Shape Distortion Produced by Isolated Mismatch Between Vision and Proprioception

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Malfait N, Henriques DY, Gribble PL. Shape distortion produced by isolated mismatch between vision and proprioception. *J Neurophysiol* 99: 231–243, 2008. First published October 31, 2007; doi:10.1152/jn.00507.2007. To investigate the nature of the visuomotor transformation, previous studies have used pointing tasks and examined how adaptation to a spatially localized mismatch between vision and proprioception generalizes across the workspace. Whereas some studies found extensive spatial generalization of single-point remapping, consistent with the hypothesis of a global realignment of visual and proprioceptive spaces, other studies reported limited transfer associated with variations in initial limb posture. Here, we investigated the effects of spatially localized remapping in the context of a visuomanual tracking task. Subjects tracked a visual target tracing a simple two-dimensional geometrical form without visual feedback except at a single point, where the visual display of the hand was shifted relative to its actual position. After adaptation, hand paths exhibited distortions relative to the visual templates that were inconsistent with the idea of a global realignment of visual and proprioceptive spaces. Results of a visuoproprioceptive matching task showed that these distortions were not limited to active movements but also affected perception of passive limb movements.

INTRODUCTION

Visually guided behavior requires that the nervous system transforms visuospatial information into appropriate motor commands. To investigate the mechanisms that underlie visuomotor adaptation in humans, a wide range of different perturbations in the visual display has been used (for review see, e.g., Kornheiser 1976; Redding et al. 2005). In particular, previous studies have used pointing tasks in which subjects receive concurrent visual and proprioceptive information only at isolated locations (Baraduc and Wolpert 2002; Bedford 1989, 1993; Ghahramani et al. 1996; Magescas and Prablanc 2006; Vetter et al. 1999). These studies examined how single-point remapping affects pointing to other locations of the workspace with the goal of inferring, from the observed patterns of generalization, the nature of the visuomotor transformation (Imamizu et al. 1995).

Using wedge prisms, Bedford (1989, 1993) reported spatially extensive transfer of adaptation to localized remapping, interpreted as "a preference for changes in space perception that shift space rigidly everywhere" (Bedford 1999). Vetter et al. (1999) introduced a localized discrepancy between felt and seen position of the fingertip using a virtual-reality setup. Consistent with Bedford's findings, "this induced significant changes in subjects' pointing behavior over the entire workspace that did not decay significantly with distance from the remapped location" (Vetter et al. 1999). However, a straightforward interpretation of these findings is precluded because other studies—also using localized remapping paradigms—reported a gradient of generalization associated with variations in initial limb posture (Baraduc and Wolpert 2002; Ghahramani et al. 1996).

In the present study, we examined visuomotor adaptation in a manual tracking task. Previous research studied tracing and tracking under altered visual feedback, in particular, to assess the respective roles of visuoproprioceptive and visuomotor conflicts in adaptive changes of the relationship between visual and sensorimotor spaces (e.g., Baslev et al. 2004; Guédon et al. 1998; Lajoie et al. 1992; Miall and Cole 2006; Prablanc et al. 1975; Scheidemann 1950; Tsao 1950). Also, tracking tasks—with or without visual perturbation—have been used to examine eye–hand coordination—that is, the interaction of two motor systems driven by different sources of spatial information (e.g., Gowen and Miall 2006; Vercher et al. 1996, 2003). Here, our goal was to use a tracking task—instead of a pointing task—to explore the patterns of generalization associated with adaptation to spatially localized remapping. It has indeed been suggested that the spatial information used in the motor production of a form/object (e.g., tracing/drawing and writing) and that involved in reaching to a target/object may fundamentally differ (see e.g., Paillard 1971).

Our subjects were instructed to track, with their unseen hand, a visual target moving along the contour of a simple two-dimensional (2D) geometrical form (circle or square). They were not provided with visual feedback about their limb position except at a single point along the contour of the form, where the cursor controlled by the hand was shown at a position that was shifted relative to its actual position. Our idea was to test whether subjects would respond to the single-point remapping by shifting the entire form/object (i.e., adaptation of its location)—consistent with the idea of a global realignment—or whether, instead, adaptation would remain limited and induce alteration of the spatial relationship between the different parts of the form (i.e., adaptation of its shape), consistent with local adaptation processes.

