Internalizing Agency of Self-Action: Perception of One’s Own Hand Movements Depends on an Adaptable Prediction About the Sensory Action Outcome

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Synofzik, Matthias, Peter Thier, and Axel Lindner. Internalizing agency of self-action: perception of one’s own hand movements depends on an adaptable prediction about the sensory action outcome. J Neurophysiol 96: 1592–1601, 2006. First published May 31, 2006; doi:10.1152/jn.00104.2006. Extensive work on learning in reaching and pointing tasks has demonstrated high degrees of plasticity in our ability to optimize goal-directed motor behavior. However, studies focusing on the perceptual awareness of our own actions during motor adaptation are still rare. Here we present the first simultaneous investigation of sensorimotor adaptation on both levels, i.e., action and action perception. We hypothesized that self-action perception relies on internal predictions about the sensory action outcome that are updated in a way similar to that of motor control. Twenty human subjects performed out-and-back pointing movements that were fed back visually. Feedback was initially presented in spatiotemporal correspondence with respect to the actual finger position, but later rotated by a constant angle. When distorted feedback was applied repetitively, subjects’ perceived pointing direction shifted in the direction of the trajectory rotation. A comparable perceptual reinterpretation was observed in control trials without visual feedback, indicating that subjects learned to predict the new visual outcome of their actions based on nonvisual, internal information. The perception of the world, however, remained unchanged. The changes in perception of one’s own movements were accompanied by adaptive changes in motor performance of the same amount, i.e., a secondary motor compensation opposite to the direction of the imposed visual rotation. Our results show that the perception of one’s own actions depends on adaptable internal predictions about the sensory action outcome, allowing us to attribute new sensory consequences of our actions to our own agency. Furthermore, they indicate that the updated sensory prediction can be used to optimize motor control.

INTRODUCTION

An organism’s behavior critically depends on correctly judging the origin of afferent information as resulting from either the outside world (exaff erence) or from one’s own actions (reaffer ence). It is suggested that for this distinction the brain resorts to internal predictions about the expected sensory consequences of one’s own behavior (Holst and Mittelstaedt 1950). If sensory feedback is incongruent with the expected reaff erence an external attribution of the causation of the sensory stimuli occurs and these sensations are accentuated (Blakemore et al. 1998a; Farrer et al. 2003; Frith 1992). If sensory events are congruent with this internal prediction, however, they are attributed to one’s own agency. This is reflected, for example, by the attenuation of self-produced somatosensory stimulation whenever we touch ourselves (Bays et al. 2005; Blakemore et al. 1998b, 1999; Shergill et al. 2003). Another well-known example is the perceptual cancellation of self-induced optical flow while we perform eye movements (see, e.g., Haarmeier et al. 2001; von Helmholtz 1867).

One and the same movement, however, can have different sensory consequences depending on context or changing body conditions such as fatigue, aging, or disease. How then can the brain still adequately inform perceptual evaluation? In particular, how can it predict the altered reaff erence and attribute it to its own actions rather than to events occurring from the outside world? To account for these challenges one has to postulate a plastic mechanism for the attribution of self-agency that optimizes the predicted sensory outcome of one’s own movements. Such a mechanism should align the reaff erences with the respective action by constantly recalibrating sensorimotor interrelations.

Elegant work in the field of prism adaptation has shown that the perception of one’s movements can change as part of a global recalibration of the perception of the world (for review see Redding et al. 2005), especially under conditions of active exploration and sensorimotor adaptation (Held 1965; Held and Freedman 1963). Yet the idea of a separate perceptual recalibration process that specifically confines to the perception of one’s own movements (reafferences only) and that is not secondary to a global change in visual perception (all afferences) still lacks compelling empirical support, even though it may be intriguing and conceptually very useful. To provide evidence for the existence of such a mechanism, we studied the perception of one’s own hand movements: we propose that the perceptual awareness of one’s own hand movements is an inferential process building on a comparison between internal predictions of the upcoming sensory consequences and the actual sensory feedback. Moreover, we hypothesize that this is a highly plastic process. If the reaff erent feedback about one’s hand movements is constantly altered, predictions on one’s sensory action outcome will be correspondingly updated. This makes the surprising prediction that sensory consequences of one’s actions coming with a large, but constant spatial distortion will then be perceived to correspond to the action. Additionally, we asked whether the internal predictions underlying...
the perception of one’s own hand movements might accordingly optimize motor performance.

As will be shown in the following, subjects’ perception of their own hand movements changed in the same way as the visual feedback on the action that we manipulated experimentally. The change in perception of one’s movements could be observed even in control trials without visual feedback, which indicates that the perceptual awareness of one’s movements relies on an inferential mechanism that integrates various types of internal and external information related to the action. More specifically, it supports the hypothesis that internal, nonvisual predictions about the action outcome are constantly recalibrated by external, visual feedback. Because the perception of the world remained unchanged, this recalibration process is specifically confined to the reafference, i.e., to the perception of one’s own actions. Furthermore, the optimization of sensory predictions seems to induce motor learning.

