Articles in PresS. J Neurophysiol (January 30, 2013). doi:10.1152/jn.01052.2012

Mechanisms of responsibility assignment during redundant reaching movements

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Abstract

When the two hands act together to achieve a goal, the redundancy of the system makes it necessary to distribute the responsibility for error corrections across the two hands. In an experiment in which participants control a single cursor with the movements of both hands, we show that right-handed individuals correct for movement errors more with their non-dominant left than with their right hand, even though the dominant right hand corrects the same errors more quickly and efficiently when each hand acts in isolation. By measuring the responses to rapid cursor and target displacements using force channels, we demonstrate that this shift is due to a modulation of the feedback gains of each hand, rather than to a shift in the onset of the corrective response. We also show that the shift towards left-hand corrections is more pronounced for errors which lead to adaptation (cursor displacements) than for perturbations which do not (target displacements). This finding provides some support for the idea that motor system assigns the correction to the most likely source of the error to induce learning and to optimize future performance. Finally, we find that the relative strength of the feedback corrections in the redundant task correlates positively with those found for the non-redundant tasks. Thus, the process of responsibility assignment modulates the processes that normally determine the gains of feedback correction, rather than completely overwriting them.

Keywords

Reaching movements, redundancy, online corrections, visual perturbations

Introduction

Human movements often involve a number of effectors or joints. When reaching for an object, we normally use a combination of trunk, shoulder, elbow, wrist, and finger movements to efficiently achieve our goal (Bernstein 1967; Diedrichsen et al. 2010). Indeed, one may argue that reaching movements that are limited to shoulder and elbow joints, are only found in the laboratory setting, where additional degrees of freedom are constrained to allow for a simplified kinematics and dynamic analysis (Bhushan and Shadmehr 1999). In natural, free movements, most goal positions can be achieved using a range of different joint combinations (Cirstea and Levin 2000). Given this natural redundancy, motor commands have to be distributed across effectors. Furthermore, errors that occur during the movement in one joint can be compensated for by adjustments in a combination of other joints (Kurtzer et al. 2008). Thus, the motor system also needs to distribute responsibility for correcting movement errors across the involved effectors.

How does the motor system solve this problem? One possibility is that the motor system distributes the correction in such a way that it optimizes the performance for the *current* movement. This can be achieved by using a control policy (Todorov and Jordan 2002) that minimizes the influence of signal-dependent noise and the overall effort (Harris and Wolpert 1998; O'Sullivan et al. 2009). This leads to solutions in which the faster and more accurate effectors contribute more to the correction than the slower and less accurate ones. Alternatively, the motor system may assign the error to the joints according to their probability of having caused the error, thereby adapting the presumably maladapted joints and improving *future* performance of the whole system. This solution would require a dedicated mechanism that assigns the error across effectors.

White & Diedrichsen (2010) studied the process of responsibility assignment using a bi-manual reaching task. In the redundant version, participants had to hit one target with a single cursor, which was displayed at the spatial midpoint between both hands. In this condition, a deviation of the cursor from its desired path could have been caused by either the left or the right hand, or any combination of the two. Accordingly, any combination of left or right hand movements could also correct for the error. In this redundant situation, the motor system has to assign the responsibility to correct for the error to the involved effectors. In the non-redundant version of the task, each hand moved independently to a separate target. Errors therefore had to be corrected with the hand that encountered the error. In the latter condition, corrections with the dominant right hand were faster and more precise (Elliott et al.

1999; Mieschke et al. 2001; Todor and Cisneros 1985). However, in the redundant task, right-handed participants corrected for visually induced errors (cursor rotations) more with their non-dominant, left hand. This suggests that the motor system assigned a larger portion of the correction to the hand that more likely caused the error (the noisier left hand). This would have the advantage that the adaptive change predominantly occurs in the appropriate effector. In favor of this interpretation, the authors found a clear correlation between the distribution of corrections and the distribution of adaptive changes on the next trial. In the present study, we now address three important questions about the mechanism that underlies the assignment of responsibility for error corrections during redundant movements.

First, we ask whether the process of responsibility assignment acts by modulating the time that each effector needs to respond to the error, or whether it changes the feedback control gains, i.e. the strength of the correction. While both would lead to a shift in the distribution of the overall correction in the end of the movement, they would imply different neural mechanisms. The gradual nature of the visual perturbation (cursor rotation) used by White & Diedrichsen (2010) does not allow disentanglement of the temporal onset of a correction from its gain. In the present experiment, we therefore displaced the visual cursors laterally at a specific time point during the first half of the movement (Franklin and Wolpert 2008; Sarlegna et al. 2003; Sarlegna et al. 2004). To further improve the measurements of the early corrective movement, we used “force channel” trials (Smith et al. 2006), in which the reaching hands were constrained on a straight path to their respective targets. The onset time and strength of the corrective action could therefore be determined from the force participants exerted against the wall of the channel (Franklin and Wolpert 2008).

The hypothesis that the error is assigned to the most likely cause of the error (the non-dominant hand) raises a second question. This assignment strategy certainly only makes sense for errors that may be caused by internal noise or mis-calibration of the visuomotor system, and therefore actually require learning (Diedrichsen et al. 2005). By contrast, one would expect that any error that does not require an adaptive change should simply be corrected in the most effective manner, i.e. predominantly with the dominant hand. White & Diedrichsen (2010) compared visual rotations of the cursors, i.e. internally attributed errors that lead to strong adaptation responses, to displacements of the visual target (Goodale et al. 1986; Prablanc and Martin 1992), i.e. externally attributed errors that do not lead to visuomotor adaptation. While they found no difference in responsibility assignment in these two cases, the finding is tempered by the fact that the cursor rotations and target displacements differed in their temporal dynamics (gradual vs. abrupt). Here, we reinvestigate this question using abrupt lateral displacements of the visual cursor instead of cursor rotations. This allowed us to directly compare corrective movements in response to these two types of errors, because both perturbations had precisely defined temporal onsets, comparable time courses, and the same magnitude.