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We found that subjects did not respond to the visual shift by globally translating the traced forms. Instead, after adaptation, hand paths exhibited clear distortions relative to the visual templates. A follow-up visuoproprioceptive matching test (*experiment* 2) showed that these distortions were not limited to the production of active hand paths, but also extended to the perception of passive hand displacements.

METHODS

Experimental setup

Forty-eight healthy subjects, right-hand dominant for writing, participated in the study. All subjects provided informed consent to procedures that complied with guidelines set by the University of Western Ontario Research Ethics Board. Subjects were naïve to the purpose of the experiment. Thirty-six subjects (20 women and 16 men, aged 19–25 yr) participated in *experiment* 1 and 12 different subjects (6 women and 6 men, aged 23–36 yr) participated in *experiment* 2.

Subjects were seated and held the handle of a two-link manipulandum (Interactive Motion, Cambridge, MA). Position signals were obtained from 16-bit encoders (Gurley Precision Instruments), providing endpoint accuracy within ±0.1°. Subjects produced arm movements in a horizontal plane with their right arm supported by an air sled. A chinrest was used to limit trunk and head motions. A visual target was presented using a semisilvered mirror placed between the arm and a back-projection screen. Thus the target appeared to float in the same plane as the hand (for a schematic, see Mattar and Gribble 2005). The target was a 1-cm-diameter white dot presented on a dark blue background. Visual feedback (given only at the end of each tracking trial; see following text) of the position of the hand was provided by displaying a white doughnut (ID and OD: 8 and 10 mm, respectively). A curtain prevented vision of the shoulders.

Experimental procedures

In *experiment* 1 and 2, subjects were instructed to track a moving visual target with their unseen hand while holding the handle of the manipulandum. The visual target was moving along the perimeter of a circle (10-cm radius) or a square (20-cm edges), centered at the origin. The origin was defined by the subject's body midline and the frontal plane 27 cm from the chinrest. For each tracking trial, the visual target first appeared stationary at one point on the perimeter of the 2D form, and then started moving around the perimeter of the form in a counterclockwise direction, for a total of eight cycles. For the circle, the target accelerated over the first half of the circle to reach an angular velocity of 144°/s (0.40 Hz). For the square, the velocity profile of the moving target was bell-shaped along each edge. The target traced the first and second edges in 1,750 and 1,500 ms, respectively, and then traced each edge in 1,250 ms (0.20 Hz). For each trial, on the last half of the last (eighth) cycle, the target decreased its moving pace in a symmetrical way to come to rest at the same position at which it initially appeared, and was then extinguished, 2 s later.

At the beginning of each tracking trial, the subjects' had their hand positioned at a point interior to the form; specifically, a point pseudorandomly sampled among the four corners of a 5 × 5-cm origin-centered square. The subjects were asked to move their hand to the target when it appeared on the perimeter of the shape and to track it as it began to move. During each trial (eight cycles) subjects saw nothing other than the moving visual target; they had no visual feedback about the position of their hand, nor did they see a visual template representing the circle or the square. It was only at the end of the trial, once the target was stationary again, that the doughnut cursor representing the position of the hand was revealed. The target

and the doughnut hand cursor were visible simultaneously for 2 s, after which they were both extinguished. The subjects' arm was then guided by the manipulandum pseudorandomly to one of the four corners of the 5 × 5-cm origin-centered square.

Unbeknown to subjects, we introduced systematic shifts between the position of the hand cursor and the actual position of the unseen hand (see following text).

Experiment 1

The goal was to test whether a localized remapping between vision and proprioception would result in a translation of the complete form. In *experiment* 1, 36 subjects were divided into two groups; 12 subjects tracked a target moving around a circle and 24 subjects tracked a target moving along the edges of a square. Each of the two groups was further divided into four adaptation conditions, defined by two visual shifts and two locations of visual feedback per shift (see Figs. 1 and 2, *top row*).