METHODS

Subjects

Twenty right-handed and healthy subjects (eleven females and nine males between the ages of 20 and 32), who gave their informed consent before their inclusion, participated in this study.

Experimental apparatus

Subjects were seated in front of a large horizontal board with their heads being stabilized in a head and chin rest. They looked down onto a rectangular mirror, placed horizontally halfway between the board and a computer screen, which was fixed above the mirror. Subjects always viewed the stimulus screen by the mirror device. For geometrical reasons this screen appeared as lying in the plane of the tabletop (see Fig. 1). Both hands of the subjects were placed on the board, below the mirror, and thus were invisible to them. Furthermore, orientation clues from the surroundings were prevented by carrying out our experiments in complete darkness. On the top of the subjects’ right index finger an ultrasound emitter was mounted. Its position was transferred to the stimulator computer to feed back the position of the index finger visually by the monitor-mirror device. The feedback stimulus consisted of a 0.4°-diameter gray disc that appeared to be in spatial correspondence with subjects’ index finger tip as long as we kept the feedback veridical. The position of the disc was updated on-line at a frame rate of 60 Hz.

Experimental procedure

The basic task of the subjects was to carry out straight out-and-back pointing-movements with their arm. Depending on the experimental phase (see following text) the position of the pointing index finger was either fed back veridically (i.e., in spatial correspondence with the actual finger position) or, alternatively, rotated by a certain degree around the starting point of the movement. The direction of the pointing movement was not constrained except by our instructions: Subjects were asked to perform movements to a self-chosen position on the top right arc (90°) of a briefly flashed circle and afterward to return immediately to the starting point. After each of these trials subjects were asked to indicate the perceived pointing direction of the movement they had actually performed, i.e., the movement for which they claimed agency. This was done by placing a mouse-guided cursor in that direction with their left hand.

Visual feedback was always veridical in the beginning of the experiment—the “preadaptation phase.” This phase constituted a total of 100 trials and four different experimental conditions (described in detail below). Different conditions were presented in randomly interleaved trials with an equal share of 25%. Visual feedback of the hand movement was always presented in only one of the four conditions, i.e., the “feedback trials.” The “preadaptation phase” was followed by a “built-up phase” for adaptation. In this phase we gradually increased the spatial discrepancy (i.e., the rotation) between the actual finger position and the corresponding position of the visual cursor reflecting it. Over a sequence of 20 consecutive feedback trials the rotation angle was increased in fixed steps of 1.5° up to the final rotation of −30° (negative angles denote rotations in the clockwise direction (cl), positive angles in the counterclockwise direction (ccl)). This gradual adaptation was introduced to limit the possibility of subjects becoming aware of the imposed rotation. Such manipulations are usually detected for angular differences of about 14° to 24° (Jannerod 2003; Slachcnevsky et al. 2001). Finally, in the “postadaptation phase” feedback was constantly rotated by −30°. Feedback trials held a share of 70%, whereas the other three conditions, identical to those presented during the preadaptation phase, each contributed to 10% of the postadaptation trials. The total number of trials during the postadaptation phase was always 110 trials.

Experimental conditions

Four experimental conditions were used to induce sensorimotor adaptation and to test for both perceptual and motor aspects of such adaptation in the pre- and postadaptation phases, respectively. The different conditions were indicated to the subjects by the color of a central spot. This color cue was always visible throughout each individual trial and meanwhile served as a fixation target (see Eye movement control below).

FEEDBACK TRIALS (FTs). These trials were indicated to the subject by a green fixation point. Subjects’ task was simply to make a fast, continuous out-and-back pointing movement, while the position of the pointing index finger was fed back visually (Fig. 2A). In the beginning of each trial subjects were asked to place their right index finger on the center point of the board, which was defined by a tactile cue (small nail head on the board). This center point of the board corresponded to the position of the fixation target. Pointing distance was cued by briefly flashing (300 ms) a white circle (9° diameter) centered on the fixation point. Subjects were free to point on any location on the (subjective) top right arc of the circle (corresponding to a region

FIG. 1. Experimental apparatus. By watching the feedback monitor by a mirror (solid orange line) subjects perceived a virtual image of their index finger, which appeared as lying in the same plane as their actual finger (broken orange line). Visual feedback (solid gray arrow) was either veridical (i.e., in spatiotemporal correspondence) or, as in this example, rotated with respect to the actual movement (dotted black arrow). Subjects were asked to perform pointing movements onto the top right quarter of a briefly flashed circle (white circle).
Subjects were asked to perform a center-out pointing movement. Pointing distance of 9° was indicated by a briefly flashed white circle. There was no specific visual target that could have served as a goal for the hand movement (exemplary pointing direction [PD], dotted gray arrow). Only the second half of the movement was fed back visually (bold white arrow); visual feedback during the first half was blocked by an invisible occluder (dotted white circle, 4.5° diameter). Visual feedback was either veridical or, as in this example, rotated by a certain amount depending on the state of the experiment. Subsequently, subjects had to estimate their perceived pointing direction (PPD) by placing a cursor. Note that the PPD is depicted as a gray arrow just for illustrational purposes. Cursor itself was a gray dot of the same size as the fixation target.

