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Alignment to natural and imposed mismatches between the senses

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van der Kooij K, Brenner E, van Beers RJ, Schot WD, Smeets JB. Alignment to natural and imposed mismatches between the senses. *J Neurophysiol* 109: 1890–1899, 2013. First published January 23, 2013; doi:10.1152/jn.00845.2012.—Does the nervous system continuously realign the senses so that objects are seen and felt in the same place? Conflicting answers to this question have been given. Research imposing a sensory mismatch has provided evidence that the nervous system realigns the senses to reduce the mismatch. Other studies have shown that when subjects point with the unseen hand to visual targets, their end points show visual-proprioceptive biases that do not disappear after episodes of visual feedback. These biases are indicative of intersensory mismatches that the nervous system does not align for. Here, we directly compare how the nervous system deals with natural and imposed mismatches. Subjects moved a hand-held cube to virtual cubes appearing at pseudorandom locations in three-dimensional space. We alternated blocks in which subjects moved without visual feedback of the hand with feedback blocks in which we rendered a cube representing the hand-held cube. In feedback blocks, we rotated the visual feedback by 5° relative to the subject's head, creating an imposed mismatch between vision and proprioception on top of any natural mismatches. Realignment occurred quickly but was incomplete. We found more realignment to imposed mismatches than to natural mismatches. We propose that this difference is related to the way in which the visual information changed when subjects entered the experiment: the imposed mismatches were different from the mismatch in daily life, so alignment started from scratch, whereas the natural mismatches were not imposed by the experimenter, so subjects are likely to have entered the experiment partly aligned.

visuomotor adaptation; realignment; multisensory integration; terminal feedback; continuous feedback

WE NORMALLY PERCEIVE A WORLD in which we see and feel objects in the same place. When one sense is perturbed, for instance by prism glasses, perceptual harmony is quickly restored (e.g., Fernandez-Ruiz et al. 2004; Klapp et al. 1974; Morton and Bastian 2004; Redding and Wallace 1988; Templeton et al. 1974). How the nervous system achieves such perceptual harmony is of fundamental importance to understanding multisensory processing.

When pointing at visual targets, there are at least two (not mutually exclusive) ways in which the nervous system can deal with visual-proprioceptive mismatches. If the mismatch is easily resolved in motor coordinates (e.g., always activate the biceps more strongly, regardless of the target's position), the movement plan can be updated such that we successfully reach the targets (e.g., Baraduc and Wolpert 2002; Burge et al. 2008; Galea and Miall 2006; Hinder et al. 2010; Körding and Wolpert 2004; Krakauer 2009; Saijo and Gomi 2010; Tseng et al. 2007; Wang and Sainburg 2005; Wei and Körding 2009). If the mismatch is more easily resolved in sensory coordinates (e.g., the visual position is rightward of the proprioceptive position regardless of the movement direction), the conflict can be resolved by updating the way in which sensory information is interpreted (Baraduc and Wolpert 2002; Block and Bastian 2012; Priot et al. 2010; Redding and Wallace 1988, 2006).

In the present study, we were interested in the second option, realignment of the sensory estimates, so we designed our experiment such that updating the sensory estimates would most easily resolve the intersensory mismatch. We rotated visual feedback around the cyclopean eye while the movements' starting points and directions varied between trials. If the mismatch was resolved in sensory coordinates (e.g., rotate the proprioceptive information rightward), the correction would be constant across trials. If, on the other hand, the mismatch was resolved in motor coordinates (e.g., activate the biceps more strongly), the change in muscle activation would have to be varied between trials. Therefore, the subjects' best strategy was to realign the senses.

Although it has frequently been proposed that the nervous system deals with intersensory mismatches by realigning the senses, there are conflicting claims about whether the senses are really realigned, depending on whether a visual-proprioceptive mismatch was imposed (e.g., Block and Bastian 2012; Burge et al. 2010; Cressman and Henriques 2009; Choe and Welch 1974; Harris 1965; Fernandez-Ruiz et al. 2004; Priot et al. 2010; Redding and Wallace 1988; Templeton et al. 1974) or realignment to feedback about naturally occurring mismatches was studied (Smeets et al. 2006).

Realignment is typically studied by introducing a visual-proprioceptive mismatch in a simple task such as pointing at visual targets and measuring how the nervous system responds to this. The mismatch has traditionally been introduced by prism glasses, which rotate visual information in space (for a review, see Welch 1978) but can also be imposed by perturbing a visual representative of the hand in virtual reality. When visual feedback imposes an intersensory mismatch, errors in goal-directed action decrease with experience. Once the mismatch is removed, subjects still compensate for the mismatch, resulting in an aftereffect in the opposite direction to the rotation.

Two properties of the aftereffect are indicative of sensory alignment rather than updated movement planning: the aftereffect generalizes to perceptual tasks and the aftereffect persists until new information about the mismatch is provided. Many studies have demonstrated that part of the aftereffect generalizes to perceptual tasks in which there is no active movement of the limbs (Choe and Welch 1974; Cressman and Henriques 2009, 2010; Ostry et al. 2011; Redding and

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Wallace 2006; Synofzyk et al. 2008). Fewer studies have investigated the persistence of the aftereffect, but one study showed an aftereffect that persisted over a time lapse of 20 min (Fernandez-Ruiz et al. 2004). However, aftereffects do decay over time, even in the absence of simultaneous visual and proprioceptive information about the hand (Choe and Welch 1974; Fernandez-Ruiz et al. 2004; Hamilton and Bossom 1964; Klapp et al. 1974; Taub and Goldberg 1973). It is therefore unclear whether any part of the aftereffect is really persistent and whether there is any true realignment of the senses.

Asking subjects to point to visual targets without seeing their hand reveals visual-proprioceptive biases (Rincon-Gonzales et al. 2011; Smeets et al. 2006; van Beers et al. 1999; Haggard et al. 2000), which we refer to as "natural mismatches." Smeets et al. (2006) studied how subjects respond to feedback about natural mismatches by alternating between blocks of movements without visual feedback and blocks with veridical feedback. When subjects pointed to visual targets with the unseen hand, their responses showed consistent visual-proprioceptive biases. These systematic errors were absent as long as subjects saw a representation of their hand, but the errors gradually reappeared when the feedback was removed. This was explained by a cue-combination mechanism that involves no realignment but combines proprioception with waning visual memory of hand position (Smeets et al. 2006).

In summary, generalization of aftereffects to perceptual tasks has provided evidence that the nervous system realigns the senses, whereas the reappearance of naturally occurring mismatches when feedback is removed has provided evidence that the senses do not realign. As the studies involved differences in the methods and analyses used as well as in the mismatch studied, we ask whether there is a fundamental difference between realignment to imposed and natural mismatches or whether different conclusions about realignment are due to methodological factors.

