perceptual test after force field, PT₃). Afterwards, subjects performed 150 movements, again without vision in a null field (washout without vision). After

the washout trials, a final estimate of sensed limb position was obtained (perceptual test after washout, PT₄). The trials without vision were included to enable an assessment of motor performance in which on-line correction based on visual feedback was not possible.

Subjects were assigned to one of two conditions based on the direction of the force-field during training. Sixteen

subjects were tested in each of a clockwise force field (CW) and a counter-clockwise force field (CCW) condition.

Force-field adaptation

In trials with vision of the hand (the null field with vision and the force field with vision), subjects performed reaching movements from a start to a target position, which were both shown as white circles, 1.6 cm in diameter. The target was located 20 cm in front of the start position. A yellow cursor, 0.8 cm in diameter, indicated the current handle position (Fig. 1c). Subjects were instructed to move the handle straight from the start position to the target. When the yellow cursor reached the target position, the color of the target circle changed to provide feedback about movement duration: the target turned green if the duration was within the desired range (700–800 ms), it turned red if the duration was too short (< 700 ms) and turned blue if the duration was too long (> 800 ms). The robot then returned the handle to the start position. An inter-trial interval ranged from 1000 to 1500 ms.

In the force-field trials with vision, the robot applied force to the handle as follows:

$$\begin{bmatrix} f_x \\ f_y \end{bmatrix} = D \begin{bmatrix} 0 & 20 \\ -20 & 0 \end{bmatrix} \begin{bmatrix} v_x \\ v_y \end{bmatrix},$$

where x and y are lateral and sagittal directions, f_x and f_y are commanded force to the handle in N , v_x and v_y are velocities of the handle in m/s, and D is the direction of the force field (Shadmehr and Mussa-Ivaldi 1994). A value of $D = 1$ corresponds to a clockwise force field, resulting in forces that deflected the movement to the right, while $D = -1$ corresponds to a counter-clockwise force field, that deflected the movement to the left (Fig. 1c).

In reaching trials without vision of the hand (null field without vision and washout without vision), the target and the current handle position were presented differently than when vision was provided. In trials without vision, the target position was shown as a white stripe (2 cm thick) that extended across the entire display screen. A yellow horizontal bar was presented to show the position of the handle (Fig. 1d). This configuration removed visual information about errors in a lateral direction and instead provided subjects with feedback that was restricted to movement amplitude. The subjects were instructed to make a single straight movement from the start bar to the white target stripe.

Prior to testing, subjects were pre-screened to verify that they were able to move the handle in a straight line in the absence of visual feedback. This was done to ensure that subjects started with a common movement trajectory against which adaptation-related changes could be assessed. Subjects in this test were required to move

from the start position to the target, in a null field, without vision of the limb or cursor. The criterion for inclusion was a mean maximum perpendicular distance over 30 trials of no more than 3.9 cm. This cutoff value was determined empirically, based on the distribution of the mean unsigned perpendicular deviation of all subjects. We used a Gaussian mixture model (Bishop 2006) to estimate two separate distributions that when summed predict the observed distribution of mean movement curvature. One modeled distribution corresponded to subjects who were able to move in a straight line (straight movement distribution) while the second corresponded to subjects whose average movement curvature was higher (curved movement distribution). Any subject whose mean unsigned perpendicular deviation fell above the 99th percentile of the straight movement distribution was excluded. Out of 45 subjects originally screened, 32 were retained and tested in the full experiment.

Perceptual testing

Perceptual tests (Fig. 1b), which measured sensed limb position, required that subjects identify the direction of the passive limb displacement produced by the robot. These tests were conducted without visual information of any kind. On each trial, the robot moved the subjects' right hand outward in a straight line, in a direction chosen from among a set of fan-shaped trajectories (Darainy et al. 2013). The movement was 20 cm in length and 1000 ms in duration. Subjects were instructed not to resist the movement of the robot, and on each trial to indicate whether the movement was angled to the left or right of the body midline. Following the subject's response, the robot returned the handle to the initial position. An inter-trial interval ranged from 1000 to 1500 ms.