For the group of subjects who traced circles (*n* = 12), the hand cursor was shifted either 5 cm to the left (Fig. 1, *A* and *B*) or 5 cm "up" (away from subject's body; Fig. 1, *C* and *D*) relative to the actual position of the hand. For each visual shift, two opposite locations of feedback were used. For the leftward shift, the false feedback was provided either on the left (Fig. 1*A*, subjects c1–c3) or on the right (Fig. 1*B*, subjects c4–c6). For the "upward" shift, the false feedback appeared either at the "top" (distant point) of the form (Fig. 1*C*, subjects c7–c9) or at the bottom (Fig. 1*D*, subjects c10–c12). In all cases, subjects performed six trials (each counting eight cycles around the form) without visual feedback, followed by nine trials with false feedback given at the end of each eight-cycle trial, once the target had stopped moving (see preceding text).

The subjects who traced squares (*n* = 24) were also divided into four groups (see Table 1 or Fig. 2). For half of the subjects, the visual display was shifted diagonally "up-left" (5 cm away from subject's body and 5 cm left; Table 1, *A* and *B*). For the other 12 subjects it was shifted diagonally "up-right" (5 cm away from subject's body and 5 cm right; Table 1, *C* and *D*). For each visual shift condition, subjects were further divided into two groups receiving false feedback about hand position at opposite corners of the square. For the up-left shift, 6 subjects received false feedback at the top left corner (Table 1*A*, subjects s1–s6), whereas for the other 6 subjects false feedback was shown at the bottom right corner (Table 1*B*, subjects s7–s12). For the up-right shift, half of the subjects received false feedback at the top right corner (Table 1*C*, subjects s13–s18) and the other half received it at the bottom left corner (Table 1*D*, subjects s19–s24). All subjects performed six trials (each of eight cycles) without visual feedback, followed by a series of trials in which they received false feedback at the end of each eight-cycle trial (see preceding text). The number of trials varied across subjects (9–15). The criterion for stopping was defined as three successive trials in which the visually displayed position of the hand (hand cursor) ended within a distance of 2.5 cm from the visual target.

To explore how subjects adapted to multiple locations of false feedback, two groups of subjects tracking squares underwent three additional sets of trials so that they received false feedback in all four corners of the square, one after another in a succession of separate sets of trials (subjects s1–s6, Table 1*A* and subjects s13–s18, Table 1*C*). In each of these sets subjects received false terminal feedback at a different corner. As shown in Table 1*A*, after the first two sets of trials (one without visual feedback and one with feedback at the top left corner), subjects s1–s6 performed three more sets with false feedback given at the bottom left corner, the bottom right corner, and the top right corner. Table 1*C* shows the sequence for subjects s13–s18.