On a methodological level, providing continuous visual feedback about the hand's position, as in Smeets et al. (2006), may thwart realignment. Several studies have found that there is less realignment to a prism-induced mismatch with continuous feedback about the hand than with feedback that only provides information about the movements' end point (terminal feedback) (Choe and Welch 1974; Cohen 1967; Redding and Wallace 2006; Taub and Goldberg 1973). Also, most recent studies that have found realignment used terminal feedback rather than continuous feedback (Cressman and Henriques 2009, Ostry et al. 2011, Redding and Wallace 2006, Synofzyk et al. 2008). Possibly, subjects prefer to correct their movements on the fly rather than realigning the senses when continuous visual feedback is available (Bernier et al. 2008). Another methodological factor that may underlie the different conclusions about realignment to natural and imposed mismatches is whether the realignment was measured from persistence (Smeets et al. 2006) or from generalization to perceptual tasks (e.g., Cressman and Henriques 2009; Choe and Welch 1974; Harris 1965; Ostry et al. 2008, Priot et al. 2010; Redding and Wallace 1988; Synofzik et al. 2008, Templeton et al. 1974). For instance, transient aftereffects on perceptual tasks may be explained by cue combination of sensory input and waning feedback memory (Smeets et al. 2006).

Another possibility is that there was more realignment to imposed mismatches than to natural mismatches because the imposed mismatches were easier to detect. The imposed mismatches were generally larger in amplitude than the natural mismatches. Moreover, the imposed mismatches generally were in the azimuthal direction (Cressman and Henriques 2009; Choe and Welch 1974; Harris 1965; Fernandez-Ruiz et al. 2004; Priot et al. 2010; Redding and Wallace 1988; Templeton et al. 1974), whereas natural mismatches were in diverse directions (Smeets et al. 2006). Since variability of pointing responses depends on direction (van Beers et al. 1998, 1999, 2002), the imposed mismatches may have been imposed in the direction where variability is small and where they were relatively distinguished from random variability.

In this study, we compared realignment to imposed and natural mismatches while controlling for methodological differences that may have caused different conclusions about realignment to imposed and natural mismatches. As it has been proposed that there is realignment to terminal feedback but not to continuous feedback, we compared realignment between sessions with terminal and continuous feedback. Since the realignment measured from generalization to perceptual tasks may be explained by waning memory of where the hand was last seen, we measured the realignment from the persistent aftereffect and from a perceptual task. Finally, because the imposed mismatches may have been easier to distinguish from random variability, we imposed mismatches of a size similar to the natural mismatches and examined whether the realignment is related to the variability in pointing errors.

METHODS

Subjects

Twelve subjects (10 women and 2 men) with normal or corrected-to-normal vision participated in the experiment. The experiment was conducted in accordance with the Declaration of Helsinki and was part of a program that was approved by the Ethics Committee of the Faculty of Human Movement Sciences. All subjects were postdoctoral or PhD researchers of the Faculty of Human Movement Sciences at VU University Amsterdam.

Setup

The setup was similar to the one used by Smeets et al. (2006). Subjects were seated in a dark room, where they viewed a separate CRT display (48 × 31 cm, viewing distance ~40 cm, resolution: 1,096 × 686 pixels, 160 Hz) with each eye via mirrors (Fig. 1*A*). Infrared emitting diodes (IREDs) were mounted on a cube with 5-cm edges that subjects held in their right hand, which allowed us to track the movements of the subject's hand at 100 Hz with an Optotrak 3020 motion analysis system (NDI, Waterloo, ON, Canada), that recorded the position of the IREDs. The cube was attached to a grip that subjects held, so we could render a floating cube without subjects expecting to see their fingers occluding the surface of the cube. To be able to render an adequate image of the scene without having to restrain the subject's head, IREDs were also mounted on a bite board that subjects held in their mouth but that was not fixed to the setup. For each subject, we determined the eyes' locations relative to the bite board, as described in detail elsewhere (Sousa et al. 2010). Knowing the eyes' location relative to the tracked bite board allowed us to render an appropriate new image of the three-dimensional (3-D) scene for each eye with a latency of ~25 ms between subjects' movements and the corresponding update of the display. In the experiment, we used two types of trials: pointing trials and perception trials.