A maximum-likelihood (MLL) procedure (Shen and Richards 2012) was used to select the angle of the fan-shaped displacement on each trial. This is an adaptive procedure that efficiently selects test stimuli for perceptual threshold estimation. On every trial of the procedure, a psychometric function, which models the relationship between stimuli (angular displacement directions) and subjects' binary responses, is obtained. The estimated function is based on the previous stimuli and associated responses, by estimating a threshold value α and slope β of a Gaussian logistic function. In the MLL procedure, the limb displacement direction on each trial was determined in an adaptive fashion based on the direction that provides the most information about the shape of the estimated psychometric function. In this study, the limb displacement at the first trial ranged from $\pm 30 \pm 5^\circ$. Each of the perceptual tests consisted of two 32-trial blocks (Fig. 1b).

Data analysis

As in previous work (Ostry et al. 2010), the dependent measure for reaching movements was the average lateral deviation, measured for each movement individually. Specifically, the perpendicular deviation from a line connecting the start and end of each trial (PD) was computed over the course of movement and was averaged to give a mean deviation for that trial. The start and end of a trial were defined as the time at which the tangential velocity of the hand rose above and fell below 5% of maximum velocity. Adaptation was quantified as the difference in average deviation between the first ten and last ten force-field trials ($FF_{init}-FF_{last}$ in Fig. 1a). Movements after washout were quantified as the difference in average deviation between the last ten washout trials without vision and the last ten null-field trials without vision ($WO_{last}-NF_{last}$ in Fig. 1a). A repeated-measure ANOVA with one between-subject factor (CW or CCW) and with one within-subject factor (NF_{last} , FF_{init} , FF_{last} or WO_{last}) was used to conduct statistical tests. To account for differences associated with the force-field directions, the signs of the measurements for both movement curvature and sensed limb position in the CW condition were flipped. This enabled us to perform statistical tests from the CW and CCW conditions together.

For each perceptual test, the boundary between ‘left’ and ‘right’ was estimated on a per-subject basis using a psychometric function that was obtained by fitting a logistic function to the 64 pairs of angled displacements and associated binary responses. The threshold was quantified as the 50% point of the logistic function (Fig. 1b). Perceptual thresholds were compared across the three perceptual tests (PT_2 , PT_3 and PT_4) and between the two force-field directions (CW or CCW) using a repeated-measures ANOVA. The perceptual shift associated with force-field adaptation was assessed by comparing the perceptual threshold estimate prior to and following adaptation (PT_3-PT_2 in Fig. 1a). The perceptual change following washout was assessed by comparing the perceptual threshold prior to force-field training with the one following washout without vision (PT_4-PT_2 in Fig. 1a). To account for differences associated with the force-field directions, the signs of the perceptual measurements for CW were flipped.

The relationship between movement and sensed limb position was assessed both prior to adaptation (NF_{last} versus PT_2 in Fig. 1a) and following washout ($WO_{last}-NF_{last}$ versus PT_4-PT_2). A correlation was also computed to assess the relationship between the magnitude of adaptation and the associated perceptual change ($FF_{init}-FF_{last}$ versus PT_3-PT_2). As above, the signs of the measurements for CW were flipped and then the correlation was computed. The measure following washout was the primary focus of the test for independence between perceptual and motor adaptation since it

was conducted without visual feedback to assess persistent changes to feedforward control (and eliminate on-line correction of movement) and in the absence of any ongoing perturbation.

Results

The experiment was designed to test whether changes to the somatosensory system that occur in conjunction with sensorimotor adaptation are linked to adaptation-related changes in movement.

Specifically, the goal was to test whether limb movements following post-adaptation washout trials were aligned with altered perceptual boundaries. Sensed limb position was quantified in terms of the perceptual boundary between ‘left’ and ‘right’ at the body midline, using perceptual tests that were interleaved with the null field, the force field and a long washout phase following adaptation (Fig. 1a).