Experiment 2

In the second experiment, we addressed two further issues. First, we wanted to explore possible effects of adaptation on the perception of
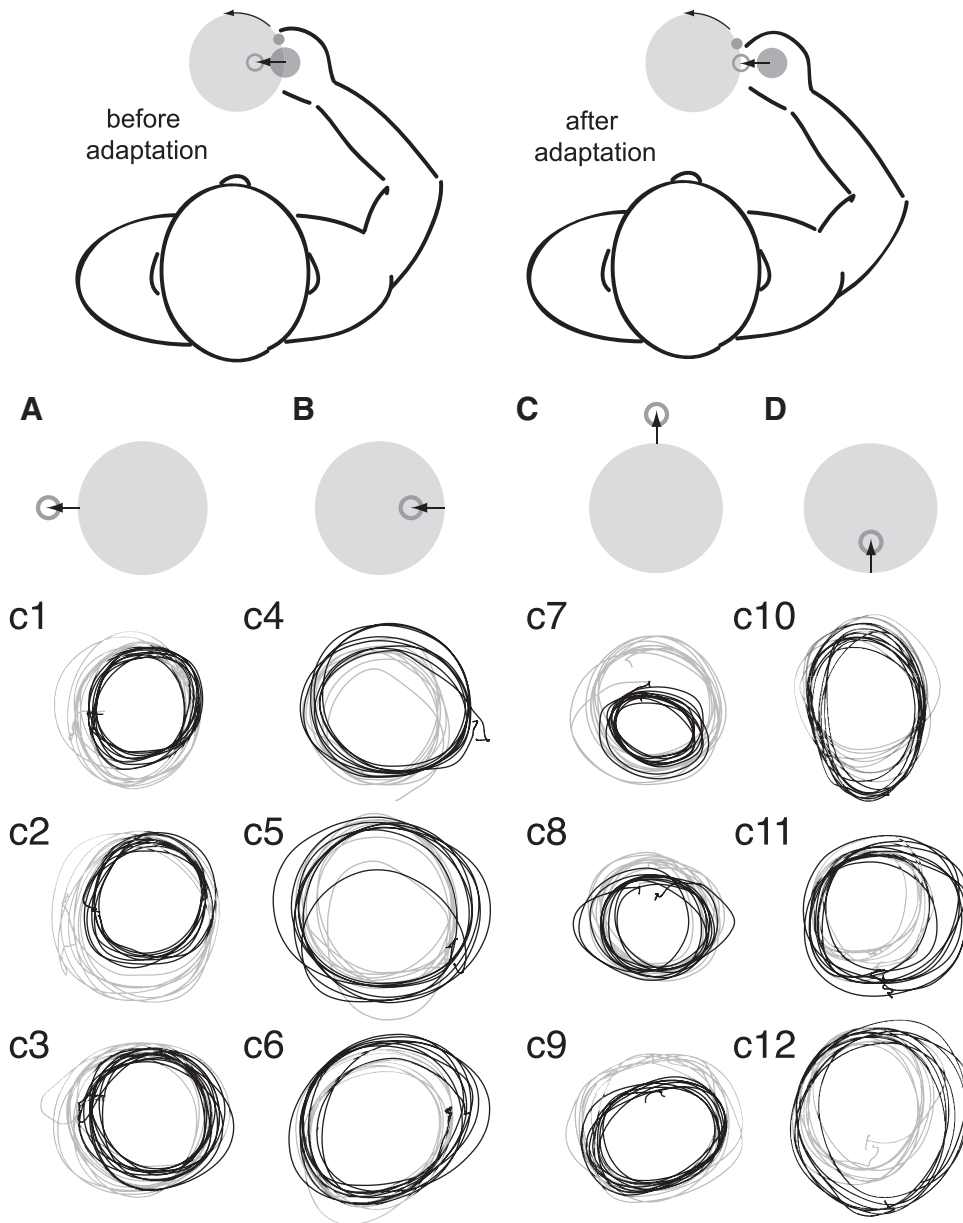
FIG. 1. In *experiment* 1, 12 different subjects tracked a target moving along a 10-cm-radius circle. Gray-filled disks correspond to the displacement of the visual target (they were not visible during the tracking task). Arrows indicate the direction of the shifts introduced in the visual display of the hand position. Small doughnuts indicate where, along the contour of the form, the hand position was shown at the end of each adaptation trial: before adaptation (*top left*) and after adaptation (*top right*). *A–D*: 2 visual shifts and 2 locations of visual feedbacks per shift were used, defining 4 adaptation conditions (3 subjects performed each condition). *Top row* presents schemas for each of the conditions. Hand paths produced in the complete absence of visual feedback are plotted in gray (last trial without vision) and black traces show subjects' tracking behavior induced by the localized remapping (last adaptation trial).

passively imposed limb displacement. Second, we wanted to examine the patterns of transfer observed across identical forms traced in adjacent workspace locations. Twelve subjects (who did not participate in *experiment* 1) participated in *experiment* 2, which consisted of two separate sessions, on different days, each lasting about 1.25 h. Each session included three phases: an adaptation period, a visuoproprioceptive matching task (passive arm movements), and a transfer test (active tracking). The two sessions differed only in the visual feedback provided during the adaptation phase.