Subjects had to make a pointing movement (PD, gray arrow) toward a given flashed target (TF, red circle). Angular difference between PD and TF is defined as the motor error \( \alpha \). No visual feedback was given.

The procedure required to obtain this perceptual estimate can be illustrated, the supposed pointing distance, as cued by a briefly flashed white circle (9° diameter), is indicated by the dotted arc.

Subjects were instructed not to base their estimates on visual information only because “it might be erroneous in some of the trials.” They should also rely on “internal” information about their movement. This instruction should ensure that subjects give an account of their own actions, i.e., the actions for which they claim self-agency, rather than simply give an account of the external visual manipulation.

The trajectory of each movement was recorded and stored on computer disc for off-line analysis. Figure 3 shows a typical example for a single feedback trial (FT). The black dots correspond to individual samples of hand position during the outward journey and the broken gray line represents the best linear fit of the samples. This fit was used to calculate the manual “pointing direction” (PD). The perceptual estimation of the pointing direction (PPD), indicated by a black arrow, deviates only slightly from the actually performed movement (PD).

**PERCEPTUAL CONTROL TRIALS (PCTs).** These trials were instructed in the same way as the feedback trials. Subjects had to carry out a fast out-and-back pointing movement, starting from the green fixation point toward any self-chosen position on the top right arc of the briefly flashed circle. However, no visual feedback was given (Fig. 2B). Subsequently, as in condition FT, the perceived pointing direction PPD had to be estimated. Thus in this condition visual feedback was missing completely and subjects had to rely solely on internal action-based subjective visual horizontal (SVH, broken blue line) by placing the cursor. Note that the broken lines are just for illustrational purposes.

FIG. 2. Experimental conditions (A–D). A: feedback trials (FTs). Subjects were asked to perform a center-out pointing movement. Pointing distance of 9° was indicated by a briefly flashed white circle. There was no specific visual target that could have served as a goal for the hand movement (exemplary pointing direction [PD], dotted gray arrow). Only the second half of the movement was fed back visually (bold white arrow); visual feedback during the first half was blocked by an invisible occluder (dotted white circle, 4.5° diameter). Visual feedback was either veridical or, as in this example, rotated by a certain amount depending on the state of the experiment. Subsequently, subjects had to estimate their perceived pointing direction (PPD) by placing a cursor. Note that the PPD is depicted as a gray arrow just for illustrational purposes. Cursor itself was a gray dot of the same size as the fixation target. B: perceptual control trials. These trials were identical to the sensorimotor adaptation condition, except that no visual feedback was given. C: sensory trials. In these trials subjects did not have to perform any movement. Instead they had to indicate their subjective visual vertical (SVV, broken red line) or subjective visual horizontal (SVH, broken blue line) by placing the cursor. Color of the fixation spot, which could be red or blue, indicated whether to estimate the SVV or the SVH, respectively. Note that the broken lines are just for illustration and were not visible to the subject. D: motor control trials. Subjects had to make a pointing movement (PD, gray arrow) toward a given flashed target (TF, red circle). Angular difference between PD and TF is defined as the motor error \( \alpha \). No visual feedback was given. E: experimental procedure; in the preadaptation phase (trials 1–100), in which visual feedback of the movement was veridical, the 4 different conditions were presented in randomly interleaved trials with an equal share of 25%. During the following “built-up phase” of adaptation (trials 101–120) the spatial discrepancy between the actual hand movement and the corresponding visual feedback was gradually increased up to the final level of −30°. To induce adaptation, only FTs were presented. In the postadaptation phase (trials 121–230), in which visual feedback was constantly rotated by −30°, the share of FTs constituted 70% of all trials to further maintain adaptation. Additional abbreviations: a, anterior; p, posterior; l, left; r, right.
related information (efference copy and proprioception) when judging their own hand movement. Thus these trials specifically tested for solely internal representations of the expected visual action outcome.

SENSORY TRIALS (STs). By means of these trials we controlled for putative changes in the visual processing of spatial information, such as that found in sensory recalibration induced by prism adaptation (Girardi et al. 2004; Held and Rekosh 1963); We also considered the possibility that in the present experiments a shift of the subject’s visual frame of reference, such as a tilt aftereffect (Held and Mikaelian 1964; Redding et al. 2005), might have been induced by the altered—in spite of the fact that the occluder was already greatly reduced—visual feedback in FT. Such a global adaptation of processing afferent information would lead to altered subjective estimates of the reafference as well (as shown by Held and Freedman 1963). To control for this possibility, we mapped the cardinal axes of our subjects’ visual reference frame during both the preadaptation and the postadaptation phases; subjects did not have to perform any movement in these conditions. When a red fixation point was presented, subjects simply had to set the mouse-controlled cursor in a vertical position, thus indicating their subjective visual “vertical” (SVV), i.e., the anterior–posterior axis. When the fixation point was blue, subjects were asked to place the cursor in a horizontal position to estimate their subjective visual “horizontal” (SVH), i.e., the left–right axis (see Fig. 2C).

