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RESEARCH ARTICLE

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# Altering the visuomotor gain

## Evidence that motor plans deal with vector quantities

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**Abstract** Two experiments investigated the effects of providing nonveridical knowledge of the results (KR) in a visuomanual task in which participants pointed to briefly (200 ms) presented targets without seeing their hand. By showing after each trial the movement endpoint displaced radially with respect to its true position, we were able to alter progressively the gain of the visuomanual loop. In experiment 1, the KR was provided only for transversal movements and for one target distance, but the effect generalized to all directions and all distances. Moreover, it also generalized to the other hand that had never been biased. In experiment 2, nonveridical KR was supplied for movements along the two major diagonals which require sharply different muscle synergies. The transfer to other directions and to the other hand was equally substantial. It is argued that the results support the vector coding hypothesis, which holds that the input to the motor execution stage is supplied by specifying independently the amplitude and the direction of the vector from the initial to the final position in an extrinsic frame of reference. We also discuss the possible brain structures involved in the biasing action of the KR.

**Keywords** Reaching movements · Vector coding · Visuomotor transformation · Amplitude control · Generalization · Human

## Introduction

Understanding how we point to a target in the near workspace is still a challenging problem. The difficulty originates from the fact that vision and motor control utilize sharply different frames of reference. Moreover, the contribution of nonvisual information is not fully elucidated. Although seeing the initial hand position vision has a beneficial effect on accuracy, the kinesthetic sense of position alone can guide pointing movements when the hand is out of sight. It is not known yet whether vision merely refines kinesthetic inputs or provides more specific information.

The problem of how the visual and kinesthetic input variables are specified ought to be distinguished from the problem of how the motor plan is set up and executed. Models of the sensorimotor transformations underlying pointing behavior differ mostly by the emphasis placed on either issue. The experiments reported here test the so-called *vector coding hypothesis* (Vindras and Viviani 1998), which focuses on the format with which the information provided jointly by vision and kinesthesia is supplied to the motor system. The basic tenets of the model are the following:

1. Both the target and the initial hand position are specified in extrinsic space, within a common frame of reference anchored to the body.
2. The relevant input to the motor system is supplied in a vector format, by specifying amplitude and direction of the shortest path from the initial to the final hand position.
3. Amplitude and direction are independently controlled parameters of the motor plan.

Ultimately, the motor plan is always implemented by acting on arm joints through a combination of active torques. Moreover, intrinsic coordinates may be involved in deriving an extrinsic representation of the initial hand position from visual and proprioceptive signals (van Beers et al. 1996; Paillard and Brouchon 1974; Rossetti et al. 1995; Vindras et al. 1998). However, according to the vector model, intrinsic coordinates (i.e., joint angles) play no direct role in the planning process. By contrast, other models (Flanders et al. 1992; Rosenbaum et al. 1995; Todorov 2000) hold that target position is mapped into

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the desired final posture defined in intrinsic coordinates already at an early stage of the planning process. The finding that, during reaching, the activity of many cells in the motor cortex correlates mostly with the associated joint angles, supports this view (Scott and Kalaska 1997). However, other data suggest that the processing involving joint angles might simply set the stage for a subsequent phase of space-based planning (Rogosky and Rosenbaum 2000; Rosenbaum et al. 2001).

Specific predictions can be derived from points 1–3 by qualifying further the nature of the system of coordinates (Cartesian, polar, etc.), the roles of visual and kinesthetic clues in determining the initial hand position, and the strategies for controlling muscles synergies. For our purposes, however, we only need to consider some key predictions of the vector coding hypothesis that are not contingent upon these further options. In particular, we focus on the expected response to experimental manipulations that alter the relationship between the hand-target distance perceived visually and the amplitude of the movement.

When pointing is accurate (i.e., under most normal circumstances), perceived distance calibrates movement amplitude so that the ratio of the latter to actual distance – usually referred to as *visuomotor gain* – is close to 1. Visuomotor gain is intrinsically unstable. In sequences of movements, unless the accuracy of the pointing is confirmed after each movement (by vision or by other means), the gain drifts spontaneously, leading to large overestimations of the hand-target distance (Vindras and Viviani 1998). Moreover, the gain can be either decreased or increased by manipulating the visual feedback. Bock (1992) has demonstrated that, if the perceived extent of a pointing movement is made larger than the actual one, the amplitude of the movement is progressively reduced. The modification of visuomanual gain induced in the adaptive phase of the experiment persists in the postadaptive phase. Although the modification was induced only along the horizontal direction, it generalized to all directions. Moreover, adaptation induced for one movement amplitude transfers to untrained amplitudes (Bock and Burghoff 1997). Adaptation to altered visual feedback has been investigated also by Pine et al. (1996), who considered both the effect of varying the visuomotor gain and the effect of shifting the perceived direction of the movement. Again, it was found that movement amplitude adapts quickly, and that the adaptation induced along one direction generalizes to all directions. By contrast, adaptation to rotations is poor. This divergent behavior has been confirmed by a more recent study (Krakauer et al. 2000).

The finding that adaptive gain changes generalize to all directions fits well with all variants of the vector coding hypothesis. Specifically, it is congruous with the behavior predicted from assumption 2 (relevant input to the motor system is supplied in a vector format, by specifying amplitude and direction of the shortest path from the initial to the final hand position). Conversely, the finding is inexplicable if one assumes that the input to the motor system is provided as a set of assignments for joint angles. However, the support to the model provided by previous experiments is somewhat weakened by the experimental conditions adopted in those studies.

Three aspects of Bock's (1992) experiment limit the general validity of its conclusions. First, movements in the preadaptation phases were dramatically hypermetric (mean gain 1.91). Such large errors – never occurring in real life – are likely to be contingent upon the experimental condition. Second, visual feedback during the adaptation phase was not perceived as veridical, because the indicated velocity of the finger was one-quarter of the real one. As a consequence, adaptation was incomplete (gain in the postadaptation phase was 1.48 instead of the required 0.5). Finally, movement amplitude (15 to 35 mm) was far smaller than that of typical pointing and reaching gestures. As for the experiments of Pine et al. (1996) and Krakauer et al. (2000), movement space (horizontal plane) was dissociated from the target space (vertical screen), introducing one additional step with respect to most real-life conditions, namely the mapping between orthogonal systems of reference. Because of this dissociation, both studies manipulated visual feedback to an extent (between 35% and 50%) that would be unrealistic when the stimulus and action plane coincide. Moreover, it is questionable that proprioceptive information can be brought to bear under these conditions.

The two experiments reported here investigate the vector hypothesis using again the altered feedback technique. Unlike previous studies, however, we attempted to reproduce as faithfully as possible the conditions prevailing in real life. Experiment 1 explores the adaptive properties of the visuomanual loop by letting, after some of the trials, the participants compare the final hand position with the actual target position. Unknown to them, however, endpoints were sometimes displaced by small, realistic amounts. The goal of the experiment was to show that an adaptation induced along the frontoparallel axis generalizes to other directions even when proprioceptive information about hand position can be directly compared with visual information about hand position. In general, hand movements such as those considered here mobilize simultaneously both elbow and shoulder joints. Furthermore, for most pairs of movement directions, there is an overlap between the required sets of synergies. Experiment 2 tests the possibility that the generalization of adaptation is due to this overlap by considering movements along the two diagonal directions (SW-NE and SE-NW) for which the synergies are as distinct as possible. The first diagonal requires mostly rotations at the elbow joint, the second one almost a pure rotation of the shoulder. Finally, both experiments test the key prediction of the vector coding hypothesis that adaptive gain modulations induced in one hand transfer also to the opposite hand.

## Methods

### Participants

Six right-handed individuals (four women, two men; aged 22–29 years) participated in experiment 1. Six different individuals (four women, two men; aged 19–41 years) participated in experiment 2. Participants had normal or corrected-to-normal vision and had never participated to similar tests. They were paid for their services. The experimental protocol was approved by the Ethical Committee of the University of Geneva. Informed consent was obtained from the participants. However, we did not disclose the goal of the experiment.

### Apparatus and data analysis

The experiments were conducted in a quiet room kept in very dim light. Participants sat in front of a large (1.1×0.8 m), translucent digitizing table (Numonics Corporation, Montgomeryville, Pa.; model 2200-2436; nominal accuracy 0.025 mm; sampling frequency 200 samples/s) mounted horizontally (Fig. 1). The position of each participant relative to the table was controlled by adjusting the height and position of an orthopedic seat, which provided a stable, comfortable support for both buttocks and knees. During the testing, the elbow of the active arm was supported by the table in the normal writing posture. By holding the recording pen (20 cm long, 1 cm in diameter, weight 20 g) with their preferred grip, participants could point to any location on the table within a distance of approximately 70 cm from the sternum. The *x*-*y* coordinates of the pen's tip were recorded as long as the tip remained within 1 cm from the table surface. In addition, a pen-up/pen-down signal was delivered when the pen was pressed gently on the table. Two 4-mm-wide laser spots were controlled independently by galvanometric mirrors (General Scanning, Watertown, Mass.; G300DT with CX660 amplifier) driven by a 12-bit DA converter. One spot, backprojected on the table from below, indicated the (invariable) starting position, which was also identified tactually by a 4-mm-wide, thin felt disc glued on the table. In some trials, this spot was also used to indicate the movement endpoint. The second spot was projected on a translucent screen placed horizontally 60 cm above the digitizing table and was used to identify the target position. A half-silvered mirror placed horizontally halfway between the screen and the table reflected this spot, providing a virtual image on the table surface. At the same time, the mirror prevented participants from seeing their hand. When the translucid screen was illuminated dimly from above, both spots were perceived against a uniform gray background. The entire workspace, including the screen, the mirror, and the table were enclosed in a light-proof box with a hole in the front side for fitting the participant's face. One end of a heavy velvet collar was fixed on the rim of the hole. The other (larger) end covered the head and the shoulders of the participant, blocking completely vision of the surrounding space. A computer controlled all phases of the experiment and provided the experimenter with real-time information on the data being acquired.