We quantified sensorimotor adaptation as the average movement deviation over the course of force-field trials with vision. Figure 1a shows a time course of these values averaged across subjects in the clockwise (CW, blue) and counter-clockwise (CCW, red) force-field conditions. The shaded area represents ± 1 standard error across the subjects for each condition. CW and CCW forces deflected movements towards the right and left, respectively. As can be seen in Fig. 1, the force-field perturbation resulted in large deviations in the first few trials that gradually decreased and reached asymptotic levels that approached those obtained in null-field conditions. Adaptation was assessed in four phases of the experiment using the mean perpendicular deviation (PD) in the last ten null-field trials without vision (before training), the initial and final ten force-field trials, and the last ten null-field trials following washout (Figs. 1a, 2). ANOVA revealed that differences in average PD across the four phases of the experiment were statistically reliable ($F_{(3,90)} = 201.59$, $p < 0.001$) and that this pattern of differences further depended on whether subjects were tested in the CW versus CCW condition which was revealed as a significant statistical interaction ($F_{(3,90)} = 6.38$, $p < 0.001$). Bonferroni-corrected post hoc tests indicated reliable differences between PD in the first and last ten trials in each of the two force-field directions ($t_{(15)} = 9.39$, $p < 0.001$ for CW and $t_{(15)} = 9.03$, $p < 0.001$ for CCW). Post hoc tests also indicated a reliable difference between PD in the last ten washout trials and the final ten null-field baseline trials for the CW force-field condition ($t_{(15)} = 5.02$, $p < 0.001$). No reliable difference was seen for the CCW force-field condition ($t_{(15)} = 0.291$, $p = 0.387$). This pattern of results is consistent with the idea that the motor system adapted to the force fields to compensate for

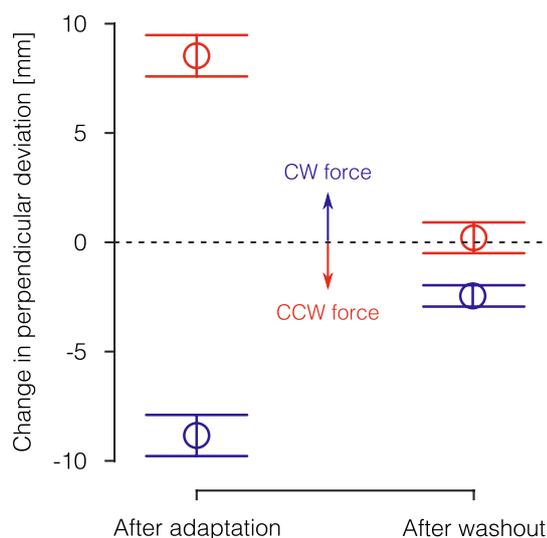


Fig. 2 Changes in motor function. Changes in motor function were assessed by differences in mean perpendicular deviation following force-field adaptation and following adaptation (see text). Values shown are averages over subjects in each condition (blue: clockwise; red: counter-clockwise) \pm SE. The left and right are associated with negative and positive values, respectively

the perturbation. In addition, in the CW condition movements following washout trials did not return to baseline.

Measures of sensed limb position were obtained at several points over the course of training, specifically, before null-field movements, before and after force-field adaptation and following washout (Fig. 1a). To assess adaptation-related changes in the perceptual boundary, the perceptual threshold estimated after adaptation was compared with threshold values obtained immediately before force-field training (PT_3 – PT_2 in Fig. 1a). Figure 3 shows the mean perceptual threshold (± 1 standard error), averaged over subjects, in each condition relative to the baseline threshold (PT_2). Following force-field training, there is a shift of the perceptual threshold in a direction opposite to that of the perturbation, that is, in the direction of applied compensatory force. ANOVA revealed statistically reliable differences between sensed limb position before adaptation, following adaptation and following washout ($F_{(2,60)} = 6.01$, $p < 0.005$), and that this pattern differed for subjects tested in the CW and CCW conditions ($F_{(2,60)} = 5.76$, $p < 0.010$). Bonferroni-corrected post hoc tests for the CW condition indicated differences in perceptual thresholds following adaptation and following washout ($t_{(15)} = 2.79$, $p < 0.015$ following adaptation, and $t_{(15)} = 4.39$, $p < 0.001$ following washout). There were no statistically reliable pair-wise differences in the CCW condition ($t_{(15)} = 1.52$, $p = 0.150$ following adaptation, and $t_{(15)} = 0.472$, $p = 0.644$ following washout). Thus, as with the movement data, on average