MOTOR CONTROL TRIALS (MCTs). An orange fixation dot indicated this specific condition, in which a red pointing target was flashed simultaneously with the white circle. The target flash could occur in four different positions on the top right quarter of the circle: at the twelve, one, two, or three o’clock position (i.e., 90, 60, 30, and 0°, respectively). Thus subjects were no longer free in choosing a movement direction as in the first two conditions but had to make a movement toward the red target as precisely as possible. Neither visual feedback nor any other feedback on movement accuracy was provided (see Fig. 2D). Because subjects were unable to visually control their movements, pointing critically depended on a previously acquired internal motor plan for the given context. To estimate the precision of this plan we calculated the motor error alpha as the difference between the actual pointing direction (PD) and the position of the target flash (TF). In addition, subjects were again asked to give a perceptual estimate of the direction of their pointing movement. However, this perceptual estimate was required only to keep uniformity across conditions and not analyzed any further.

Effects of sensorimotor adaptation on each of our behavioral measures [the perception of self-action (P) with and without visual feedback, 3) motor performance, and the 4) SVH/SVV], obtained in the four experimental conditions (1) FT, 2) PCT, 3) MCT, and 4) ST, respectively], were defined as the mean differences between the preadaptation phase (trials 1–100) and the postadaptation phase (trials 131–230). The first 10 trials of the postadaptation phase had been discarded to guarantee that adaptation had already been accomplished. Behavioral measures were analyzed on the group level (for details refer to RESULTS). To statistically test for adaptation within each subject we performed additional t-tests (H0: no difference for pre- and postadaptation phases). The resulting P values were corrected for multiple comparisons within subjects.

Eye movement control

Ocular fixation was controlled on-line using a custom-made IR video-tracker. Fixation errors >2.5° were fed back acoustically and the trial was discarded. Thus subjects were not able to track or even precede the intended hand movement with their eyes. Such oculomotor strategies might have interfered with the control and the perception of the actual hand movement (Ariff et al. 2002; Scherberger et al. 2003; Vercher et al. 1997). Although we cannot answer this question, a methodological limitation of our experiment is able to show that there was at least no difference in the control or the perception of hand movements when ocular fixation was controlled compared with uncontrolled, instructed fixation. Because of the need to direct the eyes downward and the upper lid covering much of the eyes in this position, vertical eye movements could not be reliably measured in about half of our subjects. As revealed by an ANOVA, all effects reported in RESULTS did not differ significantly between subjects in which fixation was controlled for (n = 9) and those in which it could not (n = 11; three-way ANOVA with the factors fixation, adaptation, and experimental condition; P > 0.05 for factor fixation and interactions of fixation with any of the other factors).

RESULTS

In the following we will first provide a brief, exemplary description of the results of two representative subjects before we will focus on the group of 20 subjects as a whole. In subject A the median of the difference between the performed hand movement and the perceived hand movement was about 0° in the preadaptation phase of the FT, in which veridical visual feedback was provided (see Fig. 4A). This means that the subject was able to give a very accurate perceptual estimate on his/her movement. During and shortly after the “built-up phase” of adaptation, in which visual feedback on the hand movement was gradually increased up to the final value of −30°, the perceived hand movement deviated increasingly from the actual hand movement. Already at the end of the built-up phase of adaptation (trial 120), it deviated by a difference of about −13°. This difference remained roughly constant during the whole postadaptation period and was highly significant when compared with the preadaptation period (P < 0.001; t-test). Also in the PCT, where visual feedback was absent, subject A was well able to perceptually estimate his hand movement in the preadaptation phase, with a mean deviation between the percept and the actual motor performance of only 1° (Fig. 4B; trials 1–100). Similar to his performance in the FT, subject A attained a significant difference (P < 0.001; t-test) of about −15° in the postadaptation phase (Fig. 4B). This indicates that an internal prediction about the action outcome might have been updated. Alternatively, the latter adaptation could simply arise from a purely sensory adaptation process, which might nonspecifically affect the visual estimation of the PPD, rather than from a specific sensorimotor adaptation of the perception of the own hand movement. However, subject A showed neither a difference in the SVV nor in the SVH in a comparison of preadaptation and postadaptation (P > 0.05; t-test). Both measures remained at 90° (SVV) and 0° (SVH), respectively (Fig. 4C). Thus there is no evidence for any tilt aftereffect, which could have affected processing of both efferent and reafferent information. Finally, the MCT served to monitor changes in motor performance. When plotting the difference between the position of a visual target (TF) and the direction of a pointing movement (PD) toward it (motor error alpha) as a function of trial number, in subject A there was already a bias of −4° in the preadaptation phase (Fig. 4D). This bias may indicate subject A’s problem of reaching a small target without visual feedback, relying only on nonvisual, internal reference signals. In subject A, this motor error did not significantly change during adaptation (P > 0.05; t-test). Thus the subject’s motor performance was hardly influenced by the FT, contrary to the perceptual estimate of his/her own movement in PCT.
Subject A