In both sessions, during the adaptation phase, the subjects were asked to track, without visual feedback about their hand position, the visual target whose path described a square identical to the one in *experiment* 1. This time the false visual feedback of the position of the hand was shifted 5 cm to the left (instead of diagonally as in *experiment* 1). In Session 1 the subjects received feedback, in separate sets of trials, only at the two left corners of the square, whereas in Session 2 they received feedback at all four corners (see Table 2 for the sequence of trials). The idea here was in Session 1 to induce a pattern of adaptation in which subjects traced a rectangular shape (instead of a square) and in Session 2 to produce a pattern of

adaptation in which subjects traced a square translated relative to the visual target path. As in *experiment* 1, in all cases, false feedback about hand position was given for 2 s only at the end of each eight-cycle trial, once the visual target came to rest.

The perception task and the transfer test were identical in both sessions. In the perception task, the target moved along the same square as in the adaptation phase but at a slightly slower pace (moving along each edge within 1,500 ms, instead of 1,250 ms) and cycling three times instead of eight. At the same time that the visual target was tracing the square, the manipulandum displaced the subjects' arm along the edges of an unseen rectangle with different aspect ratios from trial to trial (Fig. 7A). The subjects were asked to judge (giving a verbal response) the path of the passive hand displacement as being "too wide" or "too narrow" compared with the square traced by the moving visual target. A position servo-controller was used to passively displace the limb using stiffness and viscous damping parameters of 2,000 Nm^{-1} and 10 $Nm^{-1} \cdot s$, respectively. The robotic arm moved in synchrony with the visual target; that is, both moved from one corner to the next one in the same time (thus always moving at a slightly different speed along each individual edge). The area of the

TABLE 1.

Sequences of trial-sets for the four groups of subjects who tracked the visual target around a squared path in Experiment 1. Each trial consists of eight cycles around the shape. The gray-filled squares correspond to the displacement of the visual target. The small doughnuts show the location of altered visual feedback and the arrows indicate the direction of the visual shift introduced in the visual display of the hand position.

proprioceptive rectangles was kept constant throughout the stimulus series, but was adjusted for each subject to match the area defined by the path they traced at the end of the previous adaptation trial. The visual stimulus was always the same. [Note: one may be concerned by the difference in speed between the displacement of the visual target and that of the hand carried by the robot. Indeed, it has been shown that movement kinematics may have an influence on haptic sense (Viviani et al. 1997; although see Soechting and Poizner 2005 who did not find similar effects). However, because the conditions of the perceptual task were identical in both Sessions 1 and 2, any possible bias would be identical in both sessions.]

Each trial started at the bottom left corner of the rectangle/square. Subject's hand was positioned 5 cm to the right of the visual target, corresponding to the position at which it was positioned as a result of complete adaptation. Each subject performed 36 trials. A two-alternative forced-choice adaptive staircase algorithm was used in which two series of 18 stimuli were randomly interleaved, one starting with a "wide" rectangle (stretched horizontally by a scale factor of 1.3), the other one with a "narrow" rectangle (contracted by a factor of 0.8). On each trial, the proprioceptive stimulus was modified as a function of subject's response (Henriques and Soechting 2003; Kesten 1958; Treutwein 1995). For each series of 36 trials, the size of the initial ratio change was set such that, with correct responses, proprioceptive rectangles changed from narrow to wide (or wide to narrow) on the 6th trial. The path of the visual target did not change throughout the whole series of trials.

After the perceptual test, subjects performed a transfer test, in which they were asked to perform a single active tracking trial (of eight cycles) without any visual feedback. In this trial, they were required to track the visual target moving along the edges of a square identical to the one traced during the adaptation phase (before the perceptual task) but situated at the right of it (Fig. 8A). In particular, the "adaptation" and the "transfer" squares were positioned contigu-

ous to each other so that they had an edge in common, the left edge of the transfer square overlapping the right edge of the adaptation square (Fig. 8A). The eight-cycle transfer trial started at the top right corner of the first (adaptation) square or, equivalently, at the top left corner of the second (transfer) square. Notice that whereas tracing this edge corresponded to a movement away from the body in the adaptation phase, it corresponded to a movement toward the body in the transfer trial.