The coordinates of the movement were recorded for a period of 2 s beginning at target onset. Before computing tangential velocities and accelerations, the samples were filtered (cutoff frequency 8 Hz) with a 15-point digital convolution algorithm (Rabiner and Gold 1975). Movement onset was defined as the first time the tangential velocity exceeded 3 cm/s and remained above this threshold for at least 50 ms (peak velocity ranged across participants from 20 to 54 cm/s). The end of the movement was defined as the first time the tangential velocity remained for more than 50 ms below a 3 cm/s threshold. Because trajectories were fairly straight (see Results), we defined movement amplitude as the length of the vector from the start to the end-point, and movement direction as the angle of this vector with respect to the transversal axis of reference.

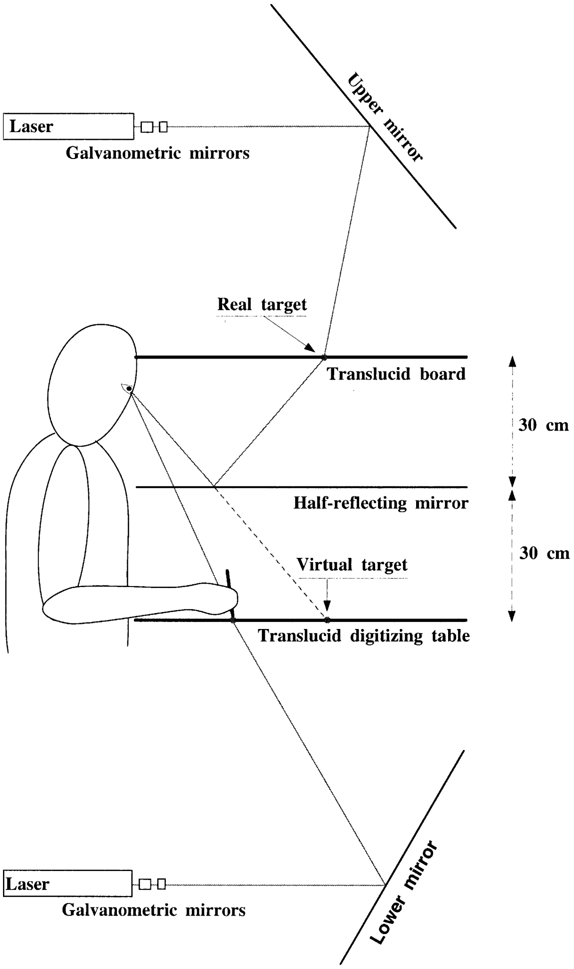

**Fig. 1** Experimental setup. Two laser beams deflected by computer-controlled galvanometric mirrors guided the pointing movements. The lower beam, backprojected on the digitizing table, indicated the initial position. The upper beam generated a virtual image of the target. A half-silvered mirror allowed both the upper and the lower beam to be perceived, but prevented the participant from seeing their hand

### Task and experimental procedure

#### *Experiment 1*

Participants were tested in three conditions, which were run in separate sessions 1 week apart. Sessions differed only in the nature of the knowledge of results (KR) provided to the participants. In the 1st session, KR was veridical. In the other two sessions, KR was biased by either magnifying or reducing the amplitude of the actual movements. Participants were unaware of this manipulation. The sequence of events within a trial was:

1. The spot from the lower laser appeared on the (invariable) starting point
2. The participant positioned the stylus on this point. The stylus was held either by the right hand (RH trials) or by the left hand (LH trials). In either case, the free hand helped locating the (invisible) felt disc on the table by using tactile cues. Two high-pitched tones signaled that the stylus tip was placed correctly (tolerance 2 mm)
3. The participant indicated his/her readiness by pressing on the stylus

4. After a random delay, distributed uniformly between 0.5 and 1.5 s, and a subsequent 1-s tone, the spot marking the initial position disappeared. At the same time, the spot from the upper laser was turned on at the selected target position, remained there for 200 ms, and then disappeared.
5. The participant moved the stylus to the target, with a single straight movement. Emphasis was placed on accuracy, but participants were also instructed to move relatively fast and not to make final corrective adjustments.

Although it was not necessary to keep the stylus in touch with the table, participants were aware of the maximum distance compatible with continuous recording and were instructed not to raise the hand too much. Depending on the response latency, the movement began sometimes before, and sometimes after the target was turned off. However, because movement time always exceeded 200 ms, the stimulus disappeared well before the hand approached the target, so that on-line processes could not affect the final hand position (Pélisson et al. 1986; Prablanc et al. 1986). Trials were repeated whenever the movement anticipated the onset of the target or when the stylus was accidentally lifted too much from the table. The participant remained in the final position for 2 s, until the lower spot reappeared at the starting point for the next trial.

In some cases (KR trials), an extra step was added at the end of this sequence. A low-pitched tone, simultaneous with the reappearance of the starting point, warned the participant not to initiate the next trial immediately. Soon after the double tone that signaled the correct positioning of the stylus, the upper spot indicated the target again. At the same time, the lower spot marked alternatively (2.5 cycles/s) for 6 s the initial point and a point that was supposed to indicate the position reached at the end of the pointing. In the session with veridical KR, this point did coincide with the final position. In the two other (biased) sessions, the point was again aligned with the initial point and with the actual final position, but the distance from the initial point was divided either by 1.15 or by 0.85. This manipulation was meant to induce participants to increase and decrease, respectively, movement amplitude by the same amount in subsequent trials. Delayed KR was used in order to focus on the planning of movement amplitude. On the one hand, on-line biasing of perceived finger motion would affect primarily velocity perception; on the other hand, showing a displaced endpoint immediately after the movement, when the hand is still close to the target, would affect more the relation between proprioceptive and visual inputs than movement planning itself. The term "KR gain" will denote the desired amount of increase or decrease in the amplitude. The disappearance of the upper spot and the return of the lower one to the initial point signaled the beginning of the next trial.

There were 12 possible targets (numbered 2–13; see Fig. 2), placed symmetrically around the central initial position, which was on the sagittal axis of the participant at 26 cm from the sternum. Targets were grouped according to their distance from the initial point: 6 cm (targets 4–7), 9 cm (targets 8–11), and 12 cm (targets 2, 3, 12, 13). KR was supplied only for trials involving the symmetrically placed right- and leftmost targets 2 and 3. This target arrangement was designed to explore the transfer of adaptation induced by KR to movements with different directions and amplitudes.

Each session comprised four successive phases ($P_1$–$P_4$). Phases $P_1$ and $P_4$ were identical (12 trials each). In these phases participants made pre- and postcalibration left-hand movements without KR. In phase $P_2$ ("calibration") the stylus was held with the right hand. There were 12 trials with KR in which targets 2 and 3 were presented in the (invariable) sequence (2, 2, 2, 2, 3, 3, 3, 3, 2, 3, 2, 3). In the second and 3rd sessions, KR in this phase was biased for the purpose of altering the visuomotor gain. In phase $P_3$ ("main") the stylus was again held with the right hand. There were 96 trials, divided into 6 blocks of 16 trials. Each block was evenly divided into 4 groups, each with the same structure. On the first trial, there was a movement toward target 2 or 3 followed by KR. In the second and 3rd sessions, this trial was supposed to refresh the gain changes induced by the previous calibration phase. In the other three trials, there were movements toward a target at one of the three possible distances, excluding targets 2 and 3, without KR. Thus, within a block, targets 2 and 3 were always selected twice and so were the other two targets at 12 cm (12 and 13); each of the other 8 targets were selected once, e.g., [(2, 8, 7, 13)(3, 5, 10, 12)(3, 13, 11, 6)(2, 4, 12, 9)]. The order of target selection for the 2nd, 3rd, and 4th trial within each group of 4 was randomized across blocks, with the constraint that each target was selected the same number of times (twice for 12 and 13, once for all the others). Altogether, in $P_3$ there were 12 movements toward each of the four targets at 12 cm (12×4=48) and 6 movements toward each of the 8 targets at 6 cm or 9 cm (6×8=48).

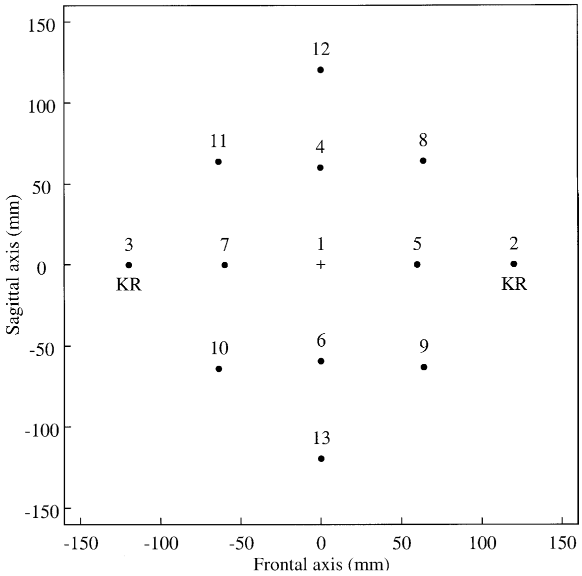

**Fig. 2** Target positions for experiment 1. Twelve targets (*2–13*) were arranged around a unique starting position (*1*). Target distance was 6 cm (targets 4–7), 9 cm (targets 8–11), or 12 cm (targets 2, 3 12, and 13). Visual feedback on accuracy (*KR*) was provided only for trials involving targets 2 and 3

Introducing two left-hand movement phases ($P_1$ and $P_4$) allowed us to assess the extent of intermanual transfer also within a session. Indeed, in the absence of visual feedback, the gain of left-hand movements might drift spontaneously between sessions. Instead, for the right hand we adopted a simple between-session design, because the KR in phases $P_2$ and $P_3$ was likely to prevent these spontaneous drifts.