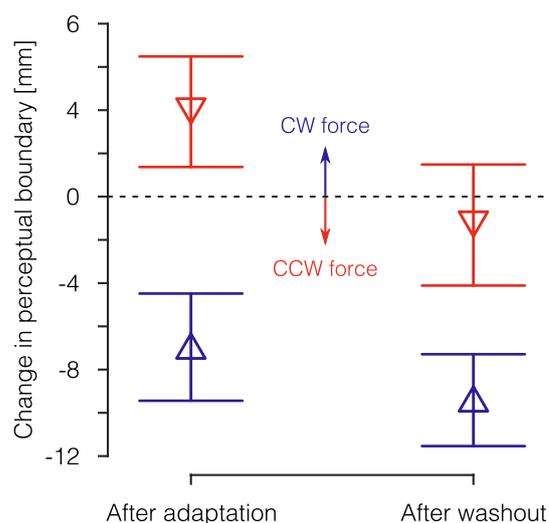


Fig. 3 Changes in somatosensory perception. Changes in somatosensory perception relative to the baseline values before null-field trials. Measurements are averaged over subjects in each condition (blue: clockwise; red: counter-clockwise) \pm SE. The left and right are shown as negative and positive, respectively

there are adaptation-related changes in sensed limb position that are restricted to the CW condition.

Of primary interest here is whether there is a link between adaptation-related changes to sensed limb position and the path of the limb following washout. We tested for this relationship by evaluating the correlation between the two measures, on a subject-by-subject basis. Figure 4 shows relationships between movements and sensed limb position before force-field training (a), following adaptation (b), and after washout (c). Blue and red filled circles in Fig. 4b, c show individual participants in the CW and CCW conditions, respectively. Regression lines for the two conditions combined are shown in black. In all cases—before training, following force-field adaptation and following washout—there are positive relationships between movement and perceptual change.

We first assessed the correlation between movements and limb perception before training (Fig. 4a). The Pearson correlation coefficient was significant ($r = 0.482$, $p < 0.005$). When the test was repeated for subjects that would subsequently train in the CW and CCW conditions, we found that the correlation was only significant for the CCW condition ($r = 0.558$, $p < 0.05$ for CCW; $r = 0.112$, $p = 0.704$ for CW). The correlation between the change in movement curvature during force-field trials and the perceptual shift following force-field trials (Fig. 4b) was significant for data from CW and CCW taken together ($r = 0.460$, $p < 0.005$). When the test was applied separately to each force-field direction, a significant correlation was observed for CCW ($r = 0.573$, $p < 0.020$), in which