Data analysis

For the active tracking tasks, hand endpoint positions were sampled at 200 Hz and low-pass filtered at 20 Hz using a Butterworth filter implemented in Matlab (The MathWorks). Data processing and statistical inference were conducted using Matlab and SAS (SAS Institute), respectively. For *experiment* 1, we measured the positional changes observed at two points on the contour of the form: the location of visual feedback and the point opposite to it (see Figs. 1, 2, and 4). Positional change was defined as the difference in hand position (averaged over eight cycles) in the direction of the visual shift observed between the last trial performed without visual feedback and the last adaptation trial. Also, as a way to assess potential changes induced by adaptation in movement directions along the edges of the squared form, we measured the angle between line segments intersecting at the corner at which false feedback was given.

In *experiment* 2, for the adaptation phase of each session, we measured changes in the position (along the frontal axis, direction of the visual shift) of the left and right edges of the traced square. For both sides of the square, the frontal-axis positions of 100 points spanning the edge were averaged for each cycle. The mean over the eight cycles was then computed. Also, for each traced form we computed an index of proprioceptive "squareness," defined as log (width/height), with width and height measured along the frontal and radial axes, respectively. Thus positive values were associated with wide rectangles and negative values with narrow rectangles. To compute height and width we used the mean of the eight endpoints (eight cycles) at each corner and computed the mean distance along the radial and frontal axes, respectively.

For the perception task, to obtain estimates of subjects' "squareness thresholds," the response profiles collected during the perception task were fitted with a logistic function (Fig. 7B) using a maximum-likelihood method (Harvey 1997). For the transfer test, we measured the frontal-axis positions of the hand paths along the "ambiguous" edge (the right edge of the adaptation square or the left edge of the transfer square; see Fig. 8A). For each cycle the frontal-axis positions of 100 points spanning the edge were averaged. We also measured the "squareness" (as indicated earlier) of the traces produced during the transfer trial.

For both experiments, *t*-tests and/or repeated-measures ANOVAs were run. For all results, the threshold for statistical significance was set at $\alpha = 0.05$; for post hoc comparisons, *P* values were compared with α-levels adjusted by using Bonferroni correction.