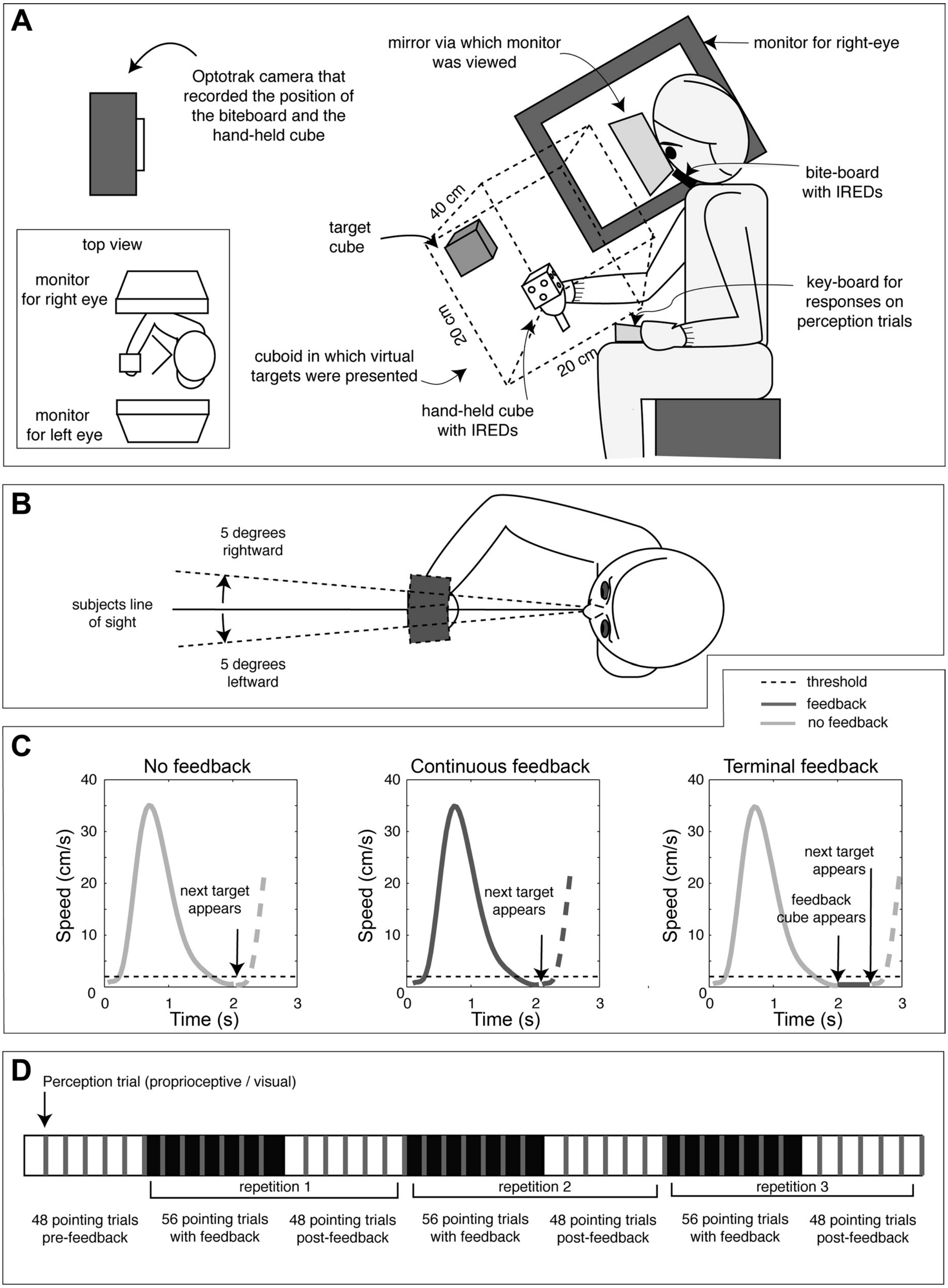

Fig. 1. Methods. *A*: experimental setup and illustration of the cuboid area in which target cubes were presented. *B*: leftward and rightward rotation conditions. *C*: the three types of feedback during pointing trials and their dependency on movement velocity. Movement ended when speed was below threshold for 300 ms. *D*: the order of the different types of trials within a single session. IREDs, Infrared emitting diodes.

Pointing Trials

Subjects were instructed to bring the hand-held cube to the position of a red virtual cube. They were told that the hand-held cube was sometimes invisible and at other times it would be visible as a blue cube.

To encourage subjects to realign the senses rather than to update motor planning, the red cubes were placed at different positions across trials so that subjects moved in many different directions in 3-D space. Thus, the sensory transformation that would correct for the mismatch was constant across trials, whereas the change in muscle activation that would correct for the mismatch varied. The intertarget distance was kept constant at 20 cm. For each subject, we created a sequence of 56 target locations. The same sequence was used in all blocks to avoid variability between blocks as a result of differences between the sequences. The target direction was chosen at random on each trial but such that all targets were within a laterally elongated 40 × 20 × 20-cm cuboid that was oriented along the subjects' line of sight (Fig. 1*A*). Thus, subjects made a pseudorandom sequence of ~20-cm movements in 3-D space. A movement was considered to have ended if movement speed was below 2 cm/s for 300 ms. There were blocks of trials without and with visual feedback. In trials without visual feedback, the hand-held cube remained invisible and the next target appeared as soon as the movement had ended. In feedback blocks, a blue cube was rendered, the position and orientation of which depended on that of the hand-held cube.

Imposed mismatches were introduced by rotating feedback of the hand-held cube around the cyclopean eye. There were two rotation conditions: in the "leftward rotation" condition feedback was rotated 5° to the left, whereas in the "rightward rotation" condition feedback was rotated 5° to the right (Fig. 1*B*). The rotational mismatch that we imposed was similar to the one imposed by prism glasses. The only difference is that in our experiment the targets existed in visual space only, whereas in prism studies the visual position of the targets can be distinguished from a "real" position.

To study whether there is more realignment to terminal than to continuous feedback, there were two feedback conditions (Fig. 1*C*). In the continuous feedback condition, the blue cube was visible throughout feedback blocks and a new target appeared as soon as the previous movement ended. In the terminal feedback condition, the blue cube only became visible after the movement had ended and remained visible at the position at which the movement had ended for 500 ms. After that, the next target appeared, and the blue cube disappeared.

Perception Trials

To measure the individual contributions of vision and proprioception to realignment, we interleaved pointing trials with perception trials in which subjects made position estimates relative to the body. These perception trials started with an auditory instruction to move the hand to a starting position close to the chest. Next, an auditory instruction was given indicating the desired position (in front of the left shoulder, nose, or right shoulder). In proprioceptive perception trials, subjects brought the unseen hand-held cube to the requested position. In visual perception trials, subjects brought a visual cube that was rendered at a distance of ~40 cm to the requested position using the arrow keys on the keyboard. They could take as long as they liked to position the cube at the requested position (in both proprioceptive and visual trials). Allowing subjects to take their time ensured that if they had updated the movement plan rather than the sensory estimates, and they had ample time to sense that their movement had brought the hand-held cube to the wrong position and to adjust its position accordingly.

Procedures

The two feedback (continuous and terminal) × two rotation (leftward and rightward) conditions were performed in separate sessions. All subjects performed all four sessions in a pseudorandom order. To minimize transfer of adaptation between rotation conditions, sessions were performed with an intersession interval of at least 4 h. A session (Fig. 1*D*) started with a prefeedback block in which natural biases were determined. Subsequently, we gave subjects the opportunity to realign vision and proprioception in a feedback block. Next, there was a postfeedback block in which realignment was measured. After that, the combination of a feedback and a postfeedback block was repeated two more times. Within each block, we introduced a perception trial after each eighth pointing trial, such that each of the three positions was indicated once using vision and once using proprioception. Blocks without feedback ended with a perception trial, but in feedback blocks, we presented eight more pointing trials so that the transition from feedback to no feedback was uninterrupted. Consequently, there were 48 pointing trials in pre- and postfeedback blocks, whereas there were 56 pointing trials in feedback blocks. The total duration of a session was 25–30 min.

Data Analysis

Mismatches. The imposed mismatch was the 3-D vector between the target and the hand-held cube's position for which the rotated feedback would show no error. To ensure that corrections to the imposed and natural mismatches were independent, we only considered natural mismatches in the plane orthogonal to the imposed mismatch. In this plane, the natural mismatch was the mean 3-D vector between the targets and end points in the prefeedback block.

End-point error components. End-point errors were defined as the difference in space between the position of the target and that of the hand-held cube at the end of the movement after adding the +5° or −5° rotation to the position of the cube. This way, each end-point error contained both a natural component and an imposed component. We isolated these components as described below.

To retrieve the imposed component, we calculated the size of the error in the direction of the imposed mismatch. Some subjects obviously had preexisting biases in this direction. For each trial in the sequence, we therefore determined the difference in response for the two rotation conditions, taking advantage of the finding that natural biases are consistent across experimental sessions (Smeets et al. 2006). We expressed the resulting value as a fraction of the imposed mismatch. Hence, we isolated the imposed component, normalized such that a value of one meant that the endpoint error was as large as the imposed mismatch (i.e., the feedback had no effect) and that a value of zero meant that the imposed mismatch was fully corrected for (i.e., in the direction of the imposed mismatches, feedback was aligned with the target).

To retrieve the natural component, we calculated the size of the error in the direction of the natural mismatch (in that session), normalized by the size of the natural mismatch. To reduce random variability, the errors in the corresponding trials from the two rotation sessions were averaged. Hence, we isolated the natural error component, normalized such that a value of one meant that the error was as large as the initial bias (i.e., the feedback had no effect) and a value of zero meant that the natural bias was fully corrected for (i.e., that in the direction orthogonal to the imposed mismatch, feedback was aligned with the target).