Finally, we asked how responsibility assignment in redundant tasks interacts with the mechanism that determines the feedback gains in non-redundant tasks. One possibility is that the principles that determine the responsibility assignment in the redundant case are separate from the principles that determine the feedback gains for both hands in the non-redundant tasks. This hypothesis predicts that the bimanual correction asymmetry in the redundant task is either not correlated with the correction asymmetry in the non-redundant task, or negatively correlated. The latter case would arise if high variability in the left hand would lead to lower feedback gains in the non-redundant task (Todorov 2005), but also to higher gains in the redundant task, as the left hand becomes the more likely cause of the error. Alternatively, the process of responsibility assignment may add to the existing underlying feedback gains for the left and right hand. It would therefore reflect a compromise between optimizing the performance on the current trial, and assigning the correction to the most likely cause of the error. This hypothesis predicts that the correction asymmetries in the redundant and non-redundant tasks correlate positively across participants.

Material and Methods

Participants

Thirty-one neurologically healthy right-handed volunteers (experimental group 1: 19 participants, 20-36 years, 7 female; experimental group 2: 12 participants, 20-28 years, 6 female) were recruited from an internal experiment database. All participants provided written informed consent prior to testing and were paid as compensation for their time expense. They were naïve to the purpose of the experiment and debriefed after the experimental sessions. The research ethics committee of University College London (United Kingdom) approved all experimental and consenting procedures.

Apparatus & Stimuli

Participants were seated comfortably in front of a virtual environment setup, leaning slightly forward with their forehead supported by a forehead rest. They made 15cm reaching movements away from their body while holding onto a robotic manipulandum (update rate 1kHz, recording of position and force data at 200Hz) with each hand. Movements were performed involving shoulder, elbow, and wrist movements in the horizontal plane at chest height. A mirror that was mounted horizontally above the manipulanda prevented direct vision of the hands, but allowed participants to view a visual scene on an LCD monitor (update rate 60Hz). The visual display was arranged such that stimuli appeared to be exactly in the depth-plane on which the hands moved. The movements were instructed using starting boxes (unfilled white squares, 0.5cm size, 6cm to the left and right from body midline) and target box(es) (unfilled white squares, 1cm size). Fixation had to be maintained on a white fixation cross (0.5cm), which was located in between the target boxes. The hand positions were represented by unfilled white circles (cursors, 0.3cm diameter) located vertically above the real positions of the hands. All visual stimuli were displayed with a time delay of 68±5 ms.

Visual perturbations

We applied two types of visual perturbation during uni-manual and bi-manual reaching movements. The perturbations occurred once the average position of the two hands had moved 15% of the forward distance to the target(s). One perturbation type consisted of a 2.5cm displacement of the visual cursor in lateral direction (defined as the x-direction) either to the left or to the right (cursor displacement, CD). The other perturbation type consisted of a 2.5cm displacement of the visual target in the lateral direction either to the left or to the right (target displacement, TD). The necessary correction magnitude for both perturbation types was equal since task success was defined in visual space. Only the direction of correction was opposite, i.e. a target displacement to the right caused a corrective response to the right while a cursor displacement to the right caused a corrective response to the left, and vice versa. Both perturbations could easily be detected and participants were informed about their occurrence before the experiment started.

Reaching conditions

We used two non-redundant conditions (“uni-manual” and “two-cursor”) and one redundant condition (“one-cursor”). The reaching conditions were blocked, and participants were informed before each block which kind of reaching movements they were supposed to perform.

Uni-manual (UM): Non-redundant uni-manual reaching movements were executed with either the left or right hand to a single target, while the other hand was static at its starting position. The target was located 15cm directly ahead of the starting position of the respective hand. Either the target or the cursor could be displaced to the left or to the right. Only participants from experimental group 1 were tested on this condition, because we did not expect further insights from testing more participants on this condition.

Two-cursor (TC): Participants executed bi-manual reaching movements, where each hand was associated with its own cursor, yielding non-redundant movements. The cursors were located above each hand, and each cursor had to reach its own target, which was located 15cm directly ahead of the respective starting positions. Both the left and right cursor or target could be displaced in independent directions (but at the same time), yielding 3 perturbation conditions: (a) a *single perturbation* was applied either to the left or right hand; (b) *symmetric perturbations* occurred, such that both hands had to respond with inward- or outward corrections (only experimental group 1); (c) *asymmetric perturbations*, such that both hands had to respond with leftward or rightward corrections. Only one type of perturbation (cursor or target) occurred within one trial. Because we did not find any significant differences between perturbation conditions, we averaged the results of all two-cursor conditions, analyzing the behavior of each hand relative to its own perturbation only.

One-cursor (OC): Redundant bi-manual reaching with a single cursor presented on the screen, which was located at the midpoint between the physical positions of both hands. Therefore, each hand contributed to half of the cursor motion. The goal of the movement was a single target located at body midline, 15cm ahead of the starting positions. As in the other conditions, either the target or cursor was displaced laterally.