A

FT: -12.7°, P<0.001

B

PCT: -14.9°, P<0.001

C

ST: SWV: -2.1°, P=0.05, SVH: -0.4°, n.s.

D

MCT: 5.7°, n.s.

Subject B

E

FT: -13.5°, P<0.001

F

PCT: -17.0°, P<0.001

G

ST: SWV: -2.0°, n.s.; SVH: 0.1°, n.s.

H

MCT: 15.4°, P<0.001

FIG. 4. Results of 2 representative subjects. For each of the 4 conditions the performance of 2 subjects (A and B) is plotted as a function of trial number. In addition, the median values (bold lines) and the quartiles (dotted lines) of the preadaptation and the postadaptation phases are shown. For FT and PCT the perceived pointing direction (PPD) is plotted relative to the actual pointing direction (PD; see A, B, and E, F). Negative angles denote shifts in clockwise direction (cl). Note the very obvious effect of adaptation (−30° cl) leading to more negative values during the built-up and adaptation phase. For ST the SSV and SVH are depicted (see C, G). Median values for perceived verticality (90°) and horizontality (0°) remained constant throughout the experiments. For motor control trials (MCTs) the motor error alpha is shown as the difference between the direction of the target flash (TF) and the actual pointing direction (PD). In Subject A (type: “perceptual adaptation”) there was no significant change between the pre- and the postadaptation phase in these MCTs (see D). In Subject B (type: “perceptual and motor adaptation”) postadaptive difference between PD and TF significantly shifted toward positive values (see H). Additional abbreviations: n.s., not significant; P > 0.05.
Also in subject B the mean postadaptive deviations of the percept from the actual motor performance were highly significant ($P < 0.001$; $t$-test) in the FT (Fig. 4E) and in the PCT (Fig. 4F), whereas the SVV and SVH remained unchanged ($P > 0.05$; $t$-test, Fig. 4G). Thus the changes in the perception of self-action in subject B are comparable to those in subject A. However, in subject B the motor error alpha changed significantly ($P < 0.001$; $t$-test) from $-6^\circ$ in the preadaptation phase toward $10^\circ$ in the postadaptation phase (Fig. 4H). This positive shift indicates a compensatory motor adjustment of pointing movements, seemingly taking into account the altered expectation of the action outcome (PCT). Thus whereas subject A learned to attribute altered feedback only to his own agency, subject B learned to update the perception of the movement as well as the movement itself to “successfully” reach the flashed target in MCT.

Interestingly, motor updating occurred even though we never provided any feedback about a potential motor error. Adaptation of subject A can be classified as behavior type “perceptual adaptation,” representing subjects adapting significantly only in FT and PCT ($P < 0.05$; $t$-test). On the other hand, subject B demonstrates the behavior type “perceptual adaptation and motor adaptation,” representative for subjects who adapted significantly in FT, PCT, and MCT ($P < 0.05$; $t$-test). Performance in these two representative subjects implies that internal predictions for perception can indeed be updated. Moreover, it suggests that the updated perception of one’s movements can trigger motor learning (subject B) although not necessarily (subject A).

Updating perception of one’s own movements

Performance across subjects was analyzed by means of a three-way ANOVA with the factors condition, adaptation, and perceived pointing direction. Significant main effects were obtained for the factors condition, adaptation, and perceived pointing direction ($P < 0.001$). Furthermore, the interaction between adaptation and condition ($P < 0.001$), the interaction between adaptation and pointing direction ($P < 0.001$), and the interaction between all three factors ($P < 0.01$) also reached the statistical threshold criteria ($P < 0.05$). In other words, the group of subjects showed significant adaptation. Adaptation thereby significantly differed for different experimental conditions and for different perceived pointing directions ($30^\circ$ bins). Furthermore, this directional tuning of adaptation differed between conditions. In the following we will focus on the differences between the behavioral measures obtained in these conditions. For further characterization of the interaction between adaptation and perceived pointing direction refer to Fig. S1 in the supplementary material (the online version of this article contains supplemental data).

FEEDBACK TRIALS. The group mean of the perceptual estimate of one’s movement showed a highly significant adaptation ($P < 0.001$; $t$-test) of about $14^\circ$ in a comparison of postadaptation with preadaptation (see Fig. 5). This effect clearly demonstrates that the relation between a given movement and its perceptual consequence can be altered: The perceptual awareness of one’s movement is not strictly linked to the movement itself (i.e., to fixed efference copies and/or proprioception), but obviously also integrates action-related visual information.