### Experiment 2

The nature of the task was the same as in experiment 1. The orientation of the targets and the structure of the sessions were modified. The target configuration of experiment 1 was rotated by 45° counterclockwise (Fig. 3). Thus, two distances (6 cm and 12 cm) could be tested along the diagonal directions. Feedback on the performance (KR) was provided either for targets 2 and 3 (SW-NE direction, D1 axis), or for targets 12 and 13 (SE-NW direction, D2 axis). The experiment included 4 sessions, each comprising the same 4 phases of experiment 1. In the first and last sessions, KR was veridical and concerned targets 2 and 3 (session 1), or targets 12 and 13 (session 4). In sessions 2 and 3, KR was biased so as to induce an increase of 15% in the movement amplitude (KR gain 1.15). For one female and two male participants, the bias was on the D1 axis in session 2 and on the D2 axis in session 3. The order was reversed for the three other participants. Sessions were run without interruptions in successive days.

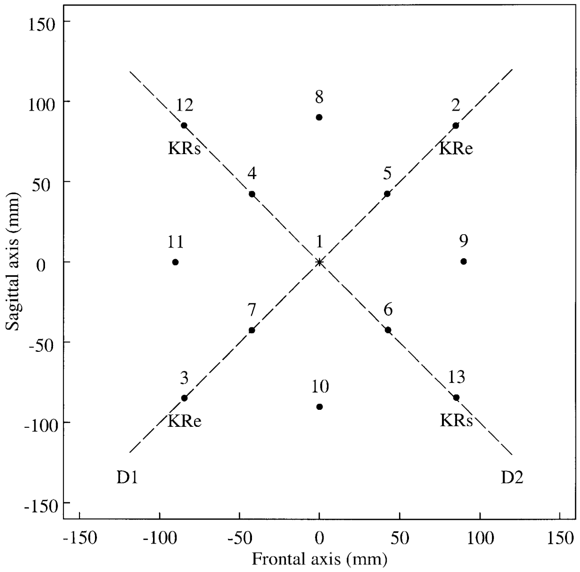

**Fig. 3** Target positions for experiment 2. Same as in experiment 1, but rotated by 45° counterclockwise. KR was provided either for targets 2 and 3 (*D1 axis*) or for targets 12 and 13 (*D2 axis*)

In both experiments, the task and the structure of the sessions were explained to the participants with the help of a written statement. Eight trials, including two with KR, were administered before the 1st session to familiarize the participants with the apparatus. Sessions lasted 40 min on average.

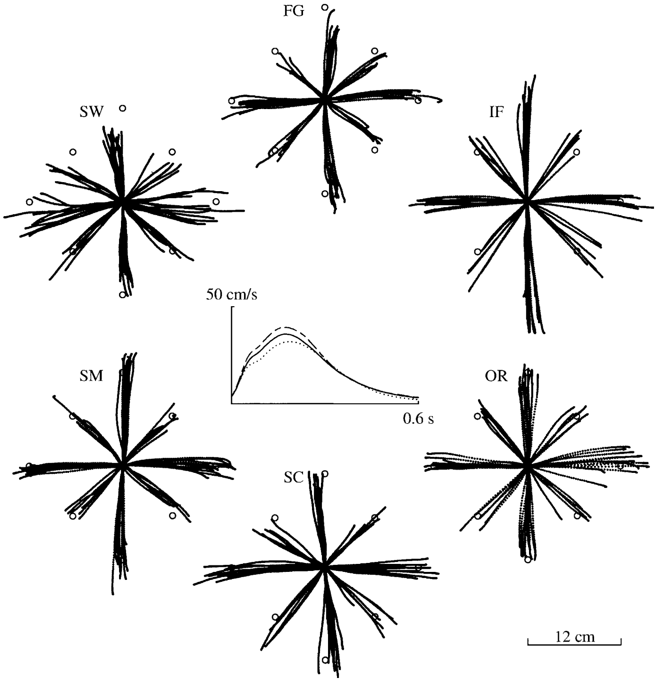

**Fig. 4** Hand paths and velocity profiles in experiment 1. Hand paths for all participants (identified by *initials*) and all trials involving targets at 9 cm and 12 cm (*open circles*) in the main phase of the veridical condition. *Inset:* nonnormalized velocity profiles in the main phase ($P_3$; mean across all participants for movements toward target 12). Results for decreased (*dotted line*), veridical (*continuous line*), and increased (*dashed line*) KR-gain conditions

## Results

### Experiment 1

### *Movement kinematics*

Pointing movements were essentially ballistic. Figure 4 shows the trajectories produced by all participants during the main phase toward the 8 most distant targets (session with veridical KR). In all cases, the hand path was fairly straight. The velocity profile (mean over all movements toward target 12 in the main phase is shown inset) was somewhat asymmetric. However, for each session the profile was single-peaked and showed no evidence of corrective submovements.

### *Direct modulation of movement gain*

We consider first the results for the right hand, whose movements had been biased directly in the calibration phase $P_2$. Figure 5 summarizes the salient findings for the main phase, $P_3$, by showing the mean pointing positions for each target and each session (means computed over all repetitions and all participants). Variability was estimated by ipsitizing and pooling the individual endpoint clusters, and computing the 0.95 confidence ellipses for the resulting population clusters. In all three sessions, directional errors were small and unsystematic [2-way ANOVA, 3 (KR gain) x 12 (target); for KR gain: $F_{2,\,10}=1.12$, P=0.364; target factor: $F_{11,\,55}=0.36$, $P=0.966$]. Moreover, comparing homologous trials in the second and third sessions for each target separately (paired *t*-test, with 5 *df*), failed to detect significant differences in direction.

The amplitudes of movements in the 1st session (veridical KR) were fairly accurate, with no systematic tendency to either undershoot or overshoot the targets. Biasing the KR (2nd and 3rd sessions) effectively altered the visuomanual gain G (movement amplitude/target distance), amplitudes being larger in the 1.15-bias session than in the 0.85-bias session. Table 1 reports the mean gains for all targets and for the three KR gains. Although KR was provided only for targets 2 and 3, the effect of the bias generalized to all targets. Figure 6 compares the gain for the two targets for which KR was supplied with the gain for all other targets. A 2-way ANOVA [3 (KR gain) x 2 (target group)] of the individual mean gains showed a large effect of the KR gain ($F_{2,\,10}=27.34$, $P<0.0001$), which was not significantly different for the two groups of targets (interaction: $F_{2,\,10}=2.17$, $P=0.101$). Adaptation was substantial but not complete. The last column in Table 1 reports for all targets the values of a mean index of adaptation *A*, defined as the ratio of actual and desired relative gain changes between the 0.85 and 1.15 sessions:

**Table 1** Experiment 1. Mean gain (movement amplitude/target distance) across participants for all targets and knowledge-of-results (KR) gains. The adaptation index is the ratio of the observed and desired relative gain changes between the sessions with KR gain 1.15 and KR gain 0.85

| Targets | | | | Mean gain | | | Adaptation index |
|---|---|---|---|---|---|---|---|
| | Direction | Distance (cm) | KR | 0.85 | 1.00 | 1.15 | |
| 2 | E | 12 | Y | 0.900 | 1.028 | 1.132 | 0.761 |
| 3 | W | 12 | Y | 0.890 | 1.030 | 1.098 | 0.699 |
| 4 | N | 6 | N | 0.944 | 1.006 | 1.069 | 0.415 |
| 5 | E | 6 | N | 0.884 | 0.996 | 1.104 | 0.737 |
| 6 | S | 6 | N | 0.971 | 1.094 | 1.128 | 0.500 |
| 7 | W | 6 | N | 0.956 | 0.988 | 1.070 | 0.375 |
| 8 | NE | 9 | N | 0.926 | 0.978 | 1.056 | 0.440 |
| 9 | SE | 9 | N | 0.942 | 1.073 | 1.152 | 0.670 |
| 10 | SW | 9 | N | 1.025 | 1.109 | 1.229 | 0.605 |
| 11 | NW | 9 | N | 0.850 | 0.987 | 1.025 | 0.622 |
| 12 | N | 12 | N | 0.845 | 0.931 | 0.995 | 0.540 |
| 13 | S | 12 | N | 0.961 | 1.030 | 1.081 | 0.390 |
| Mean | | | | 0.918 | 1.017 | 1.090 | 0.572 |