Determining realignment. We defined realignment as a persistent change in intersensory bias and therefore estimated realignment from the asymptote of an exponential equation that we fit to the error components (*equation 1*; Fig. 2). If visual feedback only produced transient effects on pointing behavior, the asymptote would be equal to the prefeedback bias (i.e., a value of 1), whereas if visual feedback induced full realignment, errors would not change when feedback was removed (i.e., a value of 0 for the asymptote). The normalized error component (p_i) as a function of the number of trials since feedback was determined as follows:

$$p_i = a\left(1 - e^{\frac{-i}{\tau}}\right) \qquad (1)$$

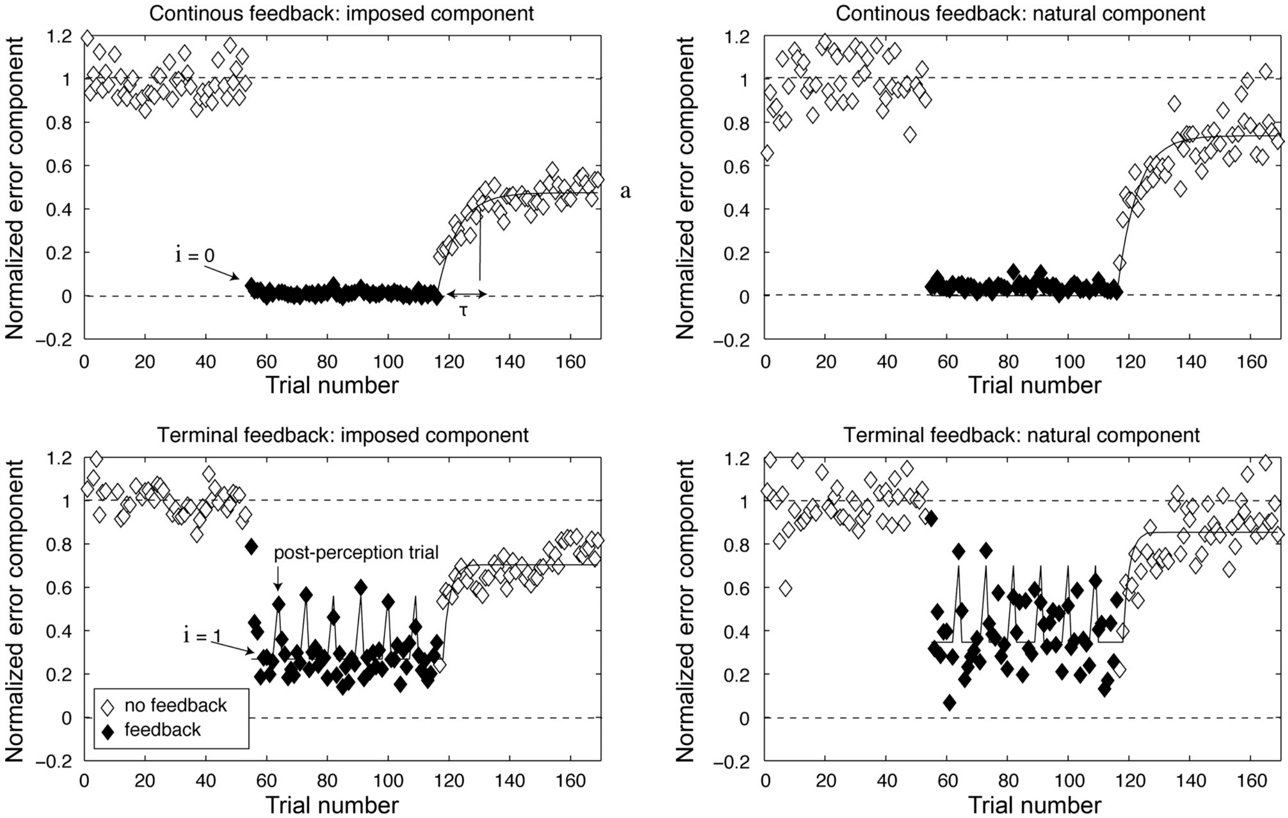

Fig. 2. Error components. Symbols indicate the normalized error components (imposed and natural) averaged over 12 subjects. Data for the feedback and postfeedback blocks are averages of the three repetitions. The continuous curves are fits of *Eq. 1* to the average data data of both the feedback and postfeedback blocks, $p_i = a[1 - e(-i/\tau)]$, where p_i is the normalized error component, a is the asymptote, i is the number of trials since the last feedback, and τ is the time constant.

In *Eq. 1*, a is the asymptote, i is the number of trials since the last feedback, and τ is the time constant. The average error in the prefeedback trials was one by definition, so $1 - a$ gives a measure of realignment. For trials in the postfeedback blocks, i was the trial number within that block. For trials with continuous feedback, i was zero because subjects had online feedback when moving their hand to the target. Thus, *Eq. 1* predicts that the average for trials with continuous feedback will be zero. For trials with terminal feedback, i was one on most trials, because the last visual feedback was from the previous movement. According to *Eq. 1*, this leads to systematic errors. Because perception trials took longer than pointing trials and allowed subjects to make multiple movements, we added the average duration of a perception trial divided by the duration of a pointing trial (2.3) to i for these trials. Figure 2 shows the fits of *Eq. 1* to the average error components. These fits were made for illustration only; all analyses were performed on similar fits to the data of individual subjects.

RESULTS

Natural Biases (Prefeedback Trials)

To analyze the consistency of natural biases within and between subjects, the three cardinal components (lateral, vertical, and sagittal) of the bias in the prefeedback block are considered separately. Natural biases differed between subjects but were reproducible across days for individual subjects. The first bias we measured for a subject was correlated to biases in the three subsequent sessions, with all r values of $>$0.44 for the lateral direction, 0.79 for the vertical direction, and 0.65 in depth (Fig. 3*A*). Different directions contributed differently to bias size, generally with the largest component in the depth direction and the smallest component in the lateral direction.

As already mentioned, we ensured independence of realignment to the imposed and natural mismatches by confining the analysis of the natural error component to the directions orthogonal to the imposed mismatches. For most subjects, the amplitude of the imposed mismatch was smaller than the amplitude of the natural mismatch (Fig. 3*B*). The natural bias parallel to the imposed mismatch, as measured in the prefeedback block, was generally smaller than the imposed mismatch.

Realignment

We defined realignment on the basis of parameter a of *Eq. 1*, which we fit to the normalized error components of individual subjects: $1 - a$ gives the realignment as a fraction of the mismatch. Repeated-measures ANOVAs on the parameters of the fits to the separate repetitions of feedback and postfeedback blocks (*blocks 1–3*) showed that repetition number had no significant effect on either a [$F_{(2,22)} = 3.05$, $P = 0.07$; Fig. 4*A*] or τ [$F_{(2,22)} = 1.96$, $P = 0.16$], so we subsequently fit *Eq. 1* with a single asymptote and τ to the data of the three repetitions and reported the latter fit.