PERCEPTUAL CONTROL TRIALS. Also in the PCTs without any visual feedback subjects showed significant adaptation of their PPD relative to their PD toward the direction of prior FT feedback rotation ($P < 0.001$, $t$-test). Similar to the FT, the relative difference of perceived pointing (PPD) with respect to the actual movement (PD) shifted to $-10^\circ$ because of adaptation (see Fig. 5). This result suggests that the altered perceptual estimate is not merely an immediate result of visual feedback, which might have governed subjects’ responses in FT, but a stable (also see Fig. S3) representation that relies on internal predictions on the action outcome as informed by proprioception and/or efference copy.

SENSORY TRIALS. Neither in the SVV nor in the SVH could significant changes between the preadaptation and postadaptation phases be observed ($P > 0.05$; $t$-test) (see Fig. 5). Thus any additional influence of general afferent adaptation on the reafferent movement estimates can be ruled out: Perceptual and motor learning in FT, PCT, and MCT were not secondary to an altered reinterpretation of sensory signals independent from the action performed (afferent perceptual adaptation). Instead, sensorimotor learning exclusively referred to sensory signals that were linked to one’s own actions (reafferent perceptual learning).

MOTOR CONTROL TRIALS. To test for the possibility that the perceptual adaptation generalizes to motor adaptation, “motor control trials” were presented randomly interleaved. Because no visual feedback was provided, subjects were dependent on exploiting their internal motor repertoire for generating goal-directed movements. If these internal motor plans were modified by the “optimized” percept, a compensatory motor adjust-

**FIG. 5.** Group data. Plot shows the mean difference between the preadaptative and postadaptative behavioral measures ($\pm 95\%$ confidence intervals) calculated across all individual subjects and separately for each condition ($***P < 0.001$; n.s., not significant, $P > 0.05$).
ment opposite to the direction of the imposed visual rotation should be expected. Indeed, the motor error alpha showed a significant ($P < 0.001$; $t$-test) adaptation-induced increase (+9°), which had a comparable absolute amount as the changes in perceptual judgments in PCT ($-10°$; see Fig. 5).

A further analysis of the distribution of pointing directions obtained in the conditions FT and PCT showed that subjects modified their motor behavior in a direction opposite to the imposed visual feedback rotation, also in these two conditions. Updating occurred even though the pointing direction was not externally guided by a visual target but had to be chosen purely “mentally” (for further details refer to Fig. S2 in the supplemental material).

Taken together, these results show that it is indeed possible to update an internal representation of the expected visual outcome of one’s own hand movements and, furthermore, that this updated internal representation is associated with compensatory motor learning.

Specificity of perceptual and motor updating?

As a next step, we asked whether motor control and sensory predictions are congreuntly updated. The mean effects (see Fig. 5), calculated across all subjects, might simply average out interindividual differences in subjects’ adaptation strategies (e.g., compare Fig. 4). To test for intraindividual congruence of both types of sensorimotor adaptation (i.e., perceptual and motor updating) we performed a correlation analysis between the individual behavioral measures obtained in FT, PCT, and MCT (see Fig. 6, A–C). Adaptation in FT correlated significantly with adaptation in PCT ($P < 0.05$; Fig. 6A). This correlation suggests that during trials with altered visual feedback subjects not only altered the perception of their movements, but also used the visual feedback to update an internal prediction of the sensory consequences of their movement, on which they had to rely in trials without visual feedback. However, perceptual adaptation in FT did not correlate ($P > 0.05$) with motor adaptation in MCT (Fig. 6B). This means that the motor behavior cannot be directly explained by visual feedback learning. Finally, adaptation in PCT also did not correlate with adaptation in MCT ($P > 0.05$; Fig. 6C). Thus it seems that, although all subjects updated their internal predictions about the sensory action outcome, they did not strictly use the acquired knowledge to update their internal representations for motor control. This was to be expected, however, if both internal representations would rely on one and the same sensorimotor underpinning and/or the same error signal.

Discussion

Extensive work on learning in reaching and pointing tasks has demonstrated that humans are able to adapt motor control to kinematic transformations, that is, spatial visuomotor transformations (Ghahramani and Wolpert 1997; Imamizu et al. 2000), to dynamic transformations (Flanagan and Wing 1997), or to both simultaneously (Flanagan et al. 1999). However, none of these studies focused on the perceptual awareness of our actions during motor adaptation and, more specifically, if such perceptual awareness relies on internal predictions about the sensory action outcome that might be updated in a similar way. To investigate this hypothesis, we here present the first simultaneous investigation of sensorimotor adaptation on both levels, i.e., action and action perception, respectively.