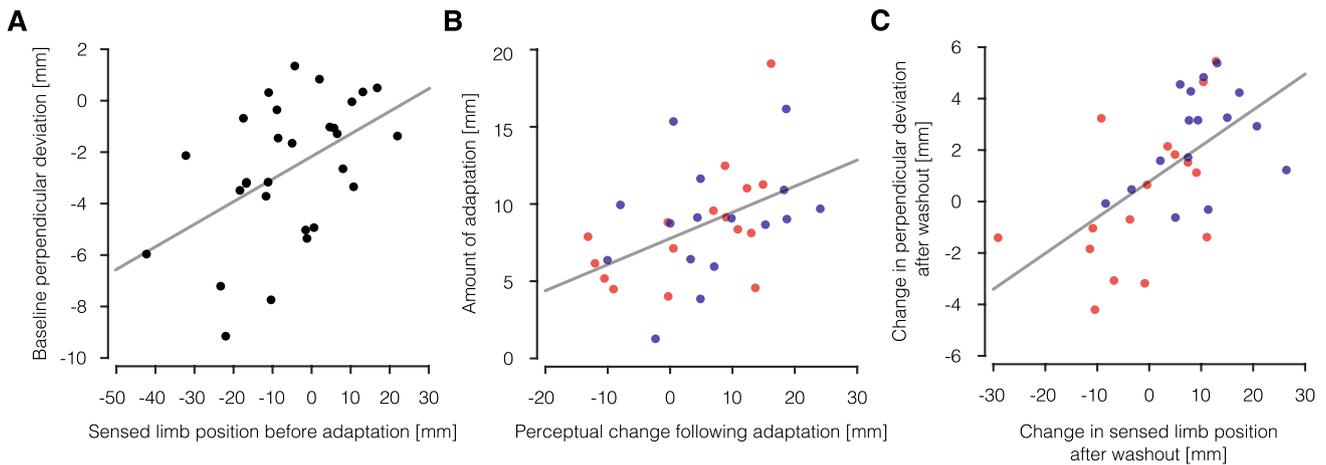


Fig. 4 Correlation between movement and sensed limb position. Relationship between movement curvature and perception before adaptation (a), between adaptation-related changes in movement curvature and the perceptual shift following the adaptation (b) and between changes in movement curvature relative to baseline and per-

ceptual change following washout (c). Blue and red circles represent CW and CCW conditions, respectively. The signs for values in the CW condition have been flipped so that both CW and CCW data can be considered together

greater movement adaptation was associated with a larger perceptual shift. No statistically reliable correlation was observed for the CW condition ($r=0.342, p=0.098$). We also computed the correlation between movement curvature following washout trials and the perceptual threshold after washout (Fig. 4c). As above, the Pearson correlation indicated a statistically reliable positive relationship when CW and CCW taken together ($r=0.591, p<0.001$). When the correlation was computed for the two conditions separately, there was a significant correlation for

CCW ($r=0.548, p<0.020$) but not for CW ($r=0.363, p=0.083$).

The tests following washout were conducted in the absence of visual feedback so as to focus on learning-related changes in feedforward control and its relationship to perceptual adaptation. To assess feedforward control more directly, we repeated all of the analyses above using movement deviation at maximum velocity as a dependent measure of motor learning. Table 1 gives the results of all tests using deviation at peak velocity and the original results using

Table 1 p values for statistical tests using both average movement deviation and movement deviation at peak velocity

Analysis		p value		
		Average	At peak velocity	
Motor performance	Difference across $NF_{last}, FF_{init}, FF_{last}$ and WO_{last}	<0.001	<0.001	
	Interaction between ($NF_{last}, FF_{init}, FF_{last}$ or WO_{last}) and (CW or CCW)	<0.001	<0.010	
	$FF_{init}-FF_{last}$	CW	<0.001	<0.001
		CCW	<0.001	<0.001
	$WO_{last}-NF_{last}$	CW	<0.001	<0.005
		CCW	0.387	0.488
Correlation	Between NF_{last} and PT_2	CW	0.704	0.998
		CCW	<0.040	<0.040
		CW and CCW	<0.005	<0.010
	Between ($FF_{init}-FF_{last}$) and (PT_3-PT_2)	CW	0.098	0.220
		CCW	<0.020	<0.050
		CW and CCW	<0.005	<0.030
	Between ($WO_{last}-NF_{last}$) and (PT_4-PT_2)	CW	0.083	0.050
		CCW	<0.020	<0.040
		CW and CCW	<0.001	<0.001

See Fig. 1 for symbol legend

average deviation. It can be seen that in statistical terms the results are equivalent for the two different ways of assessing adaptation.