R E S U L T S

Form shape/size distortion rather than form translation

In *experiment* 1, a first group of 12 subjects tracked the target moving along a circular path. Initially, without any visual feedback, subjects' hand paths (*gray traces*, Fig. 1, *A–D*) roughly matched the visual template (gray disk, *top row*). As subjects adapted to the false visual feedback of their hand position, the circles they traced became distorted (*black traces*, Fig. 1, *A–D*). Moreover, the same visual shift had very different effects depending on the location of feedback. Specifically, the circles were expanded or contracted depending on the
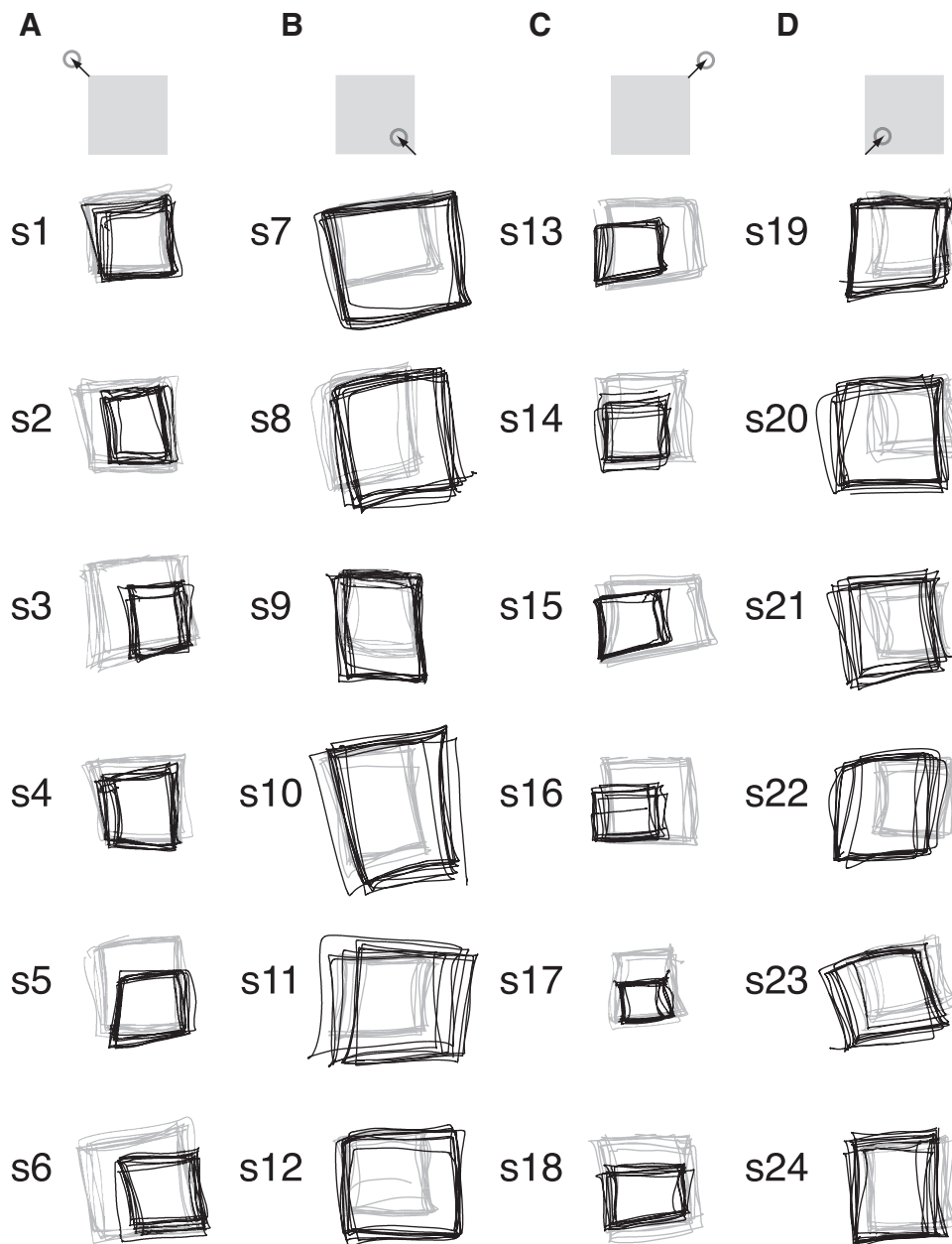
A   **B**   **C**   **D**

s1   s7   s13   s19

s2   s8   s14   s20

s3   s9   s15   s21

s4   s10   s16   s22

s5   s11   s17   s23

s6   s12   s18   s24

FIG. 2. In *experiment* 1, hand paths for 24 different subjects as they tracked a target that moved along a (not visible) square (shown by the gray-filled squares), before (*gray traces*) and after adapting to false feedback about hand position (*black traces*). Small doughnuts indicate the location of the altered visual feedback provided at the end of each 8-cycle adaptation trial. Arrow indicates the direction of the shift in the visual display. *A* and *C*: subjects who received feedback at the "top" of the square (away from subject's body) compressed their tracking movements. *B* and *D*: providing altered visual information at the "bottom" of the square (close to subject's body) induced expansion of subjects' movements.

relation between the location of feedback and the direction of the visual shift. For a 5-cm leftward shift (Fig. 1, *A* and *B*) subjects who received feedback on the left side of the circle contracted their hand paths, shifting the left side of the circular path to the right (Fig. 1*A*), whereas those for whom the shifted hand position was shown on the right, expanded their movements, shifting the right side of the circle to the right (Fig. 1*B*). Similarly, for a 5-cm shift away from the body (up, in Fig. 1, *C* and *D*), remapping the hand position at the top of the circle induced a compression of the movements, shifting the top side of the circle downward (Fig. 1*C*). In contrast, feedback provided at the bottom produced expansion (Fig. 1*D*). Also, depending on the subjects, either the forms were globally rescaled or the *x*/*y* gain was changed (subjects tracing ellipses instead of circles).