Trial procedure

Participants started a trial by moving the cursors into the starting boxes while keeping their eyes on the fixation cross. After 800ms, the target box(es) appeared 15cm straight above the starting boxes, to which participants were instructed to make fast and accurate reaching movements. In the one-cursor condition, the two cursors disappeared upon target appearance and a single cursor was displayed at the spatial midpoint between the two hands. The trial ended when the hand velocity remained below 3.5 cm/s for 40ms. A trial was considered valid when reaching time was shorter than 800ms and maximum velocity ranged between 50 and 80 cm/s. Valid trials with endpoint accuracy of at least 7mm contributed a single point each for the overall score and were rewarded with a visual target “explosion” and a pleasant tone. A running score was continuously displayed above the targets. Feedback about invalid trials, successful reaches, and increase in score was given via a color scheme at the end of each trial. Participants were encouraged to use this visual feedback to adjust their movements on the following trials if necessary.

In half of the trials, a “force channel” restricted the movements for a sensitive read-out of the feedback responses (Franklin and Wolpert 2008; Smith et al. 2006). Force data obtained with this method is more sensitive to the detection of responses to perturbations than position data from free reaching trials. The sensitivity is in the same range as velocity data with having the advantage that the force is measured directly and does not have to be derived, thus no additional noise is introduced. The force channel was implemented with a spring-like force of 7000 N/m applied in lateral direction, which guided the hands on a straight path to the targets. In these trials, the cursor or target displacements were reversed 250ms after the initial displacement in order to enable task success. In the other half of the trials, the target and cursor displacement remained, such that the participants needed to correct for the perturbations.

Session procedure

An experimental session started with training blocks of all experimental conditions, but without force channel trials in order to keep the decrease in force responses as low as possible throughout the experiment (Franklin and Wolpert 2008). Training continued until at least 75% of trials produced by the participant were valid. The participants of experimental group 1 were tested for all reaching conditions in a blocked design with block order counterbalanced across participants. The one-cursor and both uni-manual conditions were each tested in two blocks of fully randomized 48 trials each. Each block contained 4 repetitions of the full permutation of all factors perturbation type (CD/TD/no perturbation) x displacement (left/right) x force channel (yes/no). All two-cursor conditions were intermixed in six two-cursor blocks, comprising 1/9 unperturbed trials, 2/9 two-cursor symmetric and asymmetric trials each, and 4/9 single perturbation trials permuted with displacement (left/right) and force channel (yes/no). Each of these blocks contained 48 fully randomized trials, leading to overall 8 repetitions per condition. Participants were informed before each block whether the next block was uni-manual, one-cursor, or two-cursor. Participants of experimental group 2 were only tested for the one-cursor, two-cursor asymmetric, and two-cursor single conditions. Each of the 4 test blocks contained 80 trials, also resulting in 8 repetitions per condition with an equivalent ratio of trial types as experiment 1. Within each block, 24 one-cursor and 56 two-cursor trials were blocked with the order between these two conditions counterbalanced across participants. Within the one-cursor and two-cursor sub blocks, the order across trials was fully randomized.

Data analysis

Invalid trials (6%) were excluded from further analysis, as they did not meet the movement time (< 800ms) or speed (50-80 cm/s) criteria. For each condition and participant, we could average over 6 to 8 repetitions. Movement start and end time-points were defined as the velocity exceeding or falling below 2.5 cm/s for at least 40ms. All position and force traces were aligned temporally to the onset of the visual perturbations, or the point in time when the perturbation would have occurred for unperturbed trials. For all analyses, we took the display time delay (68±5 ms) into account.

To assess the size of the corrective responses, we measured the lateral forces exerted into channels (perpendicular to the reaching direction, Fig. 1). A measure of correction strength for each hand was obtained by taking the difference between the force correcting for leftward displacements and the force correcting for rightward displacements. This subtraction automatically removed any constant forces in the channel that were caused by the biomechanical properties of the arm and robot. To obtain a time-averaged single measure for each hand and correction type, we averaged the force difference in the time interval from 180 to 330 ms after perturbation onset (*CorrectionStrength*). Additionally, we calculated the size of the final correction on trials without force channels. For this measure, we also used only the component in the direction of the perturbation: the correction in lateral direction at the end of the movement. Here, we averaged over leftward and rightward corrections of the same hand, in each case coding the expected response as a positive value. Thus, a correction with an extent of 25mm constitutes a full correction for the perturbation. The onset time of the corrective movement was assessed using only the force channel trials, as this data provides the most time sensitive information about corrections. For each subject and condition, we applied t-tests between the force traces of all leftward and rightward corrections until at least 4 consecutive tests revealed differences on a significance level of $p < .05$. The time stamp of the first of those 4 consecutive tests was taken as onset time.

As the interest of this study focused on the differences between redundant and non-redundant movements, the main comparisons are between the one-cursor and two-cursor conditions. Whenever the goal of the analysis was to confirm hypotheses based on the results of previous studies, we computed one-sided t-tests according to these hypotheses. For demonstrating novel effects or interactions, we computed two-sided t-tests or repeated measures ANOVAs. Corrections for multiple comparisons were performed using Bonferroni corrections where necessary. *P* values smaller than .05 are reported as significant. All values reported are mean values across participants with their respective standard deviations unless stated otherwise.

Results

Errors in the redundant task are mostly assigned to the left hand.