To determine whether the nervous system realigned differently to natural and imposed mismatches, realignment fractions ($1 - a$; Fig. 4*B*) were entered in repeated-measures ANOVA with the factors of component (natural and imposed) and feedback type (continuous and terminal). A main effect of component showed that there was more realignment to im-

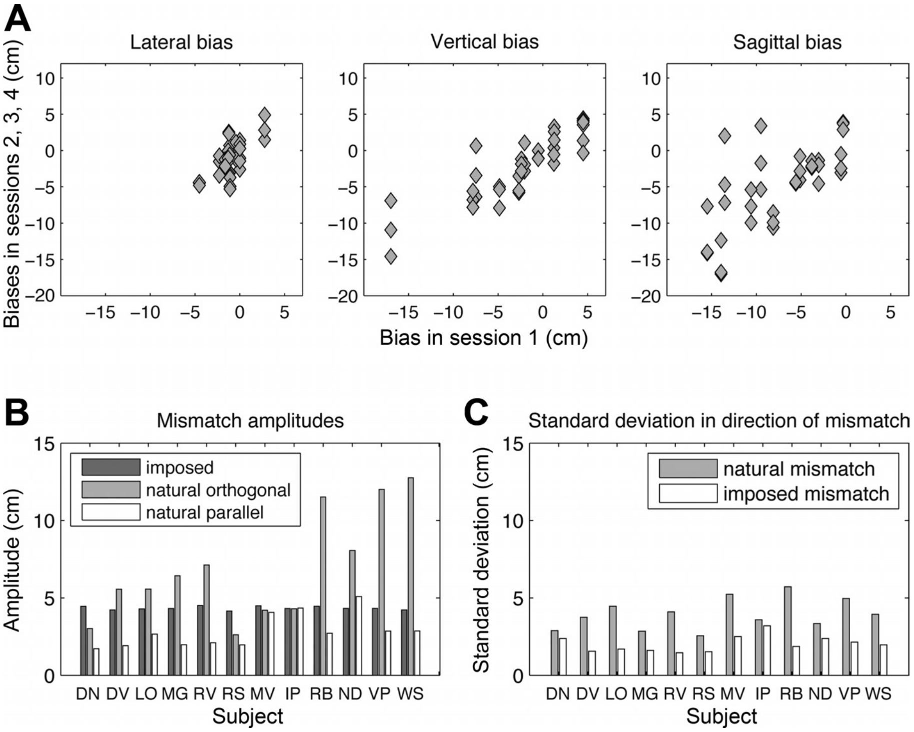

Fig. 3. Biases. *A*: natural biases in three directions. Shown is a bias of a subject in the second, third, and fourth session as a function of the bias that was measured in the first session that the subject performed. Each subject is represented by three data points with the same abscissa. Positive is rightward, upward, and away. *B*: for each subject, the bars show the amplitude of the mismatch that was imposed by the 5° rotation of visual feedback (dark shaded bars) and the mean prefeedback error both in the direction orthogonal to the imposed mismatch (light shaded bars) and in the direction parallel to the imposed mismatch (open bars). *C*: for each subject, the bars show the SD in the prefeedback block and in the direction of the natural mismatch (shaded bars) and in the direction of the imposed mismatch (open bars).

posed mismatches than to natural mismatches [$F_{(1,11)} = 23.24$, $P < 0.01$]. We also found more realignment in response to continuous than to terminal feedback [$F_{(1,11)} = 27.32$, $P < 0.01$]. Feedback type and component did not interact significantly [$F_{(1,11)} = 1.86$, $P = 0.20$], which shows that differences in realignment to the natural and imposed mismatches did not depend on the type of feedback.

We proposed in the Introduction that there may be more realignment when the mismatches are more easily discriminable from random variability. We therefore expressed the mismatch for each subject as a *z* score (dividing it by the prefeedback SD in the relevant direction; Fig. 3*C*). Such *z* scores were not significantly correlated with realignment, even when data about realignment to the imposed and natural mismatch component were pooled ($r = 0.29$, $P = 0.06$, for continuous feedback and $r = 0.16$, $P = 0.28$, for terminal feedback).

Perception Trials

To measure the individual contributions of vision and proprioception to realignment, we analyzed position estimates in perception trials. The results were comparable for the shoulder and nose position estimates, but the SD in estimates of shoulder position exceeded the SD in estimates of nose position by more than a factor three. We therefore only report the results for the nose position. Figure 5 shows average estimates of lateral positions in front of the nose as a function of feedback in the pointing trials.

Repeated-measures ANOVA on the shifts in the perceptual estimates with the factors of sense (vision and proprioception), rotation (leftward and rightward), feedback type (continuous and terminal), and block type (prefeedback, feedback, and postfeedback) showed an interaction between rotation and sense [$F_{(1,11)} = 238.13$, $P < 0.01$].

Proprioceptive estimates were shifted in the opposite direction than the imposed mismatches, whereas visual estimates were unaffected by block type. Consistent with our finding of more realignment to continuous feedback than to terminal feedback, there was an interaction between rotation and feedback type [$F_{(1,11)} = 15.98$, $P < 0.01$]. Nose position estimates were influenced more by the mismatch with continuous feedback than with terminal feedback. There was also an interaction of rotation and block type [$F_{(2,22)} = 36.1$, $P < 0.01$]: for proprioception, there were differences between rotation conditions in the feedback and postfeedback blocks but not in the prefeedback block. Interestingly, proprioceptive position estimates did not differ between the feedback and postfeedback blocks [with $t_{(11)} = -0.96$, $P = 0.17$, for continuous feedback and $t_{(11)} = -0.80$, $P = 0.57$, for terminal feedback]. Thus, proprioceptive position estimates do not follow the pointing errors, for which corrections to the imposed mismatches were larger within feedback blocks than in postfeedback blocks (see Fig. 2).

Both persistence and transfer to perceptual tasks are hallmark features of visual-proprioceptive realignment. This suggests that the change in responses on the perceptual tasks equals the postfeedback asymptote in pointing errors [$(1 - a) \times 5°$]. In our case, only the responses on the proprioceptive trials changed. Following the prediction based on realignment (dashed lines in Fig. 5), these proprioceptive responses were not significantly different from the asymptote [$t_{(11)} = 1.46$, $P = 0.15$]. The alternative is that the proprioceptive perception trials do not measure realignment but transient aftereffects on pointing. If so, the change in the proprioceptive estimates should follow the effect on pointing at the time of the perceptual trial. This effect could be calculated using *Eq. 1* as follows: $(1 - p_i) \times 5°$, with $i = 2.3$ for continuous feedback and $i = 3.3$ for terminal feedback. The proprioceptive estimates were significantly different from the prediction based on pointing [$t_{(11)} = -11.52$, $P < 0.01$; dotted lines in Fig. 5]. Thus, the proprioception was affected by realignment and not by a transient aftereffect on pointing.