To quantitatively assess the changes in movement paths, we considered the mean positional changes induced from the last trial without vision to the last adaptation trial (mean over the eight cycles), along the axis of the visual shift. We compared movement paths at two points: at the location of feedback and at the opposite point. That is, for the leftward shift (Fig. 1, *A* and *B*), we compared the changes along the frontal axis at the left and at the right of the circle. For the "upward" shift (away from subject's body; Fig. 1, *C* and *D*), we compared the changes along the sagittal axis at the "top" (furthest) and the "bottom" (closest) points of the circle. The effect of the remapping differed significantly between the two locations. Although adaptation was not complete, significant adjustments consistent with the visual shift were observed at the point of feedback [$t(11) = 11.18$, $P < 0.0001$], whereas changes at the opposite point were not statistically different from zero [$t(11) = -0.46$, $P = 0.6548$]. Mean ($\pm$SE) changes in hand position were 3.8 ± 0.4 cm for the feedback location and -0.1 ± 0.2 cm for the opposite point [$t(11) = 8.60$, $P < 0.0001$].

TABLE 2.

Session 1	Session 2
Adaptation phase	Adaptation phase

Set 1
6 trials
    Set 2
    9 trials
        Set 3
        9 trials
Set 4
2 trials
    Set 5
    2 trials
Set 6
2 trials
    Set 7
    2 trials
Set 8
2 trials
    Set 9
    2 trials

Set 1
3 trials
    Set 2
    3 trials
        Set 3
        9 trials
            Set 4
            9 trials
Set 5
2 trials
    Set 6
    2 trials
Set 7
2 trials
    Set 8
    2 trials
Set 9
2 trials
    Set 10
    2 trials
        Set 11
        2 trials
            Set 12
            2 trials

Perception task	Perception task
36 trials	36 trials
Transfer test	Transfer test
1 trial	1 trial

Experiment 2 consisted of an adaptation phase, a perception task and a transfer test. The sequences of trial-sets for the adaptation phase were different for Session 1 and 2. Note that in both Sessions 1 and 2, false feedback was given over the course of several sets of trials, in which the feedback alternated between different corners of the square. The purpose of this alternation was to prevent subjects from drifting back to their original correspondence between vision and proprioception (\zharv\Smeets et al. 2006\zharvx\). The perception task and the transfer test were the same in both sessions.

For the subjects who tracked the target moving along the edges of a square ($n = 24$) the effect of adaptation also depended on the feedback location relative to the direction of the visual shift; subjects reduced (Fig. 2, *A* and *C*) or expanded (Fig. 2, *B* and *D*), sometimes dramatically, the form they were tracing. For instance, subjects who saw the hand cursor shifted "up-left" at the top left corner of the square traced smaller squares (*black traces*, Fig. 2*A*) by the end of adaptation than during the baseline trials (*gray traces*, Fig. 2*A*). Conversely, subjects who saw the hand cursor shifted in the same way but at the bottom right corner did the opposite: they traced larger squares (*black traces*, Fig. 2*B*).

To provide some information about the time course of adaptation over trials, we show in Fig. 3 the complete learning sequence for two individuals (subjects s7 and s13, whose hand paths are shown in Fig. 2). Typically, adaptation was not instantaneous after the first exposure to the bias; rather, changes in the traced shape started after several trials. For subject s7, for example, the traced shape began to expand to accommodate the shifted visual feedback on the fifth or sixth trial. For subject s13, the traced shape began to compress on the third or fourth trial.

To quantify this pattern we compared the positional changes observed at the two opposite corners falling along the diagonal axis of the visual shift. Figure 4, *A–D* shows, for each remapping condition, all subjects' 