In summary, in tests of mean values, subjects in the CW condition showed both reliable perceptual change after washout trials and persistent non-zero movement curvature. Subjects in the CCW condition on average showed neither perceptual change nor persistent changes in movement. Thus, whenever perceptual change was present movements following adaptation did not return to baseline. Tests which examined this relationship on a subject by subject basis revealed that even subjects in the CCW condition who showed no overall mean change in sensed limb position, nevertheless, showed a statistically reliable correlation between movement curvature and sensed limb position, as was the case for subjects overall. These findings support the idea that adaptation-related changes in the somatosensory system parallel those observed in the motor system, and that this relationship is present initially and is maintained both during and after adaptation.

Discussion

In studies of sensorimotor adaptation, when perturbations are removed, washout may be incomplete and adaptation-related changes to sensed limb position can be observed. In the present study, we tested whether or not these adaptation-related changes to movement and perception are independent. We found that force-field adaptation was associated with somatosensory perceptual change, and that perceptual estimates of limb position were systematically related to movement in all phases of adaptation. Movements before training were aligned with initial estimates of limb position. Subjects showed perceptual shifts as a result of adaptation. Those that showed greater adaptation showed greater perceptual shifts. Following washout trials at the end of adaptation, movements were again aligned with the altered perceptual boundaries. At a group level, when changes in perception were observed, movements following washout did not return to baseline, whereas when changes in perception were not observed, movements following washout returned to baseline levels. At an individual subject level, movements following washout trials were correlated with changes in perceptual boundaries. The correlation between perception and movement, and between perceptual change and adaptation-related changes to movement are consistent with the hypothesis that perceptual and motor adaptation are not independent.

There are several ways in which perceptual change and movement following force-field adaptation might be organized. Adaptation-related perceptual change may result in changes to movement. Changes in movement during learning

may result in changes to sensed limb position. Force-field learning may result in coordinated changes to movement and perception. We are unable to distinguish among these alternatives based on the present results. However, in work with cats, effects have been reported in both directions. Tetanic stimulation to primary somatosensory cortex has been shown to induce long-term potentiation in superficial layers of primary motor cortex at monosynaptic latencies (Iriki et al. 1989; Keller et al. 1990a; Sakamoto et al. 1987). This shows that activity in somatosensory cortex can drive changes to motor cortex. In other work also in cats, stimulation of primary motor cortex induced long-term potentiation in area 2 of primary somatosensory cortex (Keller et al. 1990b). This shows that motor cortical activity can result in somatosensory changes as well.

In previous studies of sensorimotor adaptation involving both limb movement and speech, perceptual adaptation is consistently observed to accompany learning. However, measures of perceptual and motor adaptation have not been consistently found to be correlated. While this might indicate that processes that underlie sensory and motor adaptation are independent, it could also be a reflection of the typical experimental design in which subjects receive visual feedback during movement (and auditory in the case of speech), and as a result are able to make online corrections to movement which may be reflected in the magnitude of dependent measures of motor adaptation. Visual feedback during movement was eliminated in the present study focusing on washout trials where the perturbation was also removed and thus measures of persistence of adaptation were related to feed-forward control of the limb and not to in-flight adjustments. Under these circumstances, it was observed that measures of perceptual and motor adaptation are not independent. When one was present so was the other.

In work on visuomotor adaptation, somatosensory perceptual change is needed in a functional sense to reconcile differences in the seen and felt position of the limb, and in effect serves to keep vision and proprioception in register (Cressman and Henriques 2009). In work with prisms, it has been proposed that adaptation is fully accounted for by combined changes to vision and proprioception (Harris 1965; Wilkinson 1971). In work on perceptual change following force-field adaptation, the magnitude of change is less and indeed there seems to be no obvious reason why perception needs to change. However, the fact that it does change, and, is consistently aligned with movement, is consistent with the idea that perceptual and motor adaptations are not independent. A relationship between perceptual and motor adaptation is likewise predicted in a Bayesian model of adaptation (Haith et al. 2009).