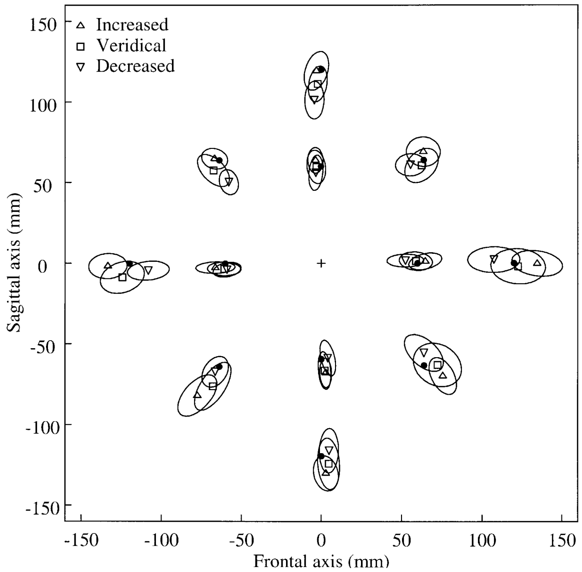

**Fig. 5** Endpoint distributions. Data points are the mean endpoints across all participants and all righthand trials of the main phase $P_3$. *Filled symbols* indicate the targets. *Empty symbols* identify the three KR-gain conditions (*upright triangle*, 1.15; *square*, 1; *inverted triangle*, 0.85). A KR gain of less than 1 forced participants to decrease the amplitude of the movements and a gain of more than 1, to increase the amplitude (see Methods). The spread of the endpoints is estimated by 0.95 confidence ellipses. Biased feedback was provided only in trials involving the leftmost and rightmost targets, but the effect generalized to all targets. Note the radial elongation of all endpoint distributions

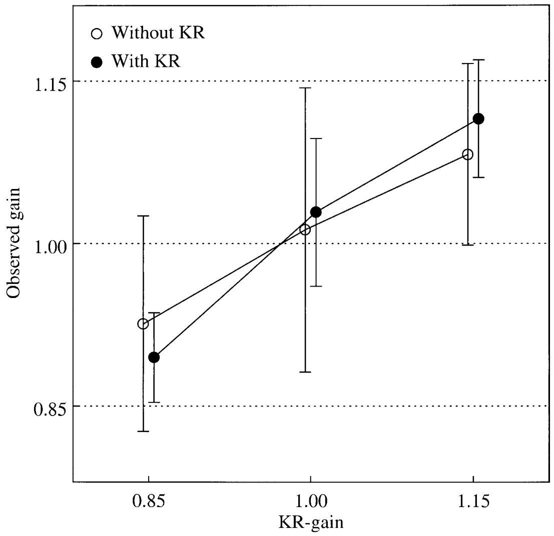

**Fig. 6** Observed gain (movement amplitude/target distance) as a function of the desired gain induced by KR. The evolution of the mean gain for targets 2 and 3 (with KR, *filled circles*) was not significantly different from that of the mean for all other targets (without KR, *empty circles*). *Vertical bars* indicate standard deviations across participants

$$A = [(G_{1.15}-G_{0.85})/(G_{1.15}+G_{0.85})]/[(1.15-0.85)/(1.15+0.85)]$$

The adaptation index was significantly greater than zero (targets with KR: $t_5$=9.63, $P$<0.001; targets without KR: $t_5$=6.93, $P$<0.001). However, full adaptation ($A$=1) was not reached (targets with KR: $t_5$=–3.56, $P$=0.016; targets without KR: $t_5$=–6.25, $P$=0.0015].

Movement amplitude varied as a function of direction. This is shown in Fig. 7A, which summarizes the results of Table 1 by pooling the results for targets along the same radii (e.g., targets 6 and 13). Because gain may vary with target distance (range effect; Slack 1953), statistical analysis of the data (Table 2) was performed separately for each distance [2-way ANOVA; for 6-cm and 9-cm targets: 3 (KR gain) × 4 (direction); for 12-cm targets: 3 (KR gain) × 2 (direction); data for targets 2 and 3 were not taken into account]. The analysis showed that the directional effect on the gain was significant for 9-cm targets. For instance, in all sessions the gain for target 10 (SW) was quite larger than that for target 11 (NW, averaged across sessions: 1.121 versus 0.959; see Table 1).

Unlike the gain itself, gain changes measured by the index A (Fig. 7B) were fairly uniform across directions, as demonstrated by the nonsignificant interactions between bias and direction (see Table 2). Because adaptation was directionally isotropic, the effect of target distance was tested by pooling the data across directions. A 2-way ANOVA of the gain for all targets with no KR

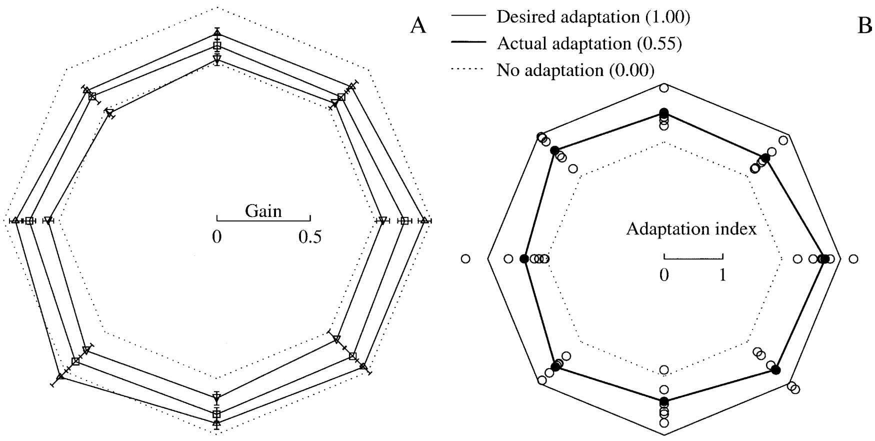

**Fig. 7A, B** Generalization of adaptation. **A** Movement gain in the main phase ($P_3$) as a function of direction. Different symbols identify the three KR-gain conditions (*upright triangles*, 1.15; *squares*, 1; *inverted triangles*, 0.85). Data points for the SE-NW and SW-NE directions are relative to targets 8–11 (distance 9 cm). Data points for the N-S and E-W directions pool the results for targets at 6 cm (4–7), and targets at 12 cm (2, 3, 12, and 13). *Bars* encompass ±1 SD. Full adaptation (*dotted lines*) was not achieved. Also, gain was not uniform across directions. **B** Adaptation index. *Empty symbols*, individual results; *filled symbols and heavy lines*, mean across participants. *Dashed lines and light lines* represent no adaptation and full adaptation, respectively. Unlike gain, gain changes were isotropic

**Table 2** Experiment 1. Summary of ANOVA results for the three target distances

| Distance (cm) | Factor | *df* | *F* | *P* |
|---|---|---|---|---|
| 6 | KR gain | 2, 10 | 5.43 | 0.025 |
| | Direction | 3, 15 | 0.51 | 0.683 |
| | KR gain × Direction | 6, 30 | 0.53 | 0.785 |
| 9 | KR gain | 2, 10 | 14.78 | 0.001 |
| | Direction | 3, 15 | 6.28 | 0.006 |
| | KR gain × Direction | 6, 30 | 0.96 | 0.958 |
| 12 | KR gain | 2, 10 | 9.88 | 0.004 |
| | Direction | 1, 5 | 4.83 | 0.073 |
| | KR gain × Direction | 2, 10 | 0.21 | 0.809 |

failed to detect a significant interaction between KR gain and target distance [3 (KR gain) × 3 (distance); $F_{4,\ 20}$=0.572, $P$=0.686). Therefore, adaptation was independent of target distance.

## *How is gain modulated?*

Movement amplitude can be controlled by varying the mean speed, the duration, or both. We estimated the relative contribution of speed and duration to gain modulation in phase $P_3$. Mean duration across participants was found to be fairly independent of KR gain (449 ms, 467 ms, and 458 ms for KR gain 0.85, 1.00, and 1.15, respectively). Thus, mean speed was the main determinant of the gain (19.8 cm/s, 21.1 cm/s, 23.1 cm/s., respectively). Actually, speed was the kinematical parameter that varied in the most consistent way across conditions. For each participant, adaptation indexes for mean velocity and duration were computed with the same formula used for the gain. Three separate sets of indexes were obtained for right-hand trials with and without KR, and for left-hand trials in phase $P_4$. Then, for each possible set pair, we computed between-participant linear correlations relative to velocity, gain, and duration. Correlation for gains (right hand with KR/right hand without KR: $r$=–0.170; right hand with KR/left hand: $r$=0.326; right hand without KR/left hand: $r$=0.477) were small and nonsignificant at the.95 confidence level. By contrast, all correlations for velocities were significant (right hand with KR/right hand without KR: $r$=0.924; right hand with KR/left hand: $r$=0.833; right hand without KR/left hand: $r$=0.851). For duration, only the first correlation was significant ($r$=0.860, $r$=0.781, and $r$=0.531, respectively). Thus, a participant with a high gain adaptation in one condition (e.g., right hand with KR) might have a low gain adaptation in another condition (e.g., left hand). Instead, velocity changes remained consistent across conditions. It should be stressed that these results are not incompatible with the presence of intermanual transfer of gain adaptation. Indeed, between-participant mean adaptation was similar for right and left hands (0.572 and 0.521, respectively). This point is addressed again in the next paragraph by considering a different way for estimating left-hand adaptation.