All participants showed fast movement corrections that specifically counteracted the displacement of cursor or target: When a cursor was displaced to the right, the hand(s) responsible for the cursor's movement pressed leftwards into the channel. By contrast, when a target was displaced to the right, the hand(s) controlling the cursor to that target pressed rightward into the channel. Figure 1 illustrates the difference in force between leftwards and rightward displacements, in such a way that positive values indicate a corrective response in the expected direction. In all conditions, the feedback correction began around 200ms after the visual perturbation.

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The amplitude of the corrective response, however, varied substantially between hands and conditions. For the non-redundant reaching conditions (two-cursor and uni-manual), the forces were usually higher for the right hand. To quantify this observation, we averaged the force difference between displacements to the left and right over the time interval from 180 to 330 ms after the visual perturbation (*CorrectionStrength*). We then used the difference in strength between the hands (right hand *CorrectionStrength* subtracted from left hand *CorrectionStrength*) as our measure of hand asymmetry (Fig 2).

<insert figure 2 about here>

In non-redundant conditions, the right hand exerted larger forces than the left hand. These differences were significant for both cursor displacement conditions (TC: $t_{30} = 2.65$, $p < .01$; UM: $t_{18} = 2.55$, $p = .01$). For target displacements, the measured left-right hand differences were smaller and did not differ significantly from symmetry (TC: $t_{30} = 1.27$, $p = .10$; UM: $t_{18} = 1.04$, $p = .16$). Overall, however, these results demonstrate that the feedback gains in non-redundant reaching are higher for the right than for the left hand.

In contrast, for the redundant one-cursor task, the left hand pushed stronger in the force channel than the right hand (Fig 1). The between-hand difference was significant for cursor ($t_{30} = 2.84$, $p < .01$), as well as for target ($t_{30} = 2.30$, $p < .05$) displacements. Importantly, a direct comparison of the asymmetry scores confirmed that participants indeed switched from stronger right-hand feedback gains for the non-redundant condition to stronger left-hand feedback gains for the redundant condition (cursor displacement: $t_{30} = 4.75$, $p < .001$; target displacement: $t_{30} = 3.50$, $p < 0.01$). This difference in the distribution of feedback corrections was not associated with a systematic change in the kinematic parameters during unperturbed movements (Table 1). Thus, we replicated the previously reported change in the assignment of corrections (White and Diedrichsen 2010).

In summary, our results show that responsibility assignment in redundant movements is not solved by each hand independently responding as strong as it would alone. Rather they indicate that feedback corrections are assigned to the effectors in a different manner in the redundant situation.

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Responsibility assignment modulates feedback gain, not temporal onset

To further characterize the mechanism of responsibility assignment, we asked whether the shift in correction asymmetry was caused by a difference in the temporal delay of correction between the hands, or only by a difference in the magnitude of corrective force applied with each hand. All results reported so far were manifest in the initial force with which the hands corrected for the sudden movement error, i.e. the correction gain of each hand. In contrast, the onset time of the corrections did not change systematically with condition (cf. Fig. 1). The mean onset time ranged from 162 to 194 ms, and a repeated-measures ANOVA with the factors reaching condition (OC/TC/UM) x perturbation (cursor/target) x hand (left/right) revealed neither a significant main effect, nor any interaction. Even though the right hand responded slightly faster to cursor displacements in the two-cursor condition ($t_{30} = 1.71$; $p < .05$), this advantage neither reversed for the redundant condition, nor was there a difference in correction onset in any other condition. Thus, the process of responsibility assignment results in a modulation of the response gain of each hand, not in a difference in the reaction time with which each hand responded to the perturbation.

Shift in correction asymmetry to the left hand when introducing redundancy is more pronounced for cursor than for target perturbations

The reasoning behind our hypothesis that right-handed participants correct more with the left hand in the redundant task is that this less-skilled hand has a higher probability of having caused the error. This would be functional, as the hand that corrects more also adapts more (White & Diedrichsen, 2010). Thus, the shift to the left-hand would ensure that the most likely source of the error experiences stronger adaptation. A prediction following from this hypothesis is that the shift towards the left hand should be stronger for perturbations requiring adaptation of future movements (an error in the internal representation of the motor system, thus most likely a systematic error) compared to perturbations not leading to visuomotor adaptation (a change in the environment, thus most likely a random error).

To test this prediction, we first had to establish that there is indeed more adaptation for cursor displacements than for target displacements. While it is well established that the *gradual* visual rotation of the cursor leads to adaptation of the next movement (Diedrichsen et al. 2005), this has not been shown for *sudden* cursor displacements as employed here. We therefore assessed the trial-by-trial adaptation rates for both cursor and target displacements. For this analysis, we only used trials in which a free-reaching trial with a perturbation was followed by another free-reaching trial. The initial deviations from a straight path to the target in the follow-up trials (measured 200ms in the movement) relative to the prior perturbations yielded the adaptation rates. A repeated-measures ANOVA confirmed that cursor displacements caused higher adaptation rates than target displacements ($F_{1,16} = 9.84$, $p < .01$; cursor: 0.13±0.23; target: 0.03±0.23).

Based on these results, our hypothesis would now predict that the asymmetry shifts more towards the non-dominant left hand for on-line corrections to cursor displacements (internal error) than to target displacements (external error). Indeed, the pattern of results (Fig 2) confirms this prediction: The on-line correction asymmetry was biased more toward the left hand for cursor than for target displacements ($t_{30} = 2.49$, $p < .05$). Furthermore, the *shift* in correction asymmetry resulting from introducing redundancy, i.e. the difference between the correction asymmetries in the redundant one-cursor and non-redundant two-cursor condition, was significantly larger for cursor than for target displacements ($t_{30} = 3.18$, $p < .01$).