Recalibration of internal predictions for perception by visual feedback

It has been suggested that our brain anticipates the sensory consequences resulting from our hand movements by use of internal predictions (Blakemore et al. 1999; Shergill et al. 2003). Perceptual awareness might be critically linked to this predictive mode of operation of the brain (Buracas 2005; Slachowsky et al. 2001). If this idea would hold true, the question remains, if and in what way the brain manages the fact that sensory consequences of one’s own movement might change as a result of changing body and context conditions (such as tiredness, growth, illness, etc.). How can it attribute the altered reafference to its own actions rather than to events occurring from the outside world (effferrence)? In fact, the present study provides evidence that the brain updates predictions about the visual action outcome in conditions of altered visual reafferent input by constantly recalibrating the interrelation between actions and their sensory consequences. This conclusion is drawn from the observation of a new interpretation of perceived hand motion that resulted from manipulated visual feedback on hand movements: When applying distorted visual feedback (in FT) the perceived pointing direction shifted significantly in the direction of the imposed trajectory rotation.

**Fig. 6.** Regressions between all individual adaptation measures obtained in FT, PCT, and MCT. Whereas the adaptation in the FT correlated with adaptation in the PCT (A), it did not correlate with adaptation in the MCT (B). Furthermore, adaptation in the PCT was not related to adaptation in MCT (C). Any significant correlation is indicated by plotting the respective regression line ($P < 0.05$, corrected for multiple comparisons).
This supports the important role of visual input for the brain when there is need to reconcile conflicting information from diverse external and internal sources and thus to confer stability on behavior (cf. Fink et al. 1999; Ramachandran and Rogers-Ramachandran 1996). However, although this visual input is used to update perception, we could show that the altered percept of one’s movements itself is partly nonvisual in origin. The change in the perceived direction of hand motion could even be observed in trials in which no external, visual feedback was provided (PCT). Thus any modification of action perception had been caused by changes in an internal representation of the predicted sensory outcome. The correlation between the perceived pointing direction in trials with visual feedback (FT) and control trials without visual feedback (PCT) furthermore shows that the modulation of perceived hand motion direction in the FT was not merely the result of a visually guided response bias or to a short-term, immediate weight shift between visual and proprioceptive inputs within a multimodal integration process of action-related sensory information. Subjects rather develop a more general and stable (but nevertheless adjustable) representation of the sensory consequences of their actions by altering their internal predictions—they update an internal model (Ito 2000; Wolpert et al. 1995, 1998) for self-action perception. That this recalibration process does indeed reflect a genuine adaptation process concerning only the perception of one’s movements (the reafference), but not the result of a more general afferent recalibration concerning the perception of the world, is shown by the stable axes (SVH/SVV) of the “low-level” visual reference frame.

Such an afferent recalibration for instance occurs during prism adaptation, which would affect ex- and reafferent visual information processing as well as visually guided motor behavior (Gibson and Radner 1937; Girardi et al. 2004; Held and Mikaelian 1964). Effects of prism adaptation are even larger (i.e., more complete) in case of 1) active exploration of the altered visual environment (Held and Freedman 1963; Held and Mikaelian 1964) or 2) when awareness of the visual displacement is being prevented (Redding et al. 2005). Although our study engaged both active movements and methods to prevent awareness of visual displacement, we observed no change in the cardinal axes of the visual reference frame, that is, the subjective visual vertical and horizontal (SVV and SVH). This is probably explained by the fact that feedback manipulations were confined to reafferent visual information only, whereas in the case of prism adaptation the global visual world is usually being manipulated.

In summary our results confirm a highly specific recalibration of the perception of one’s own movements that does not require and/or accompany changes in the perception of the world. Furthermore, we provide evidence that the perception of self-motion does not sufficiently rely on direct sensory information, such as on visual cues as stated by the direct theory of perception (Gibson 1950), but in addition builds on internal reference signals of the movement, as postulated by the inferential theory of perception (von Helmholtz 1867; von Holst and Mittelstaedt 1950; Wertheim 1994). As previously shown for smooth pursuit eye movements (Haarmeier et al. 2001) and electroreception in weakly electric fish (Bell 1981, 2001), we demonstrate with regard to hand movements that this theory has to be extended by the assumption that the internal reference signal is not a statically fixed replica, but a highly plastic “corollary discharge” (cf. Sperry 1950) of motor commands and/or proprioception. Because both the proprioceptive inputs and the motor commands are the same in the pre- and the postadaptation phases, it is not a change in proprioception or in the efference copy per se that accounts for the updated perception, but it must be a change in an internal representation that relates these internal sources of self-motion information with the expected visual action outcome.

We thus provide the first experimental evidence for a twofold theoretical assumption of internal models, recently stated by Ito (2000): 1) An internal model for perception provides a prediction about a sensory action outcome, thus being independent from (delayed and sometimes missing) afferent feedback information (as shown by the PCT). 2) Nevertheless the internal model for perception can be recalibrated by reafferent information (as shown by the FT). Thus recent criticism against the “internal model approach,” claiming that it would presuppose a rigid interdependence between perceptual predictions and corresponding motor commands (Mechsner et al. 2001), is not only conceptually misleading but also empirically invalid.