## *Transfer effects*

Figure 8 summarizes the results for movements performed with the left hand (phases $P_1$ and $P_4$). Although the left hand was not biased directly, the gain was affected by KR during the calibration and main phases in much the same way as the right hand. A 3-way ANOVA of the gains [2 (KR gain) × 2 (phase) × 2 (axis)] showed that the difference between phases $P_1$ and $P_4$ was due to the lasting biasing effect of the KR supplied in the interven-

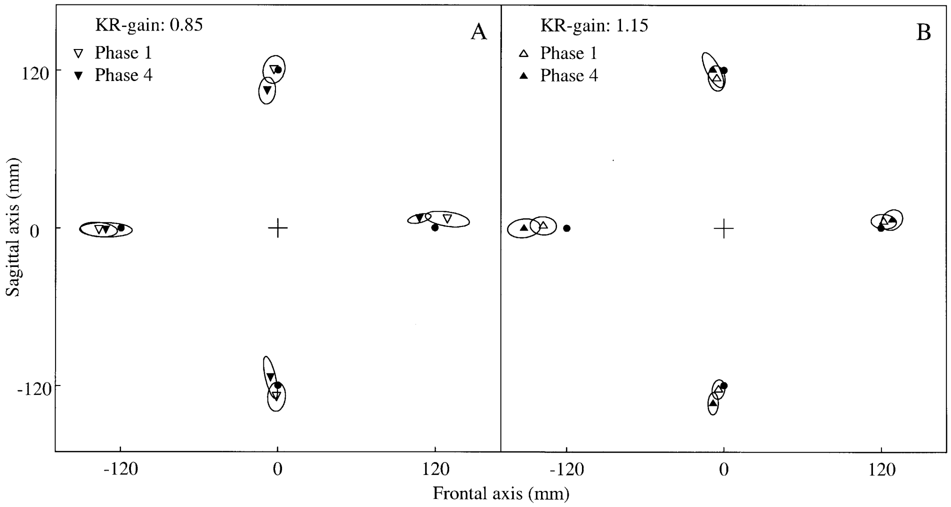

**Fig. 8A, B** Between-hands transfer. Mean movement endpoints in lefthand trials preceding (phase $P_1$, *empty upright triangles* and *inverted triangles*) and following (phase $P_4$; *filled upright triangles* and *inverted triangles*) the biased righthand trials (mean across participants). *Filled symbols* indicate the targets. The spread of the endpoints is estimated by 0.95 confidence ellipses. **A** KR gain 0.85; **B** KR gain 1.15

**Table 3** Experiment 1. Mean left-hand gain before ($P_1$) and after ($P_4$) the adaptation phases; and mean right-hand gain for the last 12 movements toward 12-cm targets in the adaptation phase $P_3$. Left-hand gain in $P_4$ increases between sessions almost as much right-hand gain

| KR gain | Direction | Left-hand gain | | | Right-hand gain |
|---|---|---|---|---|---|
| | | $P_1$ | $P_4$ | Variation (%) | $P_3$ (last 12 trials) |
| 0.85 | W | 1.1299 | 1.0771 | –4.67 | 0.8895 |
| 0.85 | E | 1.0908 | 0.9150 | –16.11 | 0.8560 |
| 0.85 | N | 1.0061 | 0.8740 | –13.13 | 0.8091 |
| 0.85 | S | 1.0660 | 0.9469 | –11.18 | 0.9295 |
| 0.85 | Mean | 1.0732 | 0.9533 | –11.18 | 0.8710 |
| 1.15 | W | 1.1336 | 1.2582 | 10.98 | 1.0932 |
| 1.15 | E | 1.0262 | 1.0878 | 6.01 | 1.1432 |
| 1.15 | N | 0.9550 | 1.0065 | 5.39 | 1.0137 |
| 1.15 | S | 1.0197 | 1.1066 | 8.53 | 1.0636 |
| 1.15 | Mean | 1.0336 | 1.1148 | 7.85 | 1.0784 |

ing phases (KR gain × phase interaction, $F_{1,5}$=15.45, $P$=0.011). It also showed that, while gains depended on the movement axis ($F_{1,5}$=15.06, $P$=0.012), the adaptation level did not (3-way interaction, $F_{1,5}$=0.04, $P$=0.857). 2-way interactions involving the axis were also not significant.

In the absence of feedback, movement amplitude could vary spontaneously between sessions. In order to neutralize these variations, adaptation for the left hand was estimated by comparing the gain in phases $P_1$ and $P_4$ (Table 3). As shown by the percentage variation between phases, the transfer of adaptation to the left hand was almost complete. The mean variations between phases $P_4$ and $P_1$ for KR gain 0.85 and KR gain 1.15 (–11.18% and 7.85%, respectively) correspond to an adaptation index $A$=0.643. By comparison, the variations for the last 12 right hand trials in $P_3$ correspond to $A$=0.691. Both values are quite close to the mean over all right hand trials in $P_3$ (Table 1, $A$=0.572).

For each axis separately, we performed a 3-way ANOVA of the gains [2 (KR gain) × 2 (hand) × 2 (direction)]. Along the N-S axis, where no KR was ever provided, only the KR gain was a significant factor ($F_{1,5}$=27.86, $P$=0.003). The KR gain × hand interaction was not significant ($F_{1,5}$=0.454, $P$=0.531), indicating that the KR had the same effect on both hands. A similar result was obtained for the E-W axis, in spite of the fact that KR had been provided only in right-hand trials (for KR gain: $F_{1,5}$=36.33, $P$=0.002). Because left hand movements were generally hypermetric (cf Table 3), the hand was also a significant factor ($F_{1,5}$=8.07, $P$=0.036). However, as in the N-S direction, there was no interaction between KR gain and hand ($F_{1,5}$=1.389, $P$=0.292).

### *Variable errors*

The confidence ellipses of Fig. 5 show that endpoints were more spread in the direction of the movement than in the orthogonal direction. The distribution of variable errors was analyzed by concentrating on the 96 trials performed with the right hand in phase $P_3$ of the 1st session. (The data from the sessions with biased KR were not included, because the ongoing gain changes could lead to overestimating the variable errors.)

First, we checked whether shape and orientation of the error ellipses were consistent across participants, direction, and target distance. The components of variable errors were computed for every participant and every target in a movement-related reference frame, with the $x$-axis passing through the starting point and the mean final position. On average, the ratio of transverse to longitu-

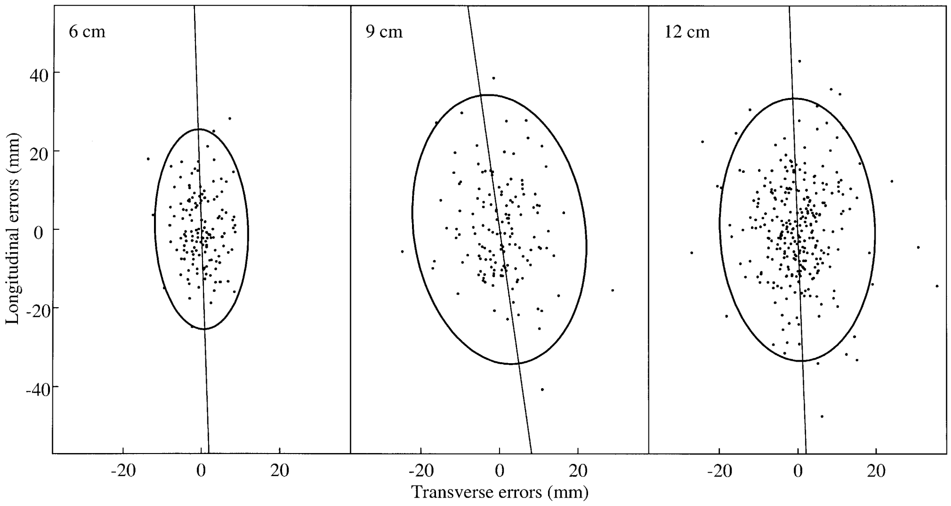

**Fig. 9** Distribution of variable errors. Results for the 96 right-hand trials in phase $P_3$ of the 1st session (veridical KR). For each indicated target distance, data were pooled over participants and directions. Data points indicate the movement final position relative to the population mean. The distributions for all directions were superimposed by aligning them with the N-S direction. The 0.95 confidence ellipses and the corresponding direction of the main axis are also shown

dinal variable error was 0.60, and exceeded 1 for only 10 of the 72 ellipses. Mean ratios were well below 1 (range of the mean: 0.40–0.79 and 0.33–0.82 for participants and targets, respectively), indicating that the ellipses were consistently elongated in the direction of the movement. The only systematic difference was the one between 9-cm targets in the diagonal directions (mean ratio 0.70), and targets in the cardinal directions (mean ratio: 0.54 and 0.56 for 6-cm and 12-cm targets, respectively).

Second, because variable errors ellipses were consistent among participants, the data were analyzed further by pooling the endpoints. First, for each target, we computed the mean endpoint over all participants. Then, for each target, the data were superposed by shifting the individual set of endpoints so that their means coincided with the population mean for that target. Finally, for each target distance separately, the resulting clusters of endpoints were pooled by a rotation aligning the vector from the starting point to the mean endpoint with the N-S direction. The resulting three clusters (one for each distance) are shown in Fig. 9 along with the corresponding 0.95 ellipses of confidence. The elongation of the clusters was estimated by the ratio $R$ of the variances of the projections of the endpoints on the axes of the confidence ellipse. For all three distances this ratio was significantly larger than 1 (6 cm: $R$=2.13, $F_{120,\ 120}$=4.53, $P$<0.0001; 9 cm: $R$=1.58, $F_{120,\ 120}$=2.39, $P$<0.0001; 12 cm: $R$=1.69, $F_{264,\ 264}$=2.85, $P$<0.0001). Moreover, the direction of the major axis of the ellipses was close to vertical, confirming that the maximum elongation occurred along the direction of the movement. For 6- and 9-cm targets the endpoint spread, estimated by the size of the ellipses, increased proportionally to distance. No further increase occurred for 12-cm targets.

Because the same general pattern of variable errors was observed in all three sessions, the elongation of the endpoint distributions cannot be credited to a progressive adaptation of the amplitude gain to (nonveridical) visual feedback. However, the common underlying reason for the radial elongation of the confidence ellipses could be a general drift of the gain in the course of the experiment (Vindras and Viviani 1998). This hypothesis was rejected by the analysis of the sequential effects described in the next section.