The asymmetry pattern found in the early corrections was sustained until the end of the movements, as visible in the free reaching trials without the force channel. In these trials, the spatial amplitude of the correction at the end of the movement was larger for the right than for the left hand in all non-redundant conditions. For corrections to cursor displacements the difference was significant (TC: $t_{30} = 2.50$, $p < .01$, LH: 13.6±6.0mm, RH: 15.8±5.7mm; UM: $t_{18} = 2.10$, $p < .05$, LH: 19.0±5.6mm, RH: 21.5±5.0mm). However, for corrections to target displacements the difference was weaker (TC: $t_{30} = 1.00$, $p > .1$, LH: 18.3±6.8mm, RH: 19.1±6.1mm; UM: $t_{18} = 0.72$, $p > .2$, LH: 20.9±7.8mm, RH: 21.7±6.2mm). Moreover, we found a similar effect for the endpoint accuracy for unperturbed movements (Table 1). The accuracy was significantly better for the right than for the left hand, both for bi-manual two-cursor (t_{30} = 8.17, $p < .001$), and for uni-manual movements (t_{18} = 5.69, $p < .001$).

For the redundant movements, the correction effect reversed: The magnitude of end correction for cursor displacements was significantly smaller for the right than for the left hand (t_{30} = 3.11, $p < .01$, LH: 20.5±10.0mm, RH: 14.4±7.1mm). Again, the difference failed to reach significance for the target displacements (t_{30} = 0.72, $p > .2$, LH: 13.8±10.2mm, RH: 12.7±8.1mm). For cursor displacements, the difference in the final amplitude between the left and right hand changed significantly from the non-redundant to the redundant condition (t_{30} = 2.81, $p = .01$). This shift was not significant for target displacements (t_{30} = 1.12, $p > .2$). Finally, the *shift* in correction asymmetry resulting from introducing redundancy was significantly larger for cursor than for target displacements (t_{30} = 4.53, $p < .001$). Therefore, the pattern of correction amplitudes at movement end closely resembled the pattern found in the early corrective movements in the force channels.

Taken together, our results argue that responsibility assignment shifts the main weight of correction towards the left hand for redundant tasks, and that is does so especially for perturbations that lead to strong visuo-motor adaptation. In contrast, we found smaller shifts in asymmetry for target displacements, for which adaptation rates were much lower.

Responsibility assignment for redundant movements modulates, rather than replaces, non-redundant feedback gains

Finally, we sought to determine how the mechanism of responsibility assignment for redundant movements interacts with the mechanism that determines the gain of feedback responses for non-redundant movements. We considered two possibilities: First, it could be that the feedback corrections for non-redundant and redundant movements are determined following two completely different principles. During non-redundant movements, each hand would show a feedback gain that reflects the accuracy of this hand. For example, participants with a large difference in accuracy between hands would exhibit larger feedback gains for the dominant right than the non-dominant left hand as compared to more ambidextrous participants. For redundant movements, those participants would assign responsibility preferentially to the noisier left hand. Following this idea, we would expect that a person who exhibits stronger feedback responses with the right than with the left hand during non-redundant tasks, should show a preference for the left hand during redundant tasks.

Alternatively, responsibility assignment may add to the existing gains of the left and right hand by biasing the preference towards the non-dominant left hand, but not completely overwriting or reversing the existing difference in feedback gains. In this case, we would expect that the correction asymmetries for redundant and non-redundant movements correlate positively – i.e. a person exhibiting stronger feedback responses with the right than with the left hand during non-redundant tasks, would exhibit a weaker preference for the left hand during redundant tasks.

Consistent with the second idea, we found significant positive correlations for both perturbation conditions (Fig. 3 middle panel; cursor displacement: $r = .42$, $p < .05$; target displacement: $r = .48$; $p < .01$). This means that the existing correction asymmetry is shifted towards the non-dominant hand upon introducing redundancy. Thus, there seems to be an individual hand preference for corrections, which is biased towards the dominant hand in non-redundant movements, and shifted towards the non-dominant hand when redundancy is introduced.

If there were stable inter-individual differences in how the feedback gains for the two hands are set, then participants with a strong asymmetry for cursor displacement should also show a strong asymmetry in the same direction for target displacements. Indeed, the correlations in hand asymmetry between corrections to cursor and target displacements were strongly positive, both for redundant ($r = .84$, $p < .001$) and non-redundant ($r = .86$, $p < .001$) reaching movements (Fig. 3 top and bottom panel). It is noteworthy to emphasize that cursor and target displacements were randomly intermixed within each block, while the reaching conditions were blocked, which might explain the more robust correlations between error types. Overall, these findings show that there is a stable individual trait, which determines the relative feedback gains for the left and right hand that applies to all conditions. Responsibility assignment then acts on top of the existing preference, depending on specific task constraints and requirements by shifting the correction asymmetry towards the non-dominant hand.

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Discussion

The present study served to further illuminate the mechanisms underlying the assignment of responsibility for movement corrections across different effectors in a redundant reaching task. Our results confirm previous reports that the dominant hand shows stronger feedback corrections than the non-dominant hand (Elliott et al. 1999; Mieschke et al. 2001; Todor and Cisneros 1985), and that this asymmetry reverses for redundant movements (White and Diedrichsen 2010).

