Spatial Realignment in Sensorimotor Adaptation: Taking the Efficiency Into Account

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The present study reviewed the modular approach in adaptive motor control by taking cognitive efficiency into account. Three experiments were conducted to compare different visuomotor learning mechanisms (modular adaptation, use-dependent plasticity, and spatial realignment) in response to visuomotor rotations. During exposure, the visual feedback of flicking movements in a single-target scenario was rotated either 30° clockwise (CW) or counterclockwise (CCW) at the left and right starting locations, respectively. Exposure to the CW and CCW rotations was carried out in an alternating order. After adaptation to the rotations, generalization was evaluated by assessing aftereffects from a set of untrained starting locations to the target (Experiments 1 and 2) or from the trained starting locations to a set of new targets (Experiment 3). Predictions made based on the different visuomotor learning mechanisms were compared to the empirical data. In spite of evidential advantages of modular structure, the current work could show a particular case of visuomotor transformation, in which modularity lacks efficiency. Results indicate that the adaptive motor control system employed the spatial realignment to accomplish adaptation more efficiently.

Keywords: visuomotor adaptation, modularity, spatial realignment, adaptive action control, visuomotor generalization

Human movement control is characterized by the capability to improve performance using sensory signals until the movement controller specifies a certain motor task in an optimal manner. Different mechanisms can account for the performance improvement depending on particular task requirements; for instance, implicit and explicit processes (Hegele & Heuer, 2010; Mazzoni & Krakauer, 2006; Sülzenbrück & Heuer, 2009), recalibrations as strategic remapping for rapid error compensation, and realignments as transformation of spatial maps to bring the origins of coordinate systems into correspondence (Redding & Wallace, 1996, 2001, 2002, 2006), or model-based and model-free learning (Diedrichsen, White, Newman, & Lally, 2010; Huang, Haith, Mazzoni, & Krakauer, 2011; for a review see Wolpert, Diedrich-sen, & Flanagan, 2011). The present work focuses on adaptation to visuomotor rotation as a particular form of motor learning distinct from force-field adaptation, sequence learning, and skill learning (Krakauer, 2009), which is believed to rely on task-dependent adjustments of the motor response to compensate for a manipulation of the working environment (Clower & Boussaoud, 2000).

Since motor learning, including visuomotor adaptation, is considered as a consequence of the acquisition of more appropriate internal representations of action (Newell, 1991), it is essential to understand how action representations are organized. Previous studies have suggested that movement control performed by the central nervous system (CNS) relies on internal representations (or models), which estimate the sensory consequences of a specific given motor command (predictors) and calculate motor commands to achieve a desired sensory effect (movement controllers; cf. Miall & Wolpert, 1996; Wolpert, Ghahramani, & Jordan, 1995). Hence, modification of an existing but currently incorrect internal model or construction of a new model forms the central stage of visuomotor adaptation in the course of dealing with changes in the environment in which the motor task is performed (action context). Given the multitude of action contexts in the everyday reality of motor behavior, it is important to understand how multiple action contexts are handled by neurocomputational mechanisms of information processing in the human CNS. Hence, key problems in the domain of movement control theory include the acquisition and modification of multiple internal representations for many action contexts, their storage, recall, and utilization in related action contexts.

The existence of multiple paired forward (predictor) and inverse models (movement controller) is believed to provide the basis for movement control in multiple action contexts (Wolpert & Kawato, 1998). A wide range of different parameters (e.g., mass and moment of inertia of the body effector, size and weight of the object and global contextual properties like gravity for a simple grasping movement) must be specified for a movement controller to determine the motor command sufficiently well. Hence, the ability to produce a variety of complex motor behaviors cannot be attained by a single controller using all the contextual information to produce an appropriate control signal, because such a controller would easily become overextended to encapsulate all the contexts. Alternatively, modular approaches offer a better resolution for this dilemma (Miall, 2002; Mussa-Ivaldi, 1999; Wolpert, 1997; Wolpert & Kawato, 1998). A central assumption of a modular approach is the coexistence of multiple controllers, with each controller suitable for one action context or a small subset of contexts. Based on evaluation of sensory signals arising from the action context (contextual cues), the proper controller could be switched on (e.g., Bock, Worringham, & Thomas, 2005; Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Krouchev & Kalaska, 2003; Rao & Shadmehr, 2001; Woolley, Tresilian, Carson, & Riek, 2007), or a set of controllers could be activated to generate the appropriate motor command (Wolpert & Kawato, 1998). Hence, multiple movement controllers can be regarded conceptually as motor primitives, which serve as building elements used to construct intricate motor behaviors. Modularity has two decisive advantages. First, modularity enables single controllers to participate in motor control without affecting or interfering with each other. And second, by combining independent modules to produce motor commands, the adaptive control repertoire can be increased sufficiently. It allows the motor control system to deal with novel situations more efficiently. To this end, when encountered with a novel context, which is derived from combinations of previously experienced contexts, the modular system can select a set of available controllers and combine them by modulating their contribution to the final motor command. Hence, selection and combination of independent controllers present the most sophisticated part of a modular architecture.

Different realizations of the modular approach were discussed and examined using computer models in previous studies. Two representative computational methods are the mixture-of-experts architecture (Jacobs, Jordan, & Barto, 1991) and the modular-selection-and-identification-for-control model (MOSAIC, cf. Haruno, Wolpert, & Kawato, 2001; Imamizu, Kuroda, Yoshioka, & Kawato, 2004). In spite of some differences, both architectures involve a prior probability distribution of responsibility estimates for each control module, based on which an appropriate control module is selected or several control modules are combined for a given action context optimally (Miall, 2002; Thoroughman & Shadmehr, 2000).

A study by Ghahramani and Wolpert (1997) was believed to provide strong evidence for the modular approach. In this study, participants learned to counteract a visuomotor rotation by reaching from two different starting positions to a common target. The rotations induced at the starting positions were opposite to each other (i.e., clockwise [CW] at the left starting position and counterclockwise [CCW] at the right, or vice versa). Following adaptation, generalization to a set of intermediate starting positions was assessed. Results demonstrated that the generalization of visuomotor adaptation followed a logistic function of starting position. The authors suggested that two different mappings were learned and retained as independent modules to prevent interference. In the test phase, both mappings were combined with each other to produce a weighted average based on responsibility estimates at a novel starting position.

However, one could question the assumption of two conflicting mappings, which were acquired and stored separately as suggested by Ghahramani and Wolpert (1997). In a study conducted in our laboratory, we used a similar spatial arrangement of start-target positions to examine motor bias of prior adaptation (Wang & Müsseler, 2012). Results showed that adaptation at one starting position caused a mirrored bias for movements at the other starting position. This was probably due to the symmetrical structure of the start-target arrangement, so that opposing rotations were concordant rather than conflicting within this particular structure. It contradicts the modular approach suggesting the acquisition of two controllers based on conflicting visuomotor mappings, at least in connection with the above-described setup. We therefore suggest an alternative approach to the modular decomposition principle for the findings of Ghahramani and Wolpert (1997), which takes the efficiency aspect into account. In particular, the present study will demonstrate the capability of the CNS to reunite conflicting movement controllers through spatial realignment in a specific experimental setup employing visuomotor rotation. Originally, spatial realignment has been found to be essential for prism adaptation (e.g., Bedford, 1989; Redding & Wallace, 1993). According to the model of adaptive eye-hand coordination suggested by Redding and Wallace (2002), realignment is mediated by feedforward–feedback comparisons that enable parametric adjustments in case of misalignments among sensorimotor coordinate systems (i.e., visual-motor and proprioceptive-motor maps). Hence, it results in fundamental changes in the evolutionarily given spatial mapping functions that normally align corresponding positions among the various spatial representations that serve perceptual-motor behavior. Consequently, once a spatial realignment is accomplished, it triggers a complete generalization in the task-work space; that is, a global change throughout the entire mapping rather than a local change at the trained location (Bedford, 1989, 1993; Redding & Wallace, 2006). This particular feature can be exploited to predict the transfer magnitude of adaptation based on spatial realignment.

Setup and Hypothesis of Experiment 1 and 2

The setup of Experiment 1 and 2 was derived from the study of Ghahramani and Wolpert (1997). Movements were made from a set of starting positions to a target as illustrated in Figure 1. The starting positions were paired regarding their locations. Each pair of starting positions was respectively located left and right of the midline with the same distance. Visuomotor rotations were applied to starting positions 3a (CW) and 3b (CCW). Participants learned to counteract the perturbation at both positions in an alternating schedule in the adaptation phase. This perturbation created a conflict in the visuomotor mapping. According to Ghahramani and Wolpert (1997), one way to resolve this conflict is to develop two separate visuomotor mappings (i.e., two experts), each for one of both starting positions. For transfer to a novel starting positions, a gating module weights and combines the outputs of the two
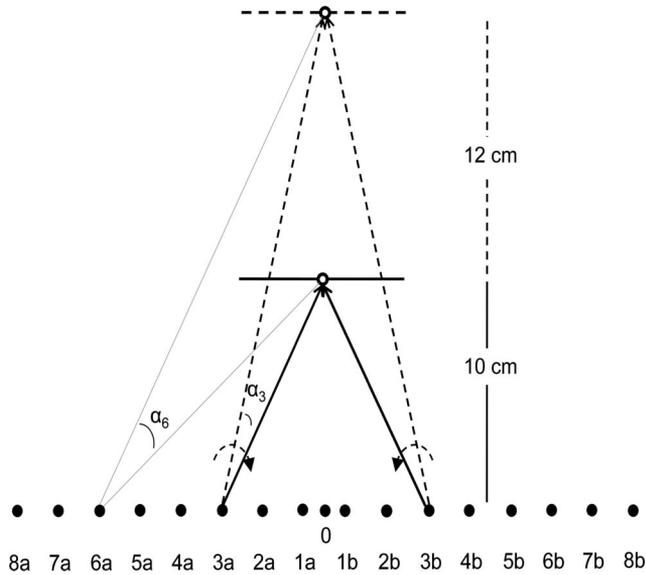
Figure 1. General setup of Experiments 1 and 2 in overview. The visual target was represented as an open circle with its periphery (horizontal line). CW and CCW rotations were applied to starting position 3a and 3b, respectively. According to the assumption of spatial realignment, in order to counteract the rotations, a fictive target (open circle with dashed line as its periphery) would be generated in the action space. A set of test locations was represented as black dots. At each test location, the motor bias caused by original rotations at 3a and 3b and the compensatory spatial realignment could be considered as the angle formed by the straight lines (e.g. the gray lines from 6a) to the visual target and to the fictive target (e.g. α_6 at location 6a).

mappings. That means a weighting algorithm computes for a given starting position S_i the relative proportion of both experts P_i and $1 - P_i$, respectively. Hence, P_i will reach its maximum of 1, if the test location is identical with the location of the expert, while P_i is set to its minimum of 0, if the test location is identical with the location of the other expert. In other words, aftereffect measured on other positions should never exceed the aftereffect on position 3a and 3b due to the modular approach.

However, the motor control system might solve the learning task in a more elegant way by accomplishing a spatial realignment. The mechanism was described as parameter adjustments in the spatial mapping functions that normally align corresponding positions among different spatial representations (e.g., visual and proprioceptive representations) that serve sensorimotor behavior (Redding & Wallace, 1996). In order to compensate for the opposing rotations, movement paths (dashed lines spreading from 3a and 3b in Figure 1) of the limb cross the midline in a larger distance compared to the distance of the visual target. Based on the as-

sumption that the sensorimotor space is coordinated in a unified amodal vectorial map (Paillard, 2005), this difference between the movement distance and the target distance would simply rescale the vectorial map. To this end, a fictive target (open circle on the top of Figure 1) for the motor map could be generated in order to compensate for the perturbation. Consequently, it is not necessary to learn two conflicting mappings. In this way, not only the perturbation is neutralized, the interference between the opposing rotations will also be harmonized by just changing one single parameter (i.e., the target height). This mechanism should be preferred by the motor control system because of its great efficiency.

Consequently, the aftereffect measured subsequent to the adaptation phase at other starting positions will be determined by their geometric location relative to the visual target and the fictive target. The aftereffect is quantified as the angular bias (α_i), which is a function of the height of the visual target (h_v), height of the fictive target (h_f), and distance of a given starting position (i) to the midline (d_i).

$$a_i = f(h_v, h_f, d_i) \qquad (1)$$

In the present study, the rotations were approximately set to $14.8°$ and h_v to 10 cm. This yielded a fictive target at a total height of 22 cm. Based on these constants, α_i can be calculated with equation 2.

$$a_i = \tan^{-1}(h_f / d_i) - \tan^{-1}(h_v / d_i) \qquad (2)$$

Magnitudes of angular bias for all starting positions are presented in Table 1.

The predictions made in Table 1 indicate that the motor bias on several test locations (i.e., 4 to 8) could be fairly greater than the aftereffect on the original adaptation location. We conducted two experiments (Exps. 1 and 2) to examine our assumption of spatial realignment by comparing the empirical data and the predictions.

Experiment 1

Experiment 1 aimed to examine the motor bias on test positions 6a and 6b following a motor learning phase on positions 3a and 3b. If the empirical data were in line with our assumption, the motor bias should be greater than the aftereffect on 3a and 3b, which cannot be explained by the modular approach. Since both modular decomposition and spatial realignment predict no aftereffect on position 0, it was included in the measure in the current experiment (as well as in Exp. 2) to serve as a plausibility check of the method.

Method

Participants. Seven right-handed students (4 females) from RWTH Aachen University volunteered to take part in Experiment

Table 1
Distance to Midline and Angular Bias of the Starting Positions

Start positions (i)	0	1	2	*3*	4	5	6	7	8
d_i (cm)	0	1	3	*5*	7	9	11	13	15
α_i (°)	0	3.26	9.57	*14.80*	18.73	21.43	23.10	23.99	24.30

1. Informed consent was solicited before participation. The mean age of participants was 21 years (ranging from 19 to 22 years) with a standard deviation of 1.2 years. Handedness was ensured with the Edinburgh Handedness Inventory (mean lateralization quotients of 71.3; Oldfield, 1971). All participants were naïve of the purpose of the study.

Apparatus and task. Participants controlled the cursor movement (a small blue disk, 4 mm in diameter) on the computer display with a stylus held in their right hand. The cursor movement was displayed on a 22" CRT color monitor (model: Iiyama Vision Master Pro514; resolution: 1024 × 768 pixels; refresh rate: 100 Hz) placed upright on the table with its center at participants' eye level and with a distance of about 65 cm in front of the participants. At the beginning of each trial, the valid starting position (5 mm in diameter) was illuminated in yellow, while the other starting positions stayed gray. After participants placed the cursor on this starting position and preserved the position for 500 ms, a pure tone (840 Hz) was released for 100 ms. It signalized that the trial was unlocked and the participants were instructed to initiate a flicking movement with their right hand as soon as possible. Participants should hit the target with the cursor as precisely as possible, by accelerating the cursor with a short flicking movement from the wrist, which determines the proximate direction of the cursor. The area within a radius of 2 cm around the starting position served as the area for movement initiation, inside of which the cursor was under control of stylus motion on the tablet. Once the cursor left this area, it began to slide on a constant velocity of 17 cm/s in a straight line holding its direction. After the cursor hit the target line, a hit score was displayed immediately next to the final cursor position to encourage the participants to execute an accurate movement. Depending on the deviation from target center, the (hit) score varied from 10 (maximum score with target center) to 0 (minimum score 50 mm or more out of range).

Procedure. A short exercise was given prior to the experiment, in order to get the participants acquainted with the stylus and the display. The experiment began with a baseline measure at five starting positions, that is, 3a, 3b, 6a, 6b, and 0. The measure was carried out in pairs and the sequence was randomized. Taking the sequence "6–3–0" for example, one block of five movements was performed at the location 6a followed by a block at the location 6b. Both blocks were performed with veridical visual feedback. After that another block was performed at 6a then at 6b; however, this time without any visual feedback. This process was repeated in the given sequence until baseline performance was measured for each starting position under each feedback condition twice. After a short break (approximately 1 min), participants adapted in 30 alternating blocks of five movements each to a CW and a CCW rotation of visual feedback, respectively, at location 3a and 3b. After the adaptation, movements were performed at all starting positions without visual feedback as postmeasure. The postmeasure was conducted again in randomized sequence for the three location pairs. As in the baseline measure, the sequence was repeated twice, so that the motor bias at each starting position was measured with two blocks à five trials.

As the dependent variable aiming errors were measured as angular deviations (in degree) from the ideal trajectory. The baseline measures with and without feedback were used to standardize the aiming error in the adaptation and postmeasure, respectively. Hereby, individual mean errors in the baseline measures were subtracted from the aiming errors in the adaptation phase and postmeasure.

The arithmetic sign of the aiming error at each location was determined relative to the rotation direction. For locations 3a and 6a, a positive angular deviation indicated a CW deviation, which was in accordance with the direction of the rotation imposed to 3a, whereas a negative value indicated a CCW deviation, which was opposite to the rotation imposed to 3a. For location 3b and 6b, a positive value indicated a CCW deviation and a negative value indicated a CW deviation, since the CCW rotation was imposed to 3b. For position 0, aiming error was positive if the deviation was clockwise and was negative if the deviation was counterclockwise.

Results and Discussion

The adaptation curve representing the angular error as a function of adaptation blocks is illustrated in Figure 2. A single power function was fitted to the data and yielded a R^2 of .86. All participants were able to adapt to the rotation by reducing the initial aiming error to a remarkably low level.

Angular deviations in the postmeasure were standardized for each individual to their respective baseline performance. A 2 (left vs. right side) × 2 (3 vs. 6 position) repeated measures ANOVA yielded a significant main effect of starting position ($F_{(1, 6)} = 34.84$, $p < .001$, $\eta^2 = .85$), but neither a main effect of side ($p > .61$) nor an interaction of both factors ($p > .21$). The angular bias at position 0 was in average $-2.58° \pm 1.28°$ (Mean ± SE) and did not differ from 0 significantly ($p > .09$; see Figure 3), which indicated that the movements at position 0 were not affected by the adaptation. At location 3a and 3b, participants showed a noticeable aftereffect of $9.94° \pm 1.78$ and 9.98 ± 1.95, respectively. More importantly, these were not as large as the motor biases at location 6a (15.62 ± 2.85) and 6b (12.31 ± 2.01). T tests confirmed significant difference regarding motor bias between 3a and 6a ($t_{(6)} = 3.43$, $p < .007$, one-tailed) and between 3b and 6b ($t_{(6)} = 2.15$, $p < .038$, one-tailed).

Obviously, the modular approach is not able to account for the findings of Experiment 1, since the weighting factor P in the course of integration of motor primitives would never exceed the maximal value of 1. Consequently, the motor bias at a test location
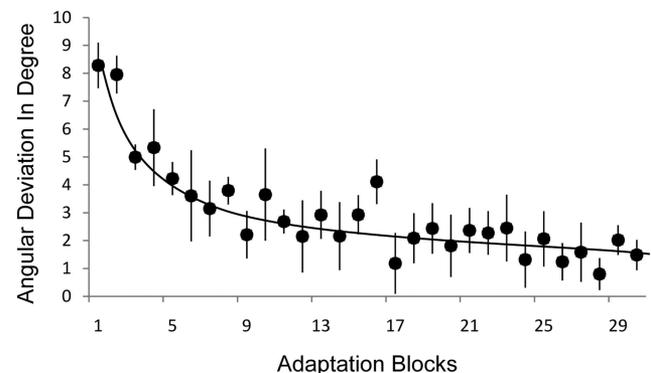

Figure 2. Mean aiming errors (with standard errors) in degree during the adaptation phase of Experiment 1. Every data point represents the average of five consecutive trials in an experimental block across all participants. A single power curve was fitted to the data.
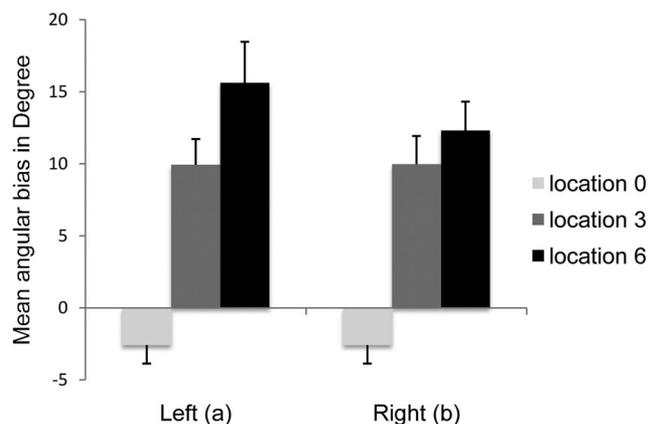
Figure 3. Mean motor bias (with standard errors) in degree at five test locations (location 0 left is equivalent to location 0 right). The motor bias at each starting position was standardized individually by subtracting the respective baseline performance from the angular deviation in the postmeasure.

could never be larger than the aftereffect at the training location. Since the aftereffect at starting positions 6a and 6b was evidently larger than that at 3a and 3b, the modular decomposition approach (Ghahramani & Wolpert, 1997) apparently cannot be applied to account for the current data. On the contrary, the spatial realignment would produce greater angular bias at starting positions 6a and 6b than at 3a and 3b, as shown in Table 2. Thus, the current result supports the spatial realignment approach.

It should be noted, however, that a similar pattern of finding could have resulted from the so-called "use-dependent learning (or plasticity)." It describes the phenomenon that repetition of the newly adapted movement induces directional biases toward the repeated movement (Verstynen & Sabes, 2011). Since no explicit model of the perturbation is necessary, it is considered to be model-free and usually "hidden" behind the learning processes based on an update of internal models (Huang et al., 2011). If the repeated movement direction at the starting position 3a or 3b (dashed arrows pointing to the fictive target in Figure 1) had been simply carried over to the ipsilateral test location 6a or 6b, as assumed by "use-dependent plasticity," the resulted motor bias would be larger than the aftereffect at the original starting position, which is, at least qualitatively, in accordance with the observed data. However, since the aftereffect was only tested at location 6a or 6b, it was not possible to distinguish between the spatial alignment approach and the use-dependent approach. This aspect was sought in the next experiment.

Experiment 2

Experiment 2 aimed to compare use-dependent plasticity and spatial realignment regarding their predictive power for the motor

biases in the postmeasure. To this end, the examination of motor bias was extended to further test positions (0, 1a, 1b to 8a, 8b as shown in Figure 1) following an adaptation phase again at positions 3a and 3b. The mean motor bias at a test location i predicted by use-dependent plasticity is quantified in equation 3, in which θ_{rep} represents the repeated movement direction and θ_i represents the actual direction from a starting position i to the target.

$$a_i = \theta_{rep} - \theta_i \qquad (3)$$

By assuming optimal adaptation and complete transfer, the predicted α_i based on use-dependent plasticity are computed and listed in Table 2. In this way, predictions based on use-dependent plasticity and on spatial realignment were compared to the empirical data.

Method

Participants. Ten right-handed students (8 females) from RWTH Aachen University volunteered to take part in Experiment 2. Informed consent was solicited before participation. The mean age of participants was 23 years (ranging from 19 to 30 years) with a standard deviation of 3.0 years. Handedness was ensured with the Edinburgh Handedness Inventory (mean lateralization quotients of 76.7; Oldfield, 1971). All participants were naïve to the purpose of the study.

Procedure. In Experiment 2 participants performed the same task with the same apparatus as in Experiment 1. The general procedure followed again a baseline, adaptation, and postmeasure schedule. However, because of the raised number of test locations and according to the increased the duration of experiment, Experiment 2 was split in two sessions separated by 3 to 5 days. The baseline measure was conducted in the first session following the same procedure as described in Experiment 1. The measure was carried out in pairs (a and b) with randomized sequence of nine locations, and baseline performance was measured for each starting position under each feedback condition twice. The second session began with an adaptation phase, which was completely identical with the adaptation phase of Experiment 1. Following the adaptation, the postmeasure was conducted again in randomized sequence for the nine location pairs. As in the baseline measure, the sequence was repeated twice, so that the motor bias at each starting position was measured with two blocks à five trials. The postmeasure was carried out without visual feedback. As a dependent variable, angular deviations α_i at each starting position i were calculated according to the same rules described in Experiment 1. The ratios $\alpha_i : \alpha_3$ were computed for statistic analysis.

Results and Discussion

Figure 4 shows the mean angular deviations as a function of adaptation blocks. A single power function was fitted to the adaptation data and yielded a R^2 of .79.

Table 2
Predicted Aftereffects (α_I) Based on Use-Dependent Plasticity

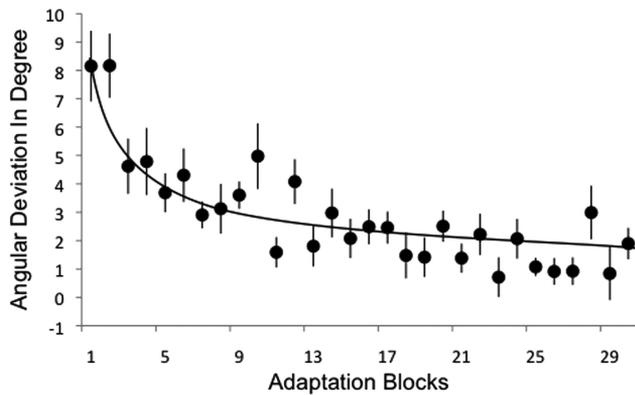| Start positions (i)	0	1	2	*3*	4	5	6	7	8
α_i (°)	0	−6.06	4.93	*14.80*	23.22	30.22	36.96	40.67	44.55

Figure 4. Mean aiming errors (with standard errors) in degree during the adaptation phase of Experiment 2. Every data point represents the average of five consecutive trials in an experimental block across all participants. A single power curve was fitted to the data.

We first analyzed the angular deviations for the starting positions at the left and right side of the midline separately. A 2 (left vs. right side) $\times$ 8 (positions 1 to 8) repeated measures ANOVA yielded a significant main effect of starting position ($F_{(7, 63)} = 8.88$, $p < .001$, partial $\eta^2 = .50$). Since the ANOVA showed neither a main effect of the factor side ($p > .22$) nor an interaction ($p > .26$), we merged the data of different side by computing a pairwise mean value α_i for each starting position pair. The average aftereffect α_3 at location 3a and 3b was approximately $11.5° \pm 1.26°$. Further, $\alpha_i:\alpha_3$ ratios were computed individually. The resulted mean ratios across all participants are listed in Table 3.

Figure 5 shows both predicted and observed $\alpha_i:\alpha_3$ ratios as a function of the starting position. *T* tests yielded significantly smaller ratios than 1 at location 0 ($t_{(9)} = 6.15$, $p < .001$, one-tailed) and location 1 ($t_{(9)} = 6.32$, $p < .001$, one-tailed), and a tendency at location 2 ($t_{(9)} = 1.40$, $p < .10$, one-tailed). More importantly, as predicted by spatial realignment, the empirical curve exceeded the crucial value of 1. *T* tests yielded significant larger ratios than 1 at location 5 ($t_{(9)} = 2.34$, $p < .026$, one-tailed) and location 6 ($t_{(9)} = 2.15$, $p < .031$, one-tailed), and a tendency at location 7 ($t_{(9)} = 1.39$, $p < .10$, one-tailed). The correlation between the predicted and observed curves was approximately .95 ($p < .001$), indicating a substantial coherency. Therefore, these results support the spatial realignment approach.

Use-dependent plasticity, on the other hand, provided prediction that was far less sufficient for the generalization across different starting locations ($r = .32$, $p > .43$). One may propose that the generalization of use-dependent plasticity decays with angular separation in a manner similar to Gaussian-like function as shown by population coding models (Georgopoulos, Schwartz, & Kettner,

1986; Tanaka, Sejnowski, & Krakauer, 2009; Verstynen & Sabes, 2011) and that the weighted generalization effect of use-dependent plasticity would provide a better fit to the empirical data. We conducted a simulation based on various Gaussian tuning widths and the results could not confirm the assumption. More importantly, adjusting the tuning width did not change the fact that a transfer of use-dependent plasticity would cause a negative aftereffect on starting position 1, which is not compatible with the empirical data.

However, the completeness of generalization of spatial realignment, as suggested by many previous studies (e.g., Redding & Wallace, 2006), has not been ensured yet. So far, the generalization was assessed for a set of novel starting positions, while the target remained the same. The generalization needs to be demonstrated to untrained targets as well, since due to the single-target scenario in Experiments 1 and 2, modification of the mapping parameters could be achieved in at least two different ways. One possibility is to relocate the target in the action space to compensate for the visual perturbation. This kind of simplified realignment is plausible, because the programming of the short-ranged and open loop flicking movements relies merely on directional information and the realignment of the target position alone would be sufficient to specify the movement direction. Hence, it modifies only one parameter of the spatial mapping, namely the target location, while all other mapping parameters remain the same. This solution is target-specific, and consequently, should not affect subsequent movements aimed to new target locations. Another possibility to establish the new mapping is to rescale the entire action space. In the scenario of the present study, it means to approximately double the y-scale of the action space. This workspace-based solution should affect all subsequent movements, even if the visual target is not the same as in the learning phase, because such parameter adjustment is characterized by complete transfer of training with a subset of positions to the entire domain of a transformation (Bedford, 1989, 1993). Experiment 3 was conducted to pursue this question by comparing both possibilities.

Experiment 3

As aforementioned, the spatial realignment observed in the prior two experiments could have been achieved either by target-related realignment or by rescaling the entire space. For the latter case, adaptation would be transferred to other targets. To this end, Experiment 3 focused on generalization of adaptation to a set of novel targets while the starting positions were kept constant.

Method

Participants. Ten right-handed students (8 females) from RWTH Aachen University volunteered to take part in Experiment 3.

Table 3
Predicted and Observed Motor Bias (Mean Value of Ratios)

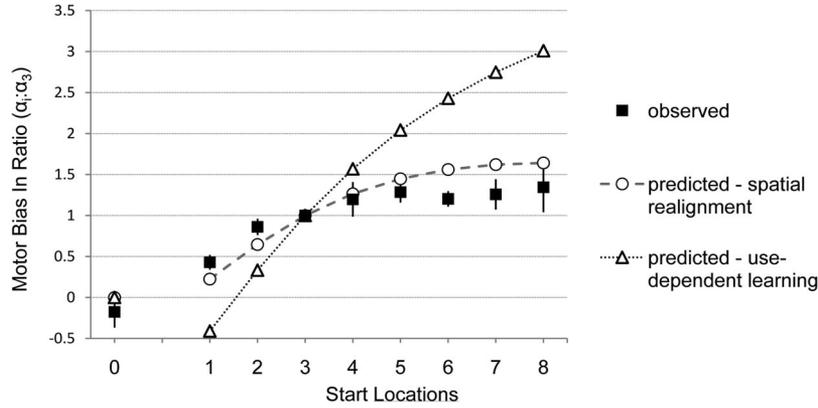| Start positions (i)	0	1	2	3	4	5	6	7	8
Prediction by spatial realignment	0	0.225	0.647	1	1.266	1.448	1.561	1.621	1.642
Prediction by use-dependent plasticity	0	−0.410	0.333	1	1.569	2.042	2.430	2.748	3.010
Observed ratio ($\alpha_i: \alpha_3$)	−0.176	0.430	0.861	1	1.197	1.286	1.202	1.258	1.345

Figure 5. Predicted data based on spatial realignment (dashed line with open circles), predicted data based on use-dependent plasticity (dotted line with open triangles), and observed (black squares) $\alpha_i:\alpha_3$ ratio for each starting position i ($i = 0, 1, 2 ... 8$). Error bars of the observed data represent the standard errors.

Informed consent was solicited before participation. The mean age of participants was 23 years (ranging from 20 to 30 years) with a standard deviation of 3.3 years. Handedness was ensured with the Edinburgh Handedness Inventory (mean lateralization quotients of 82.2; Oldfield, 1971). All participants were naïve to the purpose of the study.

Setup and procedure. The experimental setup is illustrated in Figure 6. In each trial, participants performed a flicking movement from one of two starting positions (A and B) to one of 10 targets (T_1 to T_{10}).

The experiment was scheduled in two sessions separated by 3 to 5 days. Session 1 contained a measurement of individual baseline performance with and without visual feedback for each start and target combination—four consecutive blocks for each target. The first of the four blocks consisted of five trials for a start and target combination, followed by another block to the same target but from the other starting position. In both blocks visual feedback of the cursor was provided. Subsequently, both blocks were repeated but this time without visual feedback. The targets were presented in a randomized sequence and the starting position switched after every block. The sequences of the starting position (A→B→A... vs. B→A→B...) were counterbalanced across participants. The same target sequence (i.e., each start and target combination) was measured twice. This procedure resulted in 80 blocks à five trials for the baseline measure.
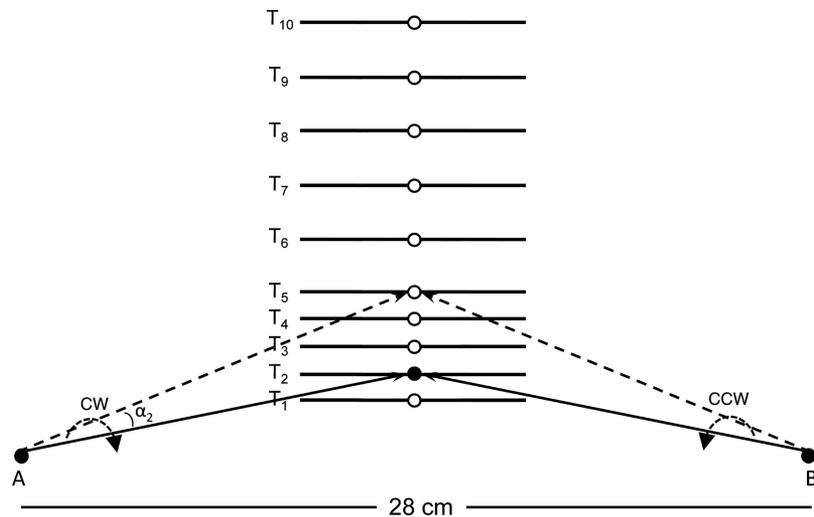

Figure 6. The experimental setup of Experiment 3. Ten visual targets (T_1 to T_{10}) were presented randomly. The heights of the targets are listed in Table 4. Flicking movements were performed to a given target either from start A or start B. The starting positions were 28 cm apart from each other. During adaptation, CW and CCW rotations (both 11.1°) were applied at starting positions A and B, respectively. According to spatial realignment, the adaptation would double the height of T_2 on the modified mapping (i.e., dashed lines to T_5). If spatial realignment is not target-related but rescales the entire workspace, it should affect the subsequent movements to the other targets and cause different aftereffects, which could be predictively quantified (Table 4).

Session 2 began with 30 blocks of visuomotor adaptation to opposing rotations: 11.1° CW on Start A and CCW of the same size at start B. The starting position switched after each block and again the sequences of the starting position were counterbalanced across participants. Since the target remained the same (T_2), which was located 3 cm above to the starting positions, adaptation to the opposing rotations should result in a virtual target (which the dashed arrows are pointing to) 6 cm to the starting positions according to spatial realignment. The height (h_i) of each given target T_i is listed in Table 4. The lateral distance (d) of the starting positions to the midline was constantly 14 cm. Hence, theoretical angular bias α_i of T_i can be calculated with equation 4 based on assumption of a fully accomplished spatial realignment.

$$a_i = \tan^{-1}(h_i/d) - \tan^{-1}(2 \times h_i/d) \qquad (4)$$

Once the adaption was completed, aftereffects without feedback were measured for each target from both starting positions in two consecutive blocks. Again, the targets were presented in a randomized sequence and the starting position switched after each block. The postmeasure procedure was also repeated twice, so that each start and target combinations was tested twice. The postmeasure was tested without visual feedback.

Empirical aiming errors (α_i) were calculated as angular separation between the optimal path and the observed trajectory for a given start and target combination. The baseline measures with and without feedback were used to normalize the individual aiming error in the adaptation and postmeasure, respectively. The arithmetic sign of the aiming error at each location was determined relative to the rotation direction: for adaptation, angular deviations in the same direction as the respective rotations were signed positive, and vice versa; for postmeasure, angular deviations in the opposite direction as the respective rotations were signed positive, and vice versa. The ratios ($\alpha_i : \alpha_2$) of postmeasures were computed and compared to the predicted values (Table 4). The predicted aftereffects were computed according to the assumption that the spatial realignment rescales the entire action space rather than target-related. If the spatial realignment is purely target-specific, there should be no generalization effect; in other words, no aftereffects to other targets should be observed. Consequently, the α_i to α_2 ratios would be always 0, or at least significantly smaller than 1.

Results and Discussion

Figure 7 illustrated the decline of aiming errors during the adaptation. The ANOVA showed a significant main effect of experimental block ($F_{(29, 261)} = 2.21$, $p < .009$, $\eta^2 = .20$). A single power function was fitted to the data ($R^2 = .53$).

As aforementioned, standardized aftereffects were computed by subtracting the baseline error from the respective angular deviation registered the postmeasure. At first, we computed the aftereffects
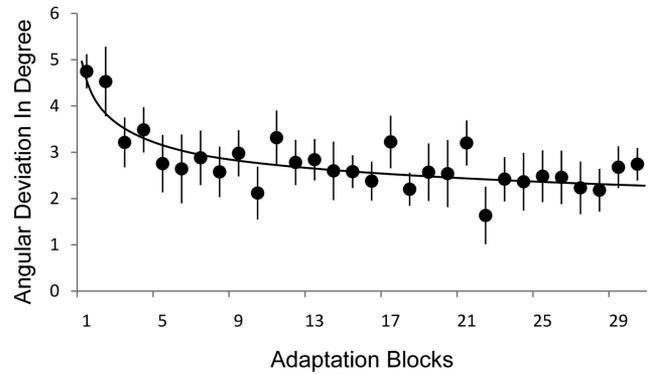

Figure 7. Mean aiming errors (with standard errors) in degree during the adaptation phase of Experiment 3. Every data point represents the average of five consecutive trials in an experimental block across all participants. A single power curve was fitted to the data.

at the starting positions A and B separately. A 2 (left vs. right side) × 10 (targets 1 to 10) repeated measures ANOVA yielded neither main effect of starting position ($p > .06$) nor any starting position by target interaction ($p > .55$), and hence we merged the data of different starting positions in pairs by computing a mean value for each target.

Observed aftereffect (α_i) to T_2 was approximately 5.7° ($\pm 1°$). Observed ratios of $\alpha_i : \alpha_2$ were calculated individually and the mean values are listed in Table 5. Figure 8 visualized the predicted (open circles) and observed ratios (filled squares). Apparently, the predicted values fit the empirical means very well. Pearson correlation showed significant fit between both datasets ($p < .001$. $r = .93$). However, the expected generally upward trend of aftereffect with increasing target height was not supported by the ANOVA, since no main effect of target was found ($p > .21$), probably due to the large variance in the data. Taken together, spatial realignment appears to affect the entire domain of transformation (Bedford, 1989, 1993). More importantly, compared to other approaches spatial realignment provides the most probable explanation for the present pattern of finding. First, there was no decline of aftereffect with increasing dissimilarity between training and generalization conditions, which would be predicted by both the modular approach (Ghahramani & Wolpert, 1997) and the population coding model regarding visuomotor generalization (Tanaka et al., 2009). Second, use-dependent plasticity would predict negative aftereffects on T_3 to T_{10}, which was obviously not the case.

General Discussion

In the present study a sensorimotor adaption scenario was reexamined and extended. It was first investigated by Ghahramani

Table 4
Predicted Directional Bias (α_I) Based on Spatial Realignment Extended to the Entire Action Space

Targets (i)	1	2	3	4	5	6	7	8	9	10
h_i (cm)	2	3	4	5	6	8	10	12	14	16
α_i (°)	7.9	11.1	13.8	15.9	17.4	19.1	19.5	19.1	18.4	17.6

Table 5

Predicted and Observed Motor Bias (Mean Value of Ratios) Based on Spatial Realignment Extended to the Entire Action Space

Targets (i)	1	2	3	4	5	6	7	8	9	10
Vertical distance (cm)	2	3	4	5	6	8	10	12	14	16
Predicted ratio by spatial realignment	0.71	1	1.24	1.43	1.57	1.71	1.75	1.72	1.66	1.58
Observed ratio (α_i: α_2)	0.88	1	1.03	1.36	1.23	1.34	1.43	1.51	1.36	1.37

and Wolpert (1997), which was considered as classical evidence for the modular organization of adaptation to visuomotor rotation. Modular approaches (Haruno et al., 2001; Jacobs et al., 1991; Miall, 2002) suggesting the acquisition and retention of two different visuomotor mappings as separated control modules were thought to perfectly account for this scenario. However, comprehensive review of prior research highlighted at least two other theoretical approaches providing alternative explanation, namely use-dependent plasticity (Huang et al., 2011; Verstynen & Sabes, 2011) and spatial realignment (Redding & Wallace, 2001, 2002, 2006). Predictions based on the three approaches regarding the transfer of acquired mapping to a subset of test locations differ strongly from each other. The predictions were compared with empirical data in the first two experiments. The results were in line with our assumption that spatial realignment should be preferred by the adaptive control system due to its efficiency. The third experiment examined whether spatial realignment is target-specific or affects the entire action space. The data suggested that spatial realignment rescaled the entire action space rather than being target-specific.

In Experiment 1, postmeasure showed significantly larger motor bias at test position 6a and 6b than the aftereffect at the original locations 3a and 3b. According to the modular approach, transfer was accomplished through weighted integration of two control modules based on a probabilistic estimation for transfer to each test location. This process entails the implication that for a given test location the weighting factor of a particular mapping would never exceed the theoretical maximum of 1. In other words, motor bias at an arbitrarily chosen test location would never be larger than the aftereffect at the original location used for adaptation. The

fact that motor bias at test locations exceeded the aftereffect at the original locations was in accordance with the prediction made by spatial realignment. Obviously, the modular approach was not able to account for the results of Experiment 1. However, it does not contradict the prediction based on use-dependent plasticity, which presumes that the repeated movement direction would be carried over to subsequent movements. Hence, the two remaining possibilities were compared in a further experiment.

In Experiment 2, the number of test locations were increased to eight pairs. Predictions made by use-dependent plasticity and by spatial realignment could be captured by a respective function of the starting position as illustrated in Figure 5. The data predicted by spatial realignment correlated with the empirical data very well and provided a much better fit than use-dependent plasticity. Furthermore, post hoc analysis strengthened arguments against modular approach by showing that transfer ratio at several test locations again exceeded the predicted maximum of 1.

In line with our hypothesis, these findings supported clearly a spatial realignment in the course of adaptation. As we argued earlier, the spatial realignment provided a most efficient solution for the adaptation and transfer scenario of the present study. According to the modular approach, two separate internal models of visuomotor mappings must be learned and stored separately. Consequently, computational resources have to be allocated, not only to learn two internal models but also to prevent the interference between them. Instead, by using spatial realignment, the same learning effect could be achieved with a linear transformation of action space coordinates. On the one hand, this simple transformation neutralizes the conflict of the opposing rotations and thereby reduces the computational load for the strategic
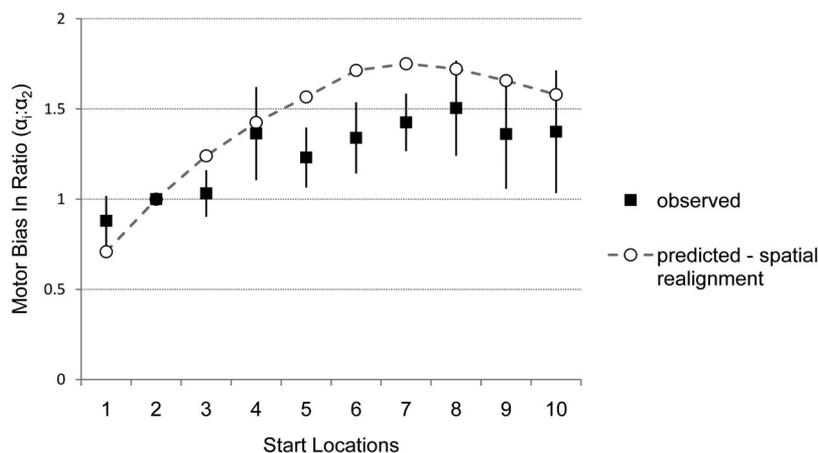

Figure 8. Predicted (dashed line with open circles) and observed (black squares) α_i:α_2 ratio for each target *i* ($i = 1, 2 \ldots 10$). Error bars of the observed data represent the standard errors.

perceptual-motor control (Redding, Rader, & Lucas, 1992; Redding & Wallace, 2002); and on the other hand, it facilitates transfer by determining the mapping parameters for later movements in the same task-work space. Considering the basic rule of efficiency, it is no wonder that the adaptive control system would prefer the spatial realignment as a more efficient way to deal with this specific situation.

At this point, an interesting question to be raised is where and how in the CNS is decided to choose one optimal option from a variety of available solutions. Actually, we think that the term *choose* cannot appropriately reflect the underlying process. It is because we envisage that in our specific experimental setup, the modification of the veridical internal model to develop two different internal models in order to compensate for the opposing rotations and the accomplishment of a new spatial alignment present two consecutive stages of adaptation rather than mutually exclusive options to be evaluated and selected by the CNS. We conjecture three distinct processes that are concurrently activated to encounter the opposing visuomotor rotations: first, explicit modification of the internal models presents the short-term process, which is centrally located and instantaneously effective to encounter a large mapping discrepancy but cognitively demanding; second, implicit adjustment of the internal models presents a long-term process and leads to the development of two different internal models; finally, spatial realignment presents another long-term process, which is driven by the spatial discordance rather than error (Ebenholtz, 1968; Redding & Wallace, 2002) and replaces the separate models through a modified spatial alignment. The first two processes are common in visuomotor adaptation (Hegele & Heuer, 2010; Mazzoni & Krakauer, 2006; Sülzenbrück & Heuer, 2009), while the spatial realignment is unique to the current experimental setup. The adaptivity of spatial alignment is supposed to have its origin in the synaptic plasticity of the multimodal neurons in the cortical associative areas, where polysensory information is processed (Paillard, 2005). Due to the changed mapping during the exposure to the visuomotor rotations, neurons in those areas show activity changes in response to sensory inputs of various origins (e.g., visual and proprioceptive) and obtain a novel coactivation pattern. According to the Hebbian theory, transmission power of repetitively coactivated synapses will be progressively reinforced (Hebb, 1961). Since the processes of the spatial alignment may possibly produce twice as many repetitions of those synaptic activations (the same activations across two opposing rotations) compared to the processes of switching between two internal models (different activations for each rotation), the spatial realignment yields increasing neural representations and replaces the processes of developing and maintaining separate models in the long term.

Based on the above postulate, the repetitive advantage of spatial alignment over the modular approach is mediated by the symmetry of the visual workspace. Consequently, this advantage is best materialized when the visual workspace is perfectly symmetric, which means that the visuomotor rations need to be symmetric as well. Namely, the opposing angles of the rotations assigned to the left and the right starting positions must have the same extent. In fact, the present experimental setup assured such symmetry. Based on these considerations, it is interesting to access the adaptation and its generalization after exposure to opposing rotations, each of which has a different magnitude, so that the symmetry is attenuated or even absent. Generally, two possibilities are conceivable.

Different rotations would prohibit the congeneric synaptic organization and the formation of a new mapping. In this case, maintaining two different internal models and contextual switching between them are necessary as suggested by the modular approach. Alternatively, a common mapping could be formed with help of linear interpolation between the two trained positions as reported by Bedford (1989, 1993). We prefer the latter case and intend to examine this assumption in future work.

We further specified the underlying mechanism of spatial realignment by comparing two alternative approaches (target-related realignment vs. rescaled action space) in the third experiment. Hereby, aftereffects to a set of different targets were quantified and compared with the predicted data based on the assumption that spatial realignment should rescale the entire action space rather than a single target. The results showed clear generalization of adaptation to subsequent movements toward other targets and substantial fit between empirical and predicted data. It could be reasoned that spatial realignment is not strictly target-related but affects the entire action space, which is apparently rescaled to fit a novel visuomotor mapping. This observation is consistent with the notion by Bedford (1989), which suggests that a mapping consists of specialized rules connecting the entire length of two dimensions rather than a collection of individual associations.

Finally, it remains open whether and to what extent the observed spatial realignments in our experiments are related to the particularity of flicking movements. These were ballistic movements, because the movement execution in our experiments was completed normally within 70 to 90 ms, which is evidently too short for movement corrections that occur in average 135 ms after the presentation of visual error information (Carlton, 1981). In this case, online error correction, and more importantly, online error monitoring were precluded. Nevertheless, the realignment observed in all three experiments together confirmed the notion (e.g., by Redding & Wallace, 1997) that the realignment is not driven by detection of movement errors (i.e., differences between desired and actual outcomes) for each specific rotation at a give target but by general misalignment detection. Normally, misalignment detection requires comparison of corresponding positions among spatial representations. For example, one can detect discordance between visual and proprioceptive spatial representations by comparing visual target coordinates that initiate a feedforward limb controller with the actual proprioceptive coordinates of the target achieved under error-corrective feedback control (Redding & Wallace, 2003). Compared to closed-loop movements (e.g., aimed reaching or pointing movements), the amount of sensory information about corresponding spatial positions during a flicking movement is very limited because of the short range of hand motions compared to that of feedback cursor motions. Therefore, it is likely that using closed-loop actions would obtain more rapid realignment. Hence, comparison between a flicking task and classical pointing task could be an interesting object for future work.

Conclusion

In three experiments, participants adapted to opposing rotations when performing aimed flicking movements. Aftereffects were measured as postadaptation directional bias and compared with predicted data based either on modular adaptation, use-dependent plasticity, or spatial realignment. Predictions based on spatial

realignment showed the best fit to the empirical data, which was consistent with our hypothesis, although the adaptation scenario applied in the current study has been considered as a typical case for modular adaptation. Consequently, efficiency appeared to be a crucial criterion for the optimal motor control and visuomotor adaptation.

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