## *Evolution of adaptation*

Figure 10A summarizes the evolution of the performance by plotting the mean gain over all participants and all trials within the successive phases and blocks of each session. A multilinear analysis of the gain for the main phase $P_3$ [3 (KR gain) × 6 (block); KR gain treated as a nominal factor), confirmed the presence of a large bias effect. In addition, it revealed a significant block × KR gain interaction ($F_{2,\ 12}$=4.28, $P$=0.040). However, linear regression analysis of the gain as a function of the block rank order showed that the slope term was significant only for KR gain 0.85 (slope=–0.0116; $F_{1,\ 4}$=9.44, $P$=0.037). In conclusion, most of the gain adaptation had taken place during the calibration phase $P_2$, but the process continued during the main phase $P_3$, in which KR was provided every 4th trial. We tested whether the movement immediately following the KR in $P_3$ was more biased than the others. An ANOVA for the 3 trials without KR [2 (KR gain) × 3 (rank)] showed no evidence of such sequential effect (rank factor: $F_{2,\ 10}$=0.27, $P$=0.789; rank × bias interaction: $F_{2,\ 10}$=0.33, $P$=0.726).

As noted previously, the gain is specified jointly by the duration and by the mean velocity of the movement, the second factor having a higher weight than the first. A further insight into the time course of the adaptation process was obtained by considering the way the adaptation index for velocity, duration, and gain changed within each session. A qualitative difference in evolution emerged by treating separately the trials with (Fig. 10B) and without KR (Fig. 10C). However, in both cases gain adaptation was mostly driven by velocity. Velocity and duration adaptations in the left hand were similar to those induced in the right hand for trials without KR. More

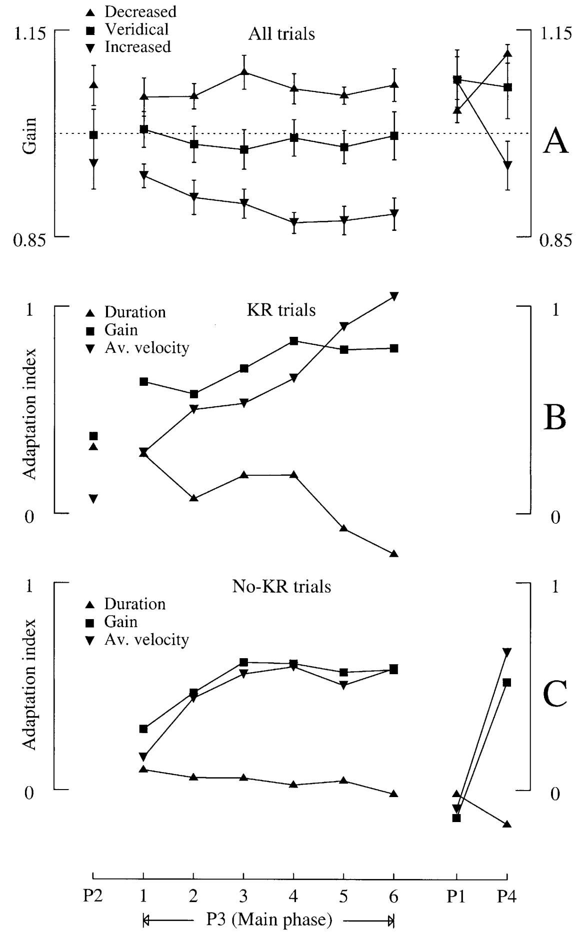

**Fig. 10A–C** Evolution of adaptation. **A** Observed gain for each phase, and each block within the main phase $P_3$ (*upright triangles*, KR gain 1.15; *squares*, KR gain 1; *inverted triangles*, KR gain 0.85). Data pooled over participants (*bars* encompass ±1 SD of the mean). Note that the adaptation level reached in the calibration phase ($P_2$) increased further during the main phase ($P_3$). Left-hand movements were hypermetric in both $P_1$ and $P_4$. **B** Adaptation index for duration, mean velocity and gain. Means over trials in phases $P_2$ and $P_3$ for which KR was provided. **C** Adaptation index for duration, mean velocity, and gain. Means over trials in phases $P_1$, $P_3$, and $P_4$, for which KR was not provided

importantly, for trials with KR, duration and velocity continued to evolve till the end of the main phase, whereas the gain leveled off in the middle of the phase. Thus, the adaptation process has a longer time constant than the one that can be inferred by looking only at movement amplitude.

## Experiment 2

### *Effectiveness of the bias*

Figure 11 shows the mean and the variability (0.95 confidence ellipses computed as in experiment 1) of the endpoints for movements of the right hand in the main phase $P_3$ of the four sessions. Movements tended to overshoot the targets by an amount that depended on movement direction. The largest overshoots were for movements directed toward the body (e.g., 12-cm target in the SW direction). However, as in experiment 1, biased KR effectively increased movement gain. For every target the mean endpoint for biased trials was further away from the center than the mean endpoint for unbiased trials. This was confirmed by a post hoc analysis showing that the difference was significant for all targets at the 0.05 level, and for 6 targets at the 0.004 level (unilateral paired *t*-test with Bonferroni threshold correction for multiple comparisons). An analysis of the variance [3-way ANOVA, 2 (KR axis) × 2 (KR gain) × 2 (target with/without KR)] demonstrated the following points: (1) there was a widespread effect of biasing the KR ($F_{1,\,5}$=177.96, $P$<0.0001); (2) the effect of the bias for targets with and without KR was not significantly different ($F_{1,\,5}$=0.647, $P$=0.458); (3) the gain for targets without KR was higher when KR was provided for movements along the axis D2 ($F_{1,\,5}$=31.04, $P$=0.003); (4) gain changes (adaptation) along either diagonal were independent of whether KR was provided on that diagonal or on the other (KR axis × KR gain interaction, $F_{1,\,5}$=1.33, $P$=0.300).

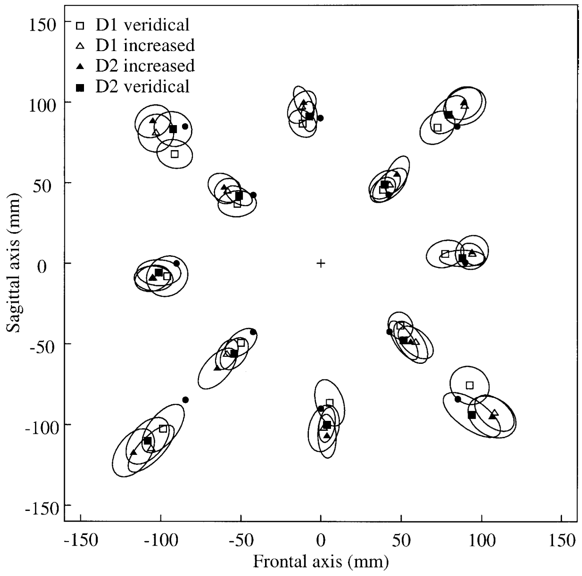

**Fig. 11** Endpoint distributions for experiment 2. Data points are the mean endpoints across all participants and all right-hand trials in the main phase ($P_3$). Different symbols identify the four sessions (*filled squares*, veridical KR, D2 axis; *empty squares*, veridical KR, D1 axis; *filled triangles*, biased KR, D2 axis; *empty triangles*, biased KR, D1 axis). Biased KR always forced participants to increase the amplitude of the movements (see Methods). The spread of the endpoints is estimated by 0.95 confidence ellipses. The effect of biased feedback generalized to all targets. As in experiment 1, endpoint distributions are elongated in the radial direction

An analysis similar to that conducted in experiment 1 confirmed that, for both KR axes, individual gain adaptations were not linearly related between any two of the three conditions (right hand with KR, right hand without KR, and left hand). By contrast, velocity and

**Table 4** Experiment 2. Movement gains for the indicated combinations of KR gain, KR axis, and hand; and the corresponding adaptation indexes (see Table 1)

| Targets | KR axis on D1 | | KR axis on D2 | | Adaptation index | |
|---|---|---|---|---|---|---|
| | 1.00 | 1.15 | 1.00 | 1.15 | KR on D1 | KR on D2 |
| Right hand | | | | | | |
| 6 cm on no KR axis | 1.066 | 1.262 | 1.176 | 1.377 | 1.209 | 1.130 |
| 6 cm on KR axis | 1.081 | 1.216 | 1.132 | 1.257 | 0.843 | 0.752 |
| 9 cm | 0.964 | 1.109 | 1.055 | 1.126 | 1.005 | 0.467 |
| 12 cm on no KR axis | 0.980 | 1.148 | 1.148 | 1.248 | 1.131 | 0.599 |
| All trials without KR | 1.006 | 1.165 | 1.119 | 1.230 | 1.054 | 0.680 |
| 12 cm trials with KR | 1.057 | 1.202 | 1.073 | 1.167 | 0.919 | 0.604 |
| Left hand | | | | | | |
| 12 cm on no KR axis | 1.155 | 1.268 | 1.132 | 1.200 | 0.668 | 0.418 |
| 12 cm on KR axis | 1.062 | 1.210 | 1.183 | 1.262 | 0.934 | 0.463 |

duration adaptations were highly correlated between conditions.