Perceptual reinterpretations of self-action trigger motor learning

Our results do not only show that the perception of our hand-movements builds on adaptable sensory predictions. They furthermore demonstrate that optimizing these predictions can be associated with an updating of internal representations for motor control. This is surprising because our experimental paradigm required subjects to update their perceptual evaluation of their actions but not necessarily to update motor control. Whereas internal error signals (i.e., errors between the actual sensory feedback of the movement and the intended sensory action outcome and/or the predicted sensory outcome) were conveyed by the distorted visual feedback in FT, a visual motor error (i.e., an error between the sensory action outcome and the visual target) could not be detected because any visual feedback about the movement was absent in MCT. Thus there was obvious need to correct for erroneous perceptual evaluation because the sensory prediction seemed to be wrong. However, there was no need to correct for motor control. These different task requirements are resembled by our results: All subjects changed the perceptual evaluation of their actions when visual feedback was present and used this information to update their internal prediction of the sensory outcome (as can be traced from the correlated changes in PCT; see Fig. 6A). Although motor adaptation also occurred, it did not strictly correspond to a simultaneous perceptual reinterpretation of self-motion in FT and PCT, but rather represented a coarse-grained, nonspecific counteradaptation as can be concluded from the uncorrelated changes in MCT (see Fig. 6, B and C). The lack of correlation implies that motor adaptation does not build on the same error signal as perceptual adaptation. However, it leaves open the possibilities that the observed changes in motor behavior might be the direct consequence of the perceptual recalibration or, alternatively, reflect the outcome of a pure “visual motor strategy,” which compensates discrepancies between the intended sensory action outcome (by imagining a visual target goal) and the perceived visual outcome (in FT). The latter interpretation can be ruled out for the following
reasons. First, it is hard to see why such an optimization strategy should be confined to motor control but not perception; otherwise, all behavioral estimates should be correlated with each other, which was clearly not the case (see above). Second, the error signal of a "visual motor strategy" would be constant for all different (perceived) pointing directions. Despite that fact, we saw significant directional effects in both motor and perceptual adaptation (compare supplementary Fig. S1). Thus it seems rather likely that perceptual adaptation might have triggered motor learning, a notion consistent with the idea that a sensory predictor can be used to train a motor controller (Flanagan et al. 2003; Haruno et al., 2001; Wolpert and Kawato 1998). Whether the sensory predictor and the motor controller are updated sequentially and whether updating depends on the conscious awareness of sensorimotor discrepancies must be clarified by further work, e.g., by lesion studies showing a dissociation in updating of both mechanisms.

Internalizing agency of the perceptual consequences of one's own movement

The need for precise and continuously optimized sensory predictions becomes evident when considering the inferential character of our perception while acting within the world (cf. Haarmeier et al. 2001; von Helmholtz 1867; von Holst und Mittelstaedt 1950; Wertheim 1994). Because there is no intrinsic difference between sensory signals arising as consequences of our actions (reafference) or as results from events in the outside world (exafference), we can differentiate only between externally produced and self-produced events on the basis of the predicted sensory consequences of our own action (Blakemore et al. 1998b; Frith et al., 2000). If—with a comparative process—the actual sensory afference matches the predicted reaferrence, we perceive the sensory event as self-produced; if they do not match, we attribute the causation of this sensory discrepancy to the environment. Elaborating on this idea, a comparison between the predicted and the actual sensory input was recently discussed as a subpersonal cognitive mechanism that underlies the subject’s experience of self-agency (Campbell 2004; Farrer et al. 2003; Gallagher 2000; Georigeiff and Jeannerod 1998; Haggard 2003; Lindner et al. 2005; Pacherie 2001). Thus in contrast to many classical philosophical concepts, self-agency is not assumed to be represented as separate from the action, but as an intrinsic property of the action itself. Because the sense of self-agency displays the implicit grasp of the causal relations between the subject and the world, it can even be seen as a constitutive part of basic self-consciousness (Campbell 2004; Churchland 2002; Gallagher 2000).

Unlike many other studies exploring the sense of agency (Daprati et al. 1997; Farrer et al. 2003; Franck et al. 2001), our experiment did not test for qualitative, dichotomic agency judgments ("Was the movement you have seen caused by yourself or not?"), but for the gradual amount of afferent information for which self-agency is claimed ("Please indicate yourself or not?"). Thus in contrast to many classical philosophical concepts, self-agency is not assumed to be represented as separate from the action, but as an intrinsic property of the action itself. Because the sense of self-agency displays the implicit grasp of the causal relations between the subject and the world, it can even be seen as a constitutive part of basic self-consciousness (Campbell 2004; Churchland 2002; Gallagher 2000).

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