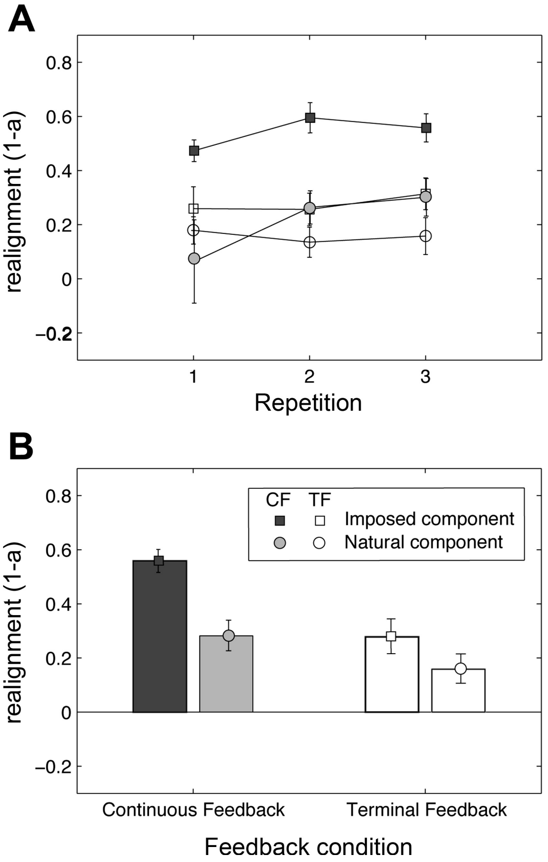

Fig. 4. Realignment. *A*: realignment did not increase when the sequence of feedback and postfeedback blocks was repeated. *B*: realignment to the imposed and natural mismatches in the terminal feedback (TF) and continuous feedback (CF) conditions averaged over the 12 subjects (with SEs). Realignment was computed as follows: 1 − *a*, where *a* is a parameter in *Eq. 1*.

DISCUSSION

We investigated whether the nervous system realigns differently to imposed than to naturally occurring visual-proprioceptive mismatches. An imposed mismatch was introduced by rotating visual feedback about hand position either rightward or leftward with respect to the cyclopean eye. Natural mismatches were estimated from the mean error orthogonal to such rotations in a prefeedback block in which subjects pointed with the unseen hand. Knowing the imposed and natural mismatches, we could decompose end-point errors into a natural and an imposed component and compare corrections with the two mismatches within the same trials.

We analyzed realignment of the sensory estimates, which has two hallmark features: it will persist in the absence of visual feedback about the mismatch (persistence) and it will affect other tasks that rely on the realigned sensory estimates (generalization). We measured both generalization and persistence. We estimated the persistent corrections to the mismatch from the asymptote of the error components in postfeedback blocks in which subjects pointed with the unseen hand. In addition, we measured how the corrections to the mismatch generalized to perceptual tasks in which subjects indicated the direction straight in front of their nose using either proprioception or vision. Consistent with the idea that both generalization and persistence are hallmark features of realignment, we found that the estimates of realignment based on the perceptual task and based on the asymptote in pointing errors were statistically indistinguishable. The perceptual task showed that subjects realigned their proprioceptive estimates of their hand location, whereas the visual estimates remained unaffected. Because success in the pointing task was entirely defined by visual feedback, the realignment of proprioception but not vision is consistent with subjects updating the inaccurate cue more strongly (Gori et al. 2008; Zaidel et al. 2011).

We will now discuss the difference in realignment as estimated from the asymptote in pointing errors, which brings forth two novel results. First, there is more realignment to imposed than to natural mismatches. Second, there is more realignment with continuous than with terminal feedback.

More Realignment for Imposed Mismatches Than for Natural Biases

Our main finding is that subjects realigned for a larger portion of the imposed mismatches than of the natural mismatches, both with terminal and continuous feedback. The amount of realignment did not just increase with the magnitude of the mismatch. The imposed mismatches were generally smaller than the natural mismatches, but we found more realignment to the imposed than to the natural mismatches. To test whether detectability rather than the absolute size of the mismatch determined realignment, we expressed the mismatches as z scores: dividing them by the (prefeedback) SD of end-point errors in the relevant direction. There was no significant relation between realignment and z scores, from which we conclude that the amount of realignment did not depend on how well the mismatch could be distinguished from random variability in movement end points.

Interestingly, we found that subjects realigned during the first feedback block but did not increase their realignment during the additional feedback blocks. We thus partially realign when we encounter a change in intersensory mismatch and do not increase the alignment further when we receive more feedback about the mismatch. As subjects have presumably already partially aligned to their natural mismatches before entering the experiment, the prefeedback block can be considered as a block following natural feedback. In contrast, subjects had not yet had feedback about the imposed mismatches before entering the experiment. We therefore propose that there was more realignment to the imposed mismatches because these mismatches changed the state of misalignment, whereas that state did not change fundamentally for the natural mismatch.

In contrast to the present finding of a small realignment to natural mismatches, Smeets et al. (2006) showed that an aftereffect of feedback on natural biases could be explained by a cue-combination mechanism that combines proprioceptive input with waning visual memory of hand position and that involves no realignment at all. The different conclusions with respect to the extent of realignment between the Smeets et al. (2006) study and the present study can be explained by differences in the analyses used. In the present study, an asymptote of the end-point errors was fitted, whereas in the Smeets et al. (2006) study, the data were compared with a cue-combination model without free parameters. When we applied our analysis to the Smeets et al. (2006) data, which were obtained with continuous feedback, we found a similar small realignment to natural mismatches as in the present experiment.