Furthermore, we demonstrate here that the asymmetry change was not driven by different onset times of the corrections between hands, but explained entirely by the feedback gains of the corrective responses. The previous study (White and Diedrichsen 2010) found changes in both strength and onset time; however, in this study the authors relied on kinematic measures relatively late in the movement. In contrast, our current study was specifically designed to detect the earliest possible responses to visual perturbations using rapid spatial displacements of cursor and target, and force channel trials to measure the reactive responses. This methodology allowed us to reliably disentangle amplitude and onset time of the corrective movements. We clearly showed that the responsibility assignment acted through a modulation of the gain of the response, leaving the onset times unchanged. In that aspect, the assignment process is similar to the up- or down-regulation of the visual reflexes with changes in model uncertainty (Franklin et al. 2012).

Based on the finding of White & Diedrichsen (2010) that the correction asymmetry in redundant movements is positively correlated with the subsequently adapted behavior, we hypothesized that the movement error and its correction is assigned preferentially to the more likely source of the error, the less reliable non-dominant hand, in order to adapt specifically this effector. In favor of the hypothesis, we found that the correction asymmetry is indeed more pronounced for internally attributable errors, for which an adaptation would be functional, than for externally attributable errors. Thus, the visuomotor system may strive to optimize not only current, but also future performance by preferentially adapting the presumably mis-calibrated joint. However, we also found a weaker, but still significant shift from stronger right-hand to stronger left-hand corrections for target displacement, for which the motor system shows a much lower adaptation rate (see our results and also Diedrichsen et al. (2005)). This low adaptation rate can be regarded as a sign that the motor system attributes these errors to an outside and unstable source (Berniker and Kording 2008). Given this, it is unclear why it still shifts the main work of the correction to the left hand. These results therefore indicate that our main hypothesis is not the complete story yet.

We therefore considered here two alternative explanations for the leftward shift of corrections during target displacements. First, using the left hand more for movement corrections in the redundant task may actually improve the performance on the current movement. This explanation is consistent with the claim that the right hemisphere (and hence the left hand) is specialized for postural tasks and endpoint corrections, whereas the left hemisphere (and therefore he right hand) is specialized for dealing with the arm dynamics and online corrections during the movement (Sainburg and Kalakanis 2000; Schaefer et al. 2012). We think that this explanation is unlikely, however. First, in non-redundant movements, the right hand was not only superior to the left hand in terms of the strength of the early corrective response, but also in the final endpoint errors, which were consistently lower for the right than for the left hand, both for perturbed and unperturbed trials. Additionally, the right-to-left shift in the feedback gains from non-redundant to redundant movements was found already in the earliest response, not only in the end of the movements when the left-hand advantage would arise.

Alternatively, it is possible that the stronger left-hand corrections in the redundant task serve to optimize future, rather than current performance – even during target displacements. While visuomotor adaptation rates were close to zero for this condition, adaptation is not the only learning mechanism that improves future performance (Huang et al. 2011). The non-dominant hand would profit more from training corrective movements: The performance of the non-dominant hand is worse than the performance of the dominant hand, as evident both in correction strength and end accuracy. Thus, skill-learning mechanisms could improve online corrections especially for the non-dominant hand. Whether this or possible alternative explanations can account for the responsibility assignment for error corrections remains a question for future research.

Our final result allows some insight into how the process of responsibility assignment interacts with the processes that determine the strength of feedback corrections during non-redundant tasks. First, we found that the right-left preference appears to be a stable intra-personal trait across all tasks and error types. Naturally, the intrinsic properties of each effector remain relatively constant across all conditions. We then found that the balance between the left and right hand corrections for the redundant task was positively correlated with the differences in correction strength in the non-redundant bi-manual task. Therefore, the shift towards the non-dominant hands was achieved by adding to existing differences in feedback gains, rather than by setting them using a completely different principle. Thus, the visuomotor system optimizes the movements in a redundant system by modulating the existing feedback mechanisms that normally determine the gain of the response.

In summary, our results confirm previous findings that right-handers correct more with their non-dominant left hand in a redundant task, while they otherwise show stronger corrections with the right hand. We further demonstrate that this change is caused by a shift in feedback gains, rather than by a change of the onset times of the corrective responses, and that it acts additively on existing left-right preferences. While the ultimate reason for the right-to-left hand shift for redundant movements remains to be further investigated, our results demonstrate that the preference for left-hand corrections in redundant movements is a replicable and stable phenomenon.

Acknowledgements

This research was supported by a postdoctoral fellowship of the Deutsche Forschungsgemeinschaft (DFG, RE 3265/1-1) to AR and a grant by the Biotechnology and Biological Science Research Council (BBSRC, BB_J009458_1) to JD.