### *Transfer of adaptation*

The degree of adaptation transfer was assessed in two ways, namely by contrasting right-hand movements along *orthogonal* diagonals, and left- and right-hand movements along the *same* diagonal. In both cases, the movements being compared involved the most different combination of elbow and shoulder rotations. For the right hand, movements along the diagonal with KR were compared with movements along the orthogonal diagonal for which there was no KR. Table 4 reports the gain (averaged over participants) for all combinations of axis, KR, and target distance. Separate analyses for target groups with the same distance from the center confirmed a pattern of generalized adaptation [3-way ANOVA: 2 (KR gain) × 2 (KR axis) × 2 (movement parallel/orthogonal to KR axis)]. For 12-cm targets there was no significant difference in adaptation whether or not movement and KR were on the same axis (interaction between first and third factor: $F_{1,\ 5}$=0.25, $P$=0.614). For 6-cm targets the bias effect was actually found to be significantly *larger* along the diagonal where no KR had been provided than along the other one (interaction between first and third factor: $F_{1,\ 5}$=9.82, $P$=0.026).

The association between direction (relative to the workspace) and joint synergies was reversed for left-hand movements. Thus, as far as transfer effects are concerned, the most relevant behavior is that of the left hand moving along the *same* direction as the right hand. Figure 12 summarizes the relevant comparisons. For each KR gain and both KR axes, the figure contrasts the mean gains for the 12 left-hand trials in phase $P_4$ and the last 12 right-hand trials for the same 12-cm targets (in all cases the data are for movements *orthogonal* to the KR axis; thus the factors (KR axis) and (movement-axis) are not independent). An analysis of the variance [3-way ANOVA, 2 (movement-axis) × 2 (KR gain) × 2 (hand)] confirmed a strong effect of the KR gain on both hands ($F_{1,\ 5}$=17.38, $P$=0.009), as well as a tendency of the left hand to be hypermetric ($F_{1,\ 5}$=7.87, $P$=0.037). However, neither the movement axis × KR gain interaction ($F_{1,\ 5}$=0.033, $P$=0.862), nor the KR gain × hand interaction ($F_{1,\ 5}$=2.356, $P$=0.185) were significant. The 3-way interaction was also not significant. Thus, even in the case of the most dissimilar synergies, KR gain affected both hands in the same way.

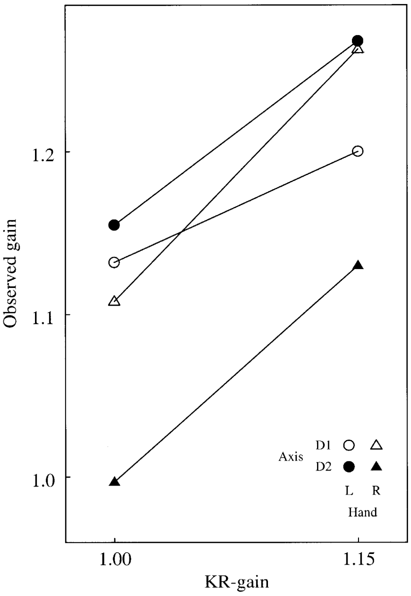

**Fig. 12** Observed gain as a function of KR gain. Data points are relative to 12-cm targets on the axis orthogonal to the KR axis. For the left hand, data points are means over all relevant trials in phase $P_4$. For the right hand, data points are means over the last 12 relevant trials in phase $P_3$. Different symbols identify movements along the two diagonals. The biasing effect of KR transferred onto the orthogonal axis similarly for the two hands

### *Biomechanical asymmetries*

Right-hand movements along axis D1 (mostly elbow rotations) are opposed by smaller inertial forces than movements along axis D2 (mostly rotations at the shoulder). The opposite is true for left-hand movements. The gain was affected by this asymmetry. Figure 13 compares movement gains along the two axes for the

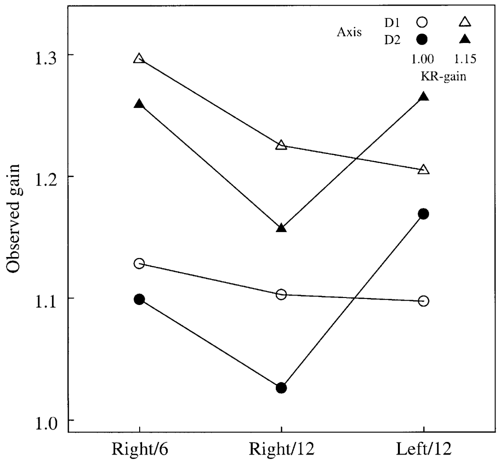

**Fig. 13** Biomechanical asymmetries affect gain. Observed gain as a function of the indicated hand-distance combinations. For the left hand, data points are means over all trials in phase $P_4$ (12-cm targets). For the right hand, data points are means over all 6- and 12-cm targets in phase $P_3$. For both KR gains and both distances, right hand movements had higher gains along D1 (low inertia, *empty symbols*) than along D2 (high inertia, *filled symbols*). The pattern was inverted for the left hand (D1, high inertia; D2, low inertia)

indicated hand/distance combinations, and for the two KR gains (pooling trials with and without KR, and averaging over both KR axes). Over and above the general modulation of movement amplitude induced by the feedback, the same pattern emerged for both KR gains. Right-hand movements toward 6- and 12-cm targets were larger along D1 than along D2. The opposite was true for left-hand movements. An ANOVA performed on the trials with 12-cm targets [2 (KR gain) × 2 (axis) × 2 (hand)] confirmed the presence of a significant interaction between axis and hand ($F_{1,\ 5}$=40.53, $P$=0.0014). This pattern of inversion was observed in all participants and in all sessions. Moreover, similar inversions were present in all kinematical parameters: maximum speed and acceleration, mean speed, movement duration, and in the time-to-peak for both speed and acceleration. The ANOVA restricted to 12-cm targets also confirmed that gain was higher for the left hand ($F_{1,\ 5}$=16.08, $P$=0.010) and that the axis had no effect ($F_{1,\ 5}$=0.03, $P$=0.870). KR gain had a highly significant effect ($F_{1,\ 5}$=33.95, $P$=0.002), but there was no interaction with the other factors (KR gain × axis: $F_{1,\ 5}$=0.01, $P$=0.939; KR gain × hand: $F_{1,\ 5}$=0.66, $P$=0.452; KR gain × axis × hand: $F_{1,\ 5}$=0.70, $P$=0.441). Thus, whatever the initial gain, KR effects applied uniformly and did not depend either on hand or on movement axis.

### *Directional errors*

The analysis of directional errors was carried out only for movements of the right hand [ANOVA: 2 (KR gain) × 2 (KR axis)]. It revealed a significant effect of the axis factor, as well as a KR gain × KR axis interaction (KR gain: $F_{1,\ 5}$=0.12, $P$=0.743; KR axis : $F_{1,\ 5}$=7.75, $P$=0.039; interaction : $F_{1,\ 5}$=15.64, $P$=0.011). Post hoc analyses revealed that these effects were mainly due to direction errors along D2 when KR was supplied along D1 (see Fig. 11). When KR was supplied along D2, directional accuracy improved along that axis, possibly because participants were aware of their systematic directional bias and managed to correct it. In fact, the significant effects disappeared when data from the 4 targets on D2 axis were not taken into account (KR gain: $F_{1,\ 5}$=0.40, $P$=0.553; KR axis : $F_{1,\ 5}$=1.60, $P$=0.261; interaction : $F_{1,\ 5}$=1.93, $P$=0.224).

Because in each session the biasing action of the KR was exerted only along a single axis, a motor control scheme based on intrinsic (joint) coordinates should give rise to systematic directional biases. We searched for evidence of such systematic biases for each target separately, and for both KR axes. Of the 24 possible comparisons (*t*-test), all but two failed to reveal a significant difference. The two exceptions were targets 12 and 13 (D2 axis) when KR was supplied for these targets (*t*=2.05, *P*=0.024 and *t*=3.25, *P*=0.007, respectively).

## Discussion

The results of experiments 1 and 2 are fully consistent with the three basic hypotheses of the parametric vector model of visuomanual control (Bhat and Sanes 1998; Bock and Eckmiller 1986; Favilla and Cecco 1996; Gordon et al. 1994; Krakauer et al. 1996, 2000; Messier and Kalaska 1997; Pine et al. 1996; Rossetti et al. 1995; Vindras and Viviani 1998). Specifically, the generalization to all directions of the biasing effect of a KR supplied along just one axis (Fig. 6) and the elongated distribution of the variable errors (Fig. 8) provide converging support to the model's basic tenet (assumption 2) that the input to the execution stage of the movement is supplied in a vectorial format. Moreover, in both experiments we were able to induce significant gain changes without affecting the directional accuracy of the movements. Thus, amplitude and direction of the vector from the initial to the final point can be specified independently, as stated by assumption 3. It should be stressed, however, that our experiments involved only movements constrained within a plane. Therefore, they cannot address the issue of whether the parametric vector model applies also to unconstrained pointing movements (Desmurget et al. 1997, 1999) or to grasping (Desmurget et al. 1995; Rosenbaum et al. 1995).