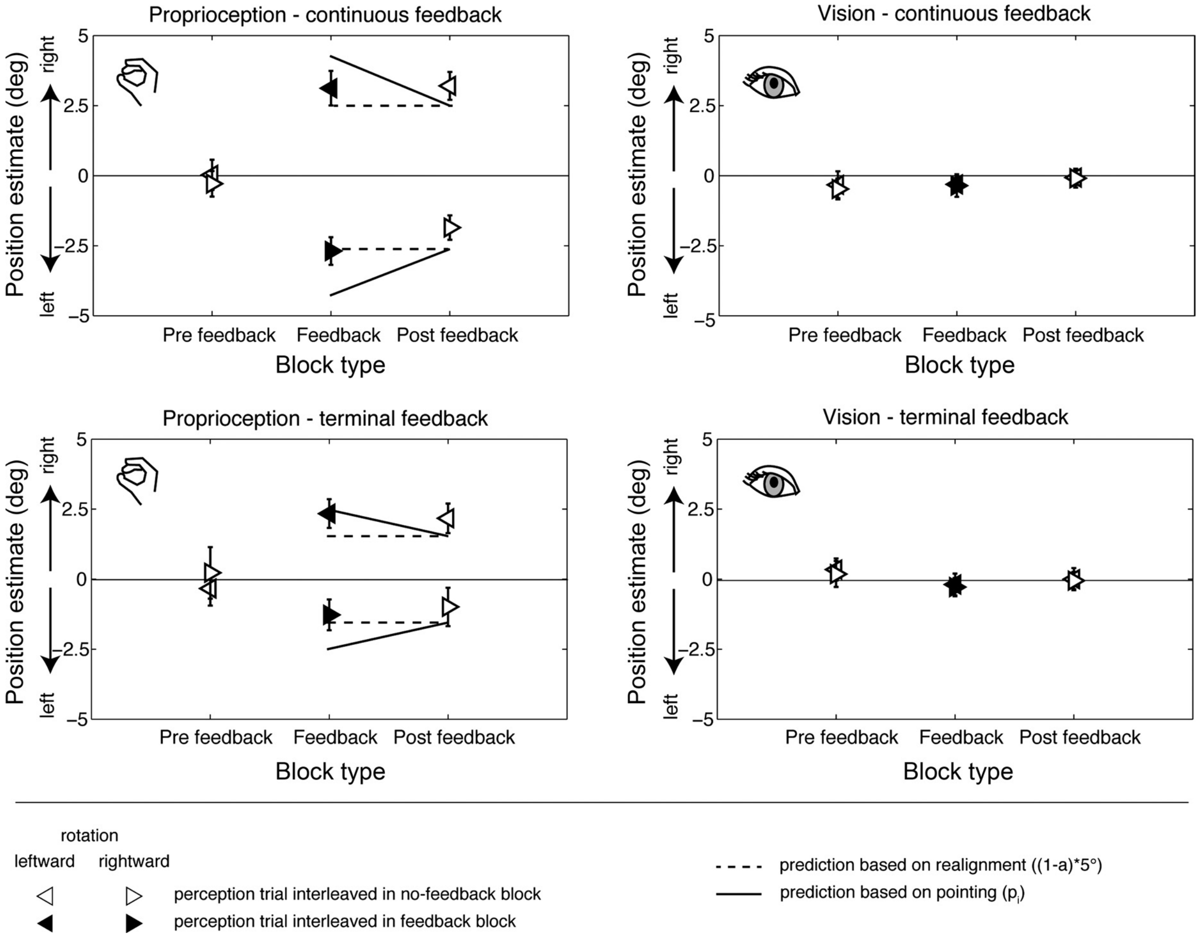

Fig. 5. Perception trials. Shown are visual and proprioceptive estimates of the lateral position that is straight in front of the nose in degrees of visual angle before, during, and after feedback. For comparison, the prediction based on realigning proprioception $[(1 - a) \times 5°]$ and the prediction based on pointing $[(1 - p_i) \times 5°]$, with i at the duration of a perception trial, are plotted as well. Data are averages of 12 subjects' estimates with SEs.

Why then was there some realignment (~20% for continuous feedback and ~10% for terminal feedback) to the natural mismatches? Had subjects not realigned to these mismatches during their everyday interactions with the environment? Visual inspection of the feedback together with the real cube (by removing occluders from behind the half-silvered mirrors) showed that the feedback of the handheld cube was well calibrated with the visual image of the real cube. Nevertheless, the small realignment to the natural mismatches may be due to the experiment introducing small changes in the sensory information. By presenting isolated visual targets in the dark, we removed natural sources of information, such as contextual cues to distance (e.g., Sousa et al. 2010), which may have introduced a different visual bias than is found in the natural situation.

Why Is Realignment Partial?

The realignment was partial, at most 60% (Fig. 4), which is consistent with the 30–60% range reported in the literature [Cressman and Henriques (2009): 30%; Fernandez-Ruiz et al. (2009): 60%; Hamilton and Bossom (1964): 50%; and Taub and Goldberg (1973): 40%]. Although we found no examples of complete realignment, the literature is unclear as to why realignment is partial. A model of realignment in which an intersensory mismatch is estimated and corrected for would predict that ultimately alignment would be complete.

If we had given subjects more time, would they have realigned completely? In macaques, prism aftereffects in depth perception were larger after 500 trials than after 250 trials of feedback (Yin and Kitazawa 2001). We saw no increase in the alignment after the first block of 56 trials with feedback. Perhaps realignment does keep increasing, after an initial fast stage, but so slowly that it was not evident from the 168 trials of feedback that subjects received in our study. Also, the learning and forgetting of the sensory alignment may be better described by two processes with different timescales than by the single process that we assumed when fitting the asymptote in pointing errors. For the updating of movement plans, it has been shown that adaptation to a force field is best described by two interacting adaptive processes with different timescales: a fast process that responds strongly to feedback but forgets rapidly and a slow process that responds weakly to feedback but has good retention (Smith et al. 2006). Unfortunately, our data do not allow for such a refined analysis of the time course of realignment.

Terminal Versus Continuous Feedback

We found more realignment with continuous than with terminal feedback. Letting subjects correct their movements on the fly did not keep them from realigning the senses, as has been proposed before (Bernier et al. 2011; Redding et al. 2005). A number of studies found more realignment with terminal than with continuous feedback (Cohen 1967; Ladavas et al. 2011; Redding et al. 2005; Taub and Goldberg 1973). The different results are difficult to compare because the differences between the studies are numerous. However, we think that an important difference is that in our study targets could appear in any direction, whereas the other studies (Cohen 1967; Ladavas et al. 2011; Redding et al. 2005; Taub and Goldberg 1973) used a more limited set of targets. It has been proposed that subjects compensate for a mismatch using a combination of realignment and motor learning, with continuous feedback facilitating motor learning at the expense of realignment (Redding et al. 2005). We thus may have seen more realignment with continuous feedback than other studies because in our experiment motor learning was not an option that would resolve the mismatch.

Why then was there less realignment with terminal feedback than with continuous feedback? One possible explanation is that the realignment is proportional to the corrections that subjects make during blocks of feedback. In blocks with continuous feedback, subjects made no errors, whereas consistent errors remained in blocks with terminal feedback. These errors may be due to subjects having to use visual feedback from a previous trial when determining the position of their hand for the planning of their movements. The visual feedback may have already partially faded in memory, leading subjects to rely less on it than if it was continuously available. Indeed, the consistent errors in blocks of terminal feedback could be considered aftereffects following one movement without visual feedback (Fig. 2). Hence, there may have been less realignment with terminal feedback because while subjects were learning from the feedback they were also partially forgetting it.

Conclusions

The nervous system partially realigns the senses in response to a change in intersensory alignment. There is more realignment to feedback about imposed mismatches than to feedback about naturally occurring mismatches. This could be because the subjects had already received feedback about the naturally occurring mismatches before entering the experiment and therefore had already partially realigned to it, whereas the experience preceding the experiment provided no feedback about the imposed mismatch.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: K.v.d.K., E.B., and J.B.J.S. conception and design of research; K.v.d.K. performed experiments; K.v.d.K. analyzed data; K.v.d.K., E.B., R.J.v.B., W.D.S., and J.B.J.S. interpreted results of experiments; K.v.d.K. prepared figures; K.v.d.K. drafted manuscript; K.v.d.K., E.B., R.J.v.B., W.D.S., and J.B.J.S. edited and revised manuscript; K.v.d.K., E.B., R.J.v.B., W.D.S., and J.B.J.S. approved final version of manuscript.

REFERENCES

Baraduc P, Wolpert DM. Adaptation to a visuomotor shift depends on the starting posture. *J Neurophysiol* 88: 973–981, 2002.