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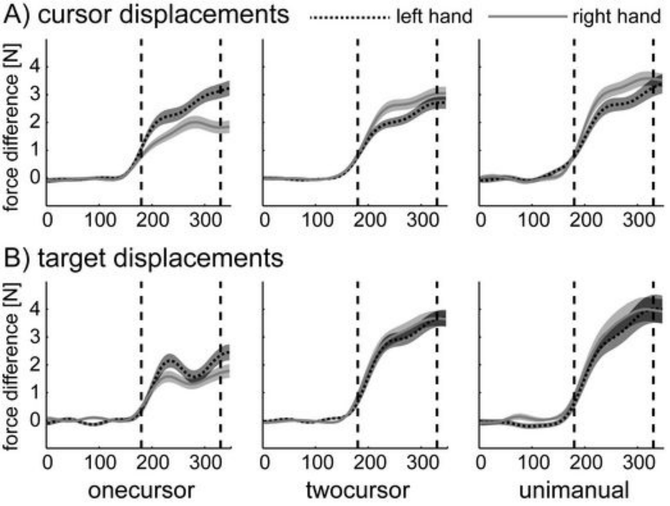
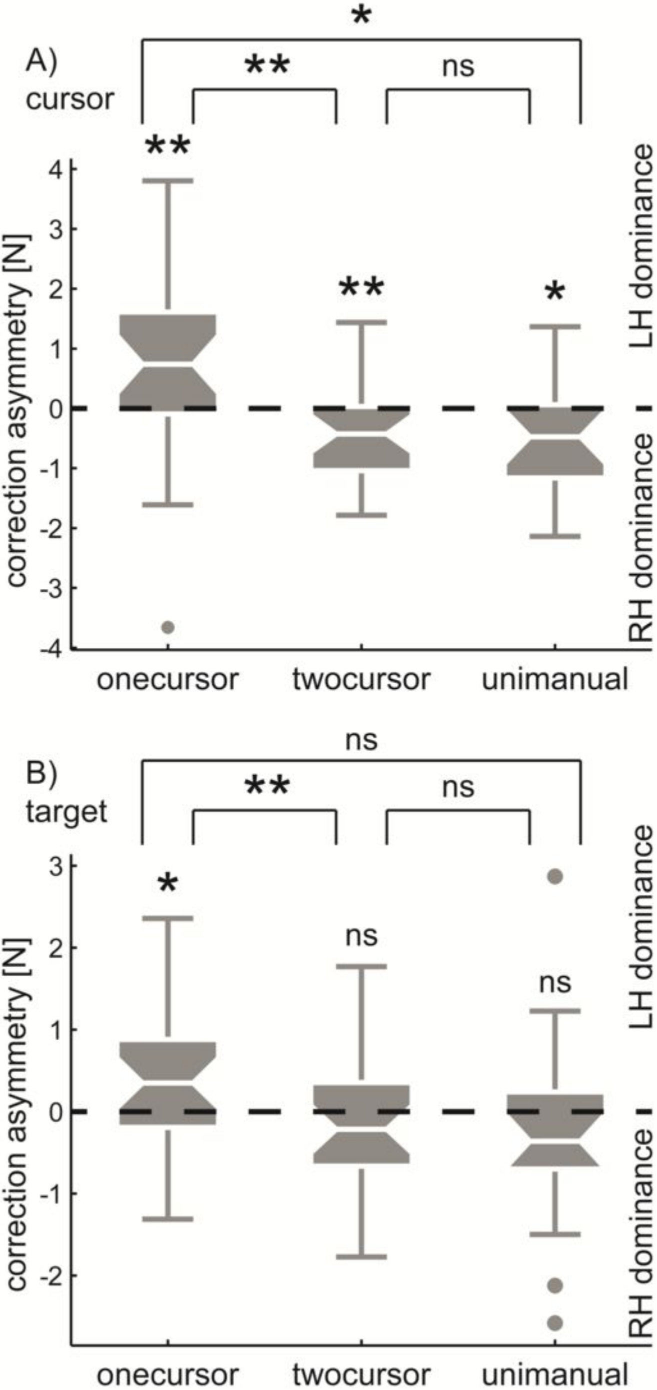
Figure captions

Figure 1 Feedback corrections for the left and the right hand in response to (A) cursor displacements and (B) target displacements in all reaching conditions. The traces depict the difference in force exerted laterally in the channel between left- and rightward displacements of each hand, aligned to the moment of visual perturbation (0ms). Note that the middle panels depict the data pooled over all two-cursor conditions. The dashed lines mark the time period, over which the forces were averaged to obtain the measure *CorrectionStrength* (180-330 ms). Shaded areas denote standard errors across participants.

Figure 2 Asymmetry in feedback correction: Differences between hands (left – right hand) for corrective force responses (*CorrectionStrength*) to cursor displacements (A) and target displacements (B) for each reaching condition. Correction asymmetry > 0N represent left hand (LH) dominance, < 0N represent right hand (RH) dominance. Above the boxes: paired t-tests left vs. right hand (one-sided according to the hypotheses). Between the boxes: interaction between hands and reaching condition. * $p < .05$; ** $p < .01$.

Figure 3 Across-subject correlations of correction asymmetry between all bi-manual conditions. The distributions of the correction asymmetries for the four conditions (error type x redundancy) are illustrated in the corners with the same conventions as in Fig. 2, while their corresponding correlations are depicted between these distributions.


A) cursor displacements
left hand
right hand
force difference [N]
0
1
2
3
4
0
100
200
300
B) target displacements
onecursor
twocursor
unimanual


A)
cursor
*
**
ns
**
**
*
4
3
2
1
0
-1
-2
-3
-4
correction asymmetry [N]
LH dominance
RH dominance
onecursor
twocursor
unimanual
B)
target
ns
**
ns
*
ns
ns
3
2
1
0
-1
-2
correction asymmetry [N]
LH dominance
RH dominance
onecursor
twocursor
unimanual