The present finding, that under baseline conditions the proprioceptive bias has motor consequences, has been reported previously, as for example in studies of tendon

vibration in which induced changes to proprioception result in changes to movement direction (Cordo et al. 1995). Similarly, a lack of proprioception leads to poor control of limb dynamics (Ghez et al. 1995). Nevertheless, the presence of this relationship underscores the alignment of sensory and motor functions in both baseline behaviors and adaptation. It also raises the possibility that accuracy of motor performance is related to somatosensory perceptual bias.

In the present study, we have described perceptual changes as relating to sensed limb position. However, perceptual report occurred after limb movement and accordingly it is possible that subjects' judgements were based on limb movement as well as/or instead of limb position. In other studies that have reported similar perceptual changes following motor learning, the perceptual judgements were based solely on sensed limb position. Specifically, in one set of studies in Ostry et al. (2010), passive limb displacements which preceded perceptual judgements were randomized so as not to provide any motion cues to the participant regarding the position of the limb. In work by Haith et al. (2009), Clayton et al. (2014) and 't Hart and Henriques (2016), participants were required to point to the sensed position of the limb using the contralateral arm, thus removing limb motion cues from the perceptual decision.

There has been some work on the neural substrates of perceptual change in conjunction with motor learning. Arce-McShane et al. (2014) reported electrophysiological evidence of changes to orofacial somatosensory cortex in conjunction with motor learning. Monkeys were trained in a novel tongue protrusion task. Rapid and long-lasting changes to primary somatosensory and motor cortex were observed in parallel. In both, there were increases in the proportion of task-modulated neurons, and reductions across trials in firing rate variability. In humans, there are electrophysiological data showing sensory change in conjunction with learning in both arm movements and speech. In particular, there are changes to somatosensory-evoked potentials following force-field adaptation (Nasir et al. 2013), following learning an arm muscle timing task (Pleger et al. 2003), and a sinusoidal tracing task (Andrew et al. 2015). There are changes to both auditory- and somatosensory-evoked potentials following adaptation to altered auditory feedback in speech (Ito et al. 2016). There is likewise neuroimaging data in work on motor and perceptual learning in human arm movement showing changes in functional connectivity in networks related to both perceptual change and motor learning (Vahdat et al. 2011, 2014). It is presently unknown whether perceptual changes reflect adaptation related to sensory feedback or to cortico-cortical connectivity or to some combination of the two.

Here, we observe changes on an individual basis in somatosensory perception following force-field adaptation. In other work, changes in visual perception have also been

observed in the context of force-field adaptation (Brown et al. 2007). Specifically, force-field adaptation influenced how participants predicted the motion of visual stimuli. Changes in visual perception have also been reported in the context of prism adaptation (Harris 1963). In the present study, measures of sensed limb position were conducted without vision of the limb. Likewise measures of movement curvature after washout were without visual feedback. Hence, it is not likely that potential visual changes affected the present results. However, it would be desirable to know more generally whether changes in visual perception contribute to movements following force-field adaptation.

An unresolved issue in the present work is the relative contribution of sensory and motor systems to learning. As noted above, in work on prism adaptation, post-exposure changes to movement are fully accounted for by the sum of changes to vision and proprioception (Harris 1965; Wilkinson 1971). This suggests that changes to the motor system per se may not be needed for prism adaptation, but rather, following learning, movements may depend solely on shifted visual alignment and altered proprioception. Part of the difficulty more generally in attributing plasticity to movement or somatosensation is that the two occur in parallel over the course of training. Accordingly changes to either or both systems could occur during learning. Differences in the rate at which learning-related changes occur in the motor and somatosensory systems are difficult to interpret. In studies involving altered somatosensory input (Cressman and Henriques 2009; Mattar et al. 2013; Zbib et al. 2016), adaptation has been studied in response to abrupt perturbations. Accordingly, this might result in the use of cognitive/explicit processes in early movement trials, which mask a more gradual intrinsic learning processes that may be better matched to the slower perceptual shift that has thus far been reported.

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