Bernier P, Chua R, Franks IM. Is proprioception calibrated during visually guided movements? *Exp Brain Res* 167: 292–296, 2008.

Block HJ, Bastian AJ. Cerebellar involvement in motor but not sensory adaptation. *Neuropsychologia* 50: 1766–1775, 2012.

Burge J, Ernst MO, Banks MS. The statistical determinants of adaptation rate in human reaching. *J Vision* 8: 1–19, 2008.

Burge J, Girshick AR, Banks MS. Visual-haptic adaptation is determined by relative reliability. *J Neurosci* 30: 7714–7721, 2010.

Choe CS, Welch RB. Variables affecting the intermanual transfer and decay of prism adaptation. *J Exp Psychol* 102: 1076–1084, 1974.

Cohen MM. Continuous versus terminal visual feedback in prism aftereffects. *Percept Motor Skills* 24: 1295–1302, 1967.

Cressman EK, Henriques DY. Sensory recalibration of hand position following visuomotor adaptation. *J Neurophysiol* 102: 3505–3518, 2009.

Cressman EK, Henriques DY. Reach adaptation and proprioceptive recalibration following exposure to misaligned sensory input. *J Neurophysiol* 103: 1888–1895, 2010.

Fernandez-Ruiz J, Diaz R, Aguilar C, Hall-Haro C. Decay of prism aftereffects under passive and active conditions. *Cogn Brain Res* 20: 92–97, 2004.

Galea JM, Miall RC. Concurrent adaptation to opposing visual displacements during an alternating movement. *Exp Brain Res* 175: 676–688, 2006.

Gori M, Del Viva M, Sandini G, Burr DC. Young children do not integrate visual and haptic information. *Curr Biol* 18: 694–698, 2008.

Haggard P, Newman C, Blundell J, Andrew H. The perceived position of the hand in space. *Percept Psychophys* 62: 363–377, 2000.

Hamilton CR, Bossom J. Decay of prism aftereffects. *J Exp Psychol* 67: 148–150, 1964.

Harris CS. Perceptual adaptation to inverted, reversed and displace vision. *Psychol Rev* 72: 419–444, 1965.

Hinder MR, Riek S, Tresilian JR, de Rugy A, Carson RG. Real-time error detection but not error correction drives automatic visuomotor adaptation. *Exp Brain Res* 201: 191–207, 2010.

Klapp ST, Nordell SA, Hoekenga KC, Patton CB. Long-lasting aftereffect of brief prism exposure. *Percept Psychophys* 15: 399–400, 1974.

Körding K, Wolpert DM. Bayesian integration in sensorimotor learning. *Nature* 427: 244–248, 2004.

Krakauer JW. Motor learning and consolidation: the case of visuomotor rotation. *Adv Experimental Med Biol* 629: 405–421, 2009.

Ladavas E, Bonifazi S, Catena L, Serino A. Neglect rehabilitation by prism adaptation: different procedures have different impacts. *Neuropsychologia* 49: 1136–1145, 2011.

Morton SM, Bastian AJ. Prism adaptation during walking generalizes to reaching and requires the cerebellum. *J Neurophysiol* 92: 2497–2509, 2004.

Ostry DJ, Darainy M, Mattar AAG, Wong J, Gribble L. Somatosensory plasticity and motor learning. *J Neurosci* 30: 5384–5393, 2010.

Peled A, Karniel A. Knowledge of performance is insufficient for implicit visuomotor rotation adaptation. *J Motor Behav* 44: 185–194, 2012.

Priot A, Laboissiere R, Plantier J, Prablanc C. Partitioning the components of visuomotor adaptation to prism-altered distance. *Neuropsychologia* 49: 498–506, 2010.

Redding GM, Rossetti Y, Wallace B. Applications of prism adaptation: a tutorial in theory and method. *Neurosci Biobehav Rev* 29: 431–444, 2005.

Redding GM, Wallace B. Components of prism adaptation in terminal and concurrent exposure: organization of the eye-hand coordination loop. *Percept Psychophys* 44: 59–68, 1988.

Redding GM, Wallace B. Generalization of prism adaptation. *J Exp Psychol* 32: 1006–1022, 2006.

Rincon-Gonzalez L, Buneo CA, Helms Tillery SI. The proprioceptive map of the arm Is systematic and stable, but idiosyncratic. *PLoS ONE* 6: e25214, 2011.

Saijo N, Gomi H. Multiple motor learning strategies in visuomotor rotation. *PLoS ONE* 5: e9399, 2010.

Shabbott BA, Sainburg RL. Learning a visuomotor rotation: simultaneous visual and proprioceptive information is crucial for visuomotor remapping. *Exp Brain Res* 203: 75–87, 2010.

Smeets JB, van den Dobbelsteen JJ, de Grave, DDJ, van Beers RJ, Brenner E. Sensory integration does not lead to sensory calibration. *Proc Natl Acad Sci USA* 103: 18781–18786, 2006.

Smith MA, Ghazizadeh A, Shadmehr R. Interacting adaptative processes with different timescales underlie short-term motor learning. *PLoS Biol* 4: 1035–1043, 2006.

Sousa R, Brenner E, Smeets JB. A new binocular cue for absolute distance: disparity relative to the most distant structure. *Vision Res* 50: 1786–1792, 2010.

Synofzik M, Lindner A, Thier P. The cerebellum updates predictions about the visual conssequences of one's behavior. *Curr Biol* 18: 814–818, 2008.

Taub E, Goldberg IA. Control of intermanual transfer by distribution of practice. *Science* 180: 755–757, 1973.

Templeton WB, Howard IP, Wilkinson DA. Additivity of components of prismatic adaptation. *Percept Psychophys* 15: 249–257, 1974.

Tseng YW, Diedrichsen J, Krakauer JW, Shadmehr R, Bastian AJ. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J Neurophysiol* 98: 54–62, 2007.

Uhlarik JJ, Canon LK. Influence of concurrent and terminal exposure conditions on the nature of perceptual adaptation. *J Exp Psychol* 91: 233–239, 1971.

Van Beers RJ, Sittig AC, Denier van der Gon JJ. Integration of proprioceptive and visual position information: an experimentally supported model. *J Neurophysiol* 81: 1355–1364, 1999.

Van Beers RJ, Wolpert DM, Haggard P. When feeling is more important than seeing in sensorimotor adaptation. *Curr Biol* 12: 834–837, 2002.

Wang RL, Sainburg J. Adaptation to visuomotor rotations remaps movement vectors, not final positions. *J Neurosci* 25: 4024–4030, 2005.

Wei K, Körding K. Relevance of error: what drives motor adaptation? *J Neurophysiol* 101: 655–664, 2009.

Welch RB. *Perceptual Modification: Adapting to Altered Sensory Environments.* New York: Academic, 1978.

Yin P, Kitazawa S. Long-lasting aftereffects of prism adaptation in the monkey. *Exp Brain Res* 141: 250–253, 2001.

Zaidel A, Turner AH, Angelaki DE. Multisensory calibration is independent of cue reliability. *J Neurosci* 31: 1349–1362, 2011.