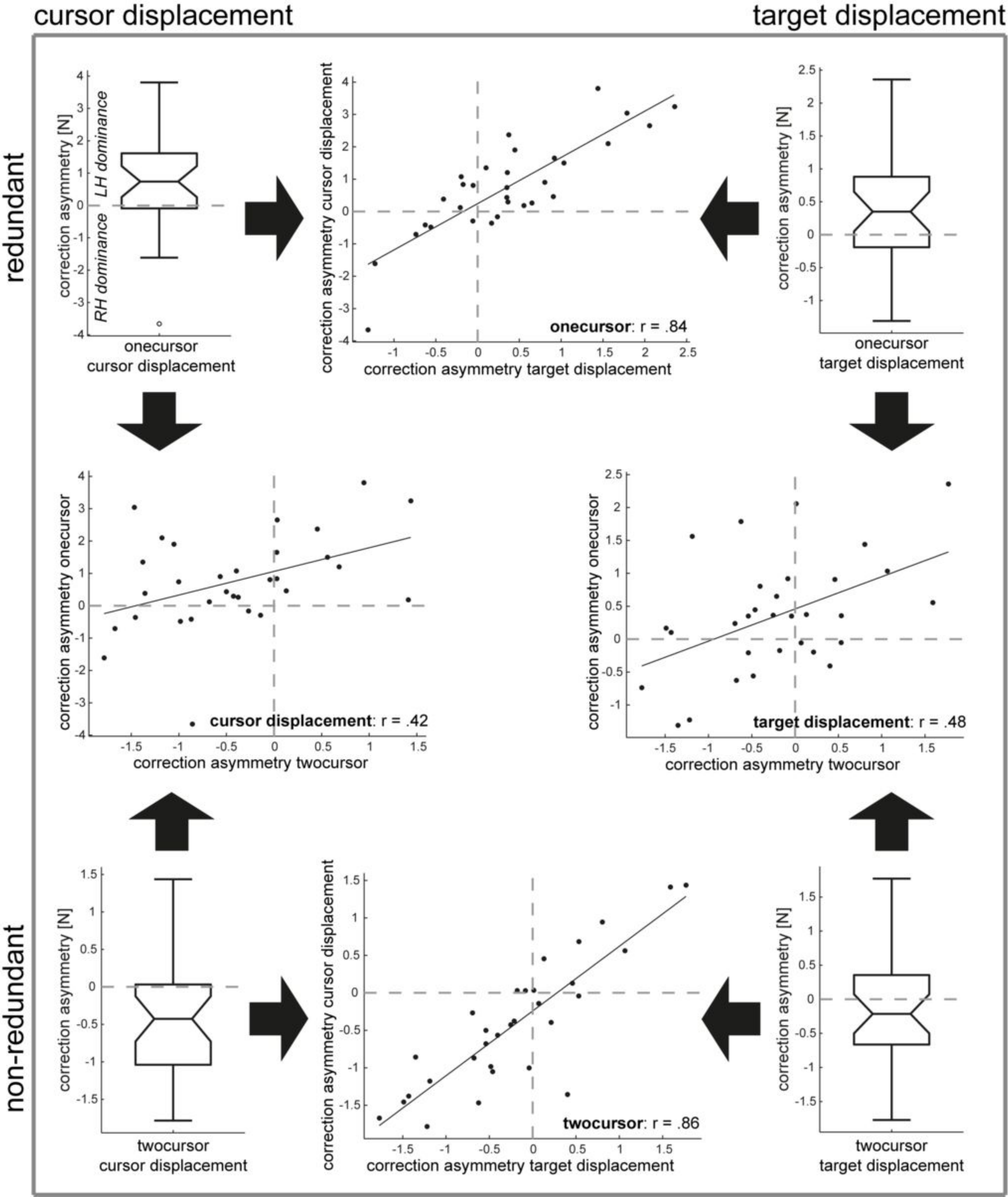

cursor displacement
target displacement
redundant
non-redundant
correction asymmetry [N]
LH dominance
RH dominance
4
3
2
1
0
-1
-2
-3
-4
onecursor
cursor displacement
correction asymmetry cursor displacement
correction asymmetry target displacement
-1
-0.5
0
0.5
1
1.5
2
2.5
onecursor: r = .84
2.5
2
1.5
1
0.5
0
-0.5
-1
onecursor
target displacement
correction asymmetry onecursor
correction asymmetry twocursor
-1.5
-1
-0.5
0
0.5
1
1.5
cursor displacement: r = .42
target displacement: r = .48
1.5
1
0.5
0
-0.5
-1
-1.5
twocursor
cursor displacement
twocursor: r = .86
twocursor
target displacement

Table 1: Additional kinematic parameters for unperturbed movements (mean ± standard deviation)

	peak velocity [cm/s]		***y-distance [mm]***		***end accuracy [mm]***	
	left hand	**right hand**	**left hand**	**right hand**	**left hand**	**right hand**
two-cursor	59.1±5.8	58.6±5.4	15.4±0.4	15.2±0.3	9.7±2.9	7.2±2.4
uni-manual	58.2±5.6	57.2±6.2	15.3±0.4	15.1±0.2	8.6±2.1	6.5±1.3
one-cursor	58.5±6.2	57.1±5.5	15.3±0.9	14.9±0.7	cursor overall: 12.3±4.5	

The peak velocity of unperturbed movements differed neither between hands nor between reaching conditions. The y-distance of unperturbed movements, defined as the difference between start and end location of each hand in direction of the reach, differed between reaching conditions ($F_{2,36} = 3.83$; $p < .05$), but was neither influenced by hand ($F_{1,18} = 3.98$; $p > .05$) nor did reaching condition interact with hand ($F_{2,36} = 0.75$; $p > .7$). The end accuracy, defined as the absolute distance between the end position(s) of the cursor(s) and the corresponding target(s), was significantly better for the right than for the left hand for all non-redundant conditions ($t > 5$; $p < .001$). This measure was calculated on unperturbed movements only in order to distinguish reaching accuracy from the size of feedback corrections.