### Relation with previous studies

Our results extend and qualify the conclusions of earlier studies of visuomotor adaptation (Bock 1992; Krakauer et al. 2000; Pine et al. 1996). In agreement with Bock

(1992), we found that modulating the visual feedback along the frontoparallel axis affects the amplitude of all movements, without affecting their direction. The novel findings were that adaptation: (1) is independent of target distance, (2) is induced irrespectively of the axis along which KR is provided, (3) can both increase and decrease the gain, and (4) transfers to the untrained hand. More importantly, we succeeded to induce adaptations even in fairly realistic operating conditions. Instead, the size of the actual movements in Bock's experiment (approximately 15–35 mm) was in the lower end of the range of typical hand movements. Moreover, the feedback in his main condition was very distorted (KR gain 2). This may be a source of concern for the interpretation of the results. Indeed, generalized adaptation can be taken to support the vectorial model only insofar as it can be excluded that conscious strategies contribute to the modulation of movement amplitude. This was the reason why we set the KR bias to a low level that could not be perceived consciously. With a KR gain of 2 (a 2-cm movement perceived as a 4-cm movement) one wonders how participants may have failed to realize that feedback was not veridical. Finally, even in the preadaptive phase, Bock's participants were strongly hypermetric (mean preadaptive gain 1.91). This may explain why the degree of adaptation was rather limited (mean postadaptive gain 1.48, instead of the theoretical 0.5). The same reason may also account for the failure to increase the vertical gain by a factor of 2, because the required feedback compensated almost exactly the large spontaneous hypermetry. The results on intermanual transfer of adaptation are sharply at variance with those reported by Bock (1992). Whereas we found that left-hand adaptation was almost as strong as the right-hand one, no significant transfer was observed in experiment B4 of Bock's study. We can offer no explanation for this discrepancy.

The extent of the adaptation (mean across targets 0.610; see Table 1) was generally comparable with that observed by Pine et al. (1996, their Fig. 3). However, the agreement should be qualified by considering that in Pine's study, as well as in a similar, later experiment (Krakauer et al. 2000), the work plane was dissociated from the (vertical) stimulus plane. Thus, unlike what happens when pointing to real objects, the experimental condition required an additional sensorimotor transformation for mapping the stimulus onto the work plane. By necessity, such a transformation is vectorial; therefore, one could argue that the experimental paradigm was not neutral with respect to the hypothesis to be tested. In addition, because the target plane was dissociated from the movement plane, it might have been difficult to compare hand position inferred from feedback and feedforward signals to visual information about target position. Pine et al. (1996) have suggested that adaptation sets in quickly and is virtually complete after approximately 20 biased trials. We did not confirm this result, possibly because we used smaller values of the bias. However, we did demonstrate that the time constant of the adaptation process is even longer than the one estimated from movement amplitude alone (Fig. 10B, C).

## Where does adaptation take place?

There is convincing evidence that selected populations of directionally tuned neurons in the primary motor cortex are involved in specifying the direction component of the movement vector (Ashe and Georgopoulos 1994; Fu et al. 1993; Georgopoulos 1991; Georgopoulos et al. 1982; Schwartz et al. 1988). The motor cortical neuronal activity also depends on the arm initial joint angles (Caminiti et al. 1990; Scott and Kalaska 1997). However, when the starting posture is held constant, the relation between individual neuronal activity and movement direction is stable and well characterized (Scott and Kalaska 1997). Although several modeling studies have questioned the current interpretation of this fact (Mussa-Ivaldi 1988; Tanaka 1994; Todorov 2000), directional information is certainly available in the primary motor cortex. By contrast, the situation is much less clear for amplitude information (Messier and Kalaska 2000). Earlier studies of single-joint movements failed to detect significant correlations between target distance and firing rate in motor and premotor cortex neurons (Hamada and Kubota 1979; Riehle and Requin 1989). Weak correlations were reported by Georgopoulos (1990) in both primary motor cortex and area 5 during the reaction time (RT) for reaching movements. More recently, experiments involving multijoint movements have confirmed that target distance modulates significantly the firing rate of both motor and premotor area neurons (Fu et al. 1993, 1995; Kurata 1993; Messier and Kalaska 2000). In addition, in approximately 40% of motor cortex cells, the firing rate correlates better with movement velocity than with direction (Ashe and Georgopoulos 1994). Because pointing velocity covaries strictly with amplitude (isochrony principle; Vindras and Viviani 1998), this invites again the conclusion that at least some information about amplitude is also present in cortical motor areas. However, no algorithm has been produced so far to predict movement amplitude from neuronal activity in these areas, as this has been done for movement direction (Georgopoulos et al. 1982). Thus, available data suggest that whatever the contribution by the motor cortex, full specification of movement amplitude must also involve other cortical or subcortical areas, which may be responsible for the phenomenon of gain adaptation. Three potential loci – parietal cortex, cerebellum, and basal ganglia– are considered in this order.

A first candidate locus is the posterior parietal cortex. On the one hand, parietal circuits are supposed to be involved in the coordinate transformation between retinotopic and head-centered space (Andersen et al. 1985; Buneo et al. 2002; Snyder et al. 1998). On the other hand, it has recently been shown that the recalibration of visually guided reaching movements induced by displacing prisms produces a selective activation of the posterior parietal cortex (Clower et al. 1996). However, lesions of posterior parietal areas in humans (Perenin and Vighetto 1988) and monkeys (Faugier-Grimaud et al. 1985) lead to optic ataxia, which results in a systematic shift of movement endpoints toward the side of the lesion (Jeannerod 1988), but does not affect constant and variable errors in movement amplitude.

The cerebellum is a also a likely candidate as a locus where adaptation takes place. Indeed, the cerebellum plays an important role in saccadic (Optican and Robinson 1980) and prism adaptation (Baizer et al. 1999; Gauthier et al. 1979; Martin et al. 1996; Weiner et al. 1983). Moreover, cerebellar lesions affect selectively the control of movement amplitude (Hallett et al. 1991; Hore et al. 1991). However, the adaptive gain changes induced in our experiments did not resemble cerebellar dysmetria. Whereas cerebellar lesions result in inappropriate timing and/or scaling of the activity in antagonist muscles (see Manto 1996), KR in our experiment affected mainly movement velocity, leaving its duration virtually unchanged. Moreover, the transfer of adaptation to the left hand is hardly compatible with the involvement of a lateralized structure.

Finally, the basal ganglia, which are likely to play a role in controlling amplitude, may also be involved in gain adaptation. Hypokinetic (e.g., Parkinson disease) and hyperkinetic (e.g., Huntington disease) movement disorders are associated with increased or decreased basal ganglia output, respectively (Alexander et al. 1990; Mink and Thach 1993; Turner and Anderson 1997; Wichmann and DeLong 1996). Also, current models of the subcortical components of the motor control system (Alexander et al. 1990) have advanced the hypothesis that scaling and termination of movements is achieved by successively inhibiting and disinhibiting the globus pallidus (internal segment) and the substantia nigra (pars reticulata). The role of the pallidus is emphasized further by the recent finding that, in approximately 80% of the cells recorded there, changes in firing rate correlated linearly with movement amplitude (Turner and Anderson 1997). However, to the extent that the basal ganglia are also lateralized, they cannot account any better than the cerebellum for between-hand transfer of adaptation.

Adaptation was very pervasive, affecting the unbiased hand even when the required synergies were as different as possible (experiment 2). Thus, if adaptation takes place in one of the three structures considered above, one has to make the additional hypothesis that gain changes spread via some bilateral projection to the motoneuronal pool. Alternatively, one can envisage the possibility that visuomotor gain is changed upstream from the motor implementation stage. In particular, noting the different degree of adaptation for amplitude and direction, Pine et al. (1996) have argued that short-term working memory is involved in recalibrating the visuomotor scaling factor. In principle, it is even possible that the gain modulation has a perceptual component arising within the visual areas. Bock (1992) has considered this possibility, but ruled it out by arguing that, contrary to his results, perceptual biases should generalize to both hands. Of course, this argument does not hold in the case of the present study. Yet there is an independent reason why a purely perceptual origin of the bias is unlikely. If gain variations resulted from an altered perception of the distances, individual variations should be more correlated across conditions (right hand with and without KR, left hand) than the concomitant variations in the kinematical parameters (maximum velocity and acceleration). In fact, for both experiments the analysis showed the opposite pattern. Gain correlations across conditions were not significant, whereas kinematical correlations were highly significant.

## Biomechanics

Pointing movements are propelled by muscles acting along several axes, the resulting force being the vector sum of the individual contributions. Thus, the assumption that amplitude and direction are controlled variables implies a highly specific pattern of covariation among the commands to the participating muscles. Because gain modulations generalize to movements with sharply different directions, the mechanisms mapping the desired controlled variables onto the required pattern of muscle contractions must include a model of the limb geometry and an estimation of its inertial properties. The model is not totally accurate, however. In experiment 1 (Fig. 7A) right-hand movements became progressively longer as their direction moved from the high-inertia (NW-SE) to the low-inertia (SW-NE) diagonal. A clear pattern of gain inversion was observed also in experiment 2 when moving along the same diagonal with the right or the left hand (Fig. 13). As already mentioned, all other kinematical parameters of the movement – duration, velocity, acceleration – were affected by the inertia of the moving limb. Velocity and acceleration were the best predictors of the gain, suggesting that gain anisotropy is the consequence of inappropriate calibration of the active torques driving the movement. Instead, gain changes brought about by KR were fairly isotropic. Therefore, whatever mechanism is responsible for biasing the gain, it must intervene before direction is specified.

One might speculate that extensive practice with gesturing in the proximal workspace calibrates the thrust impressed to the hand as a function of the distance to be covered. This calibration would be altered by nonveridical KR. Once the direction of the movement is specified, the estimated thrust (possibly biased by KR) is translated into an appropriate set of joint torques. The translation, however, is approximate, as witnessed by the gain anisotropy documented in Figs. 7A and 13. By contrast, gain changes need not to be altered. This speculation is at least compatible with the idea that information from the cortex is processed through the basal ganglia and returned to the precentral motor areas (Georgopoulos et al. 1983). If so, the basal circuits might be responsible for the calibration of the thrust and would be the target of the biasing action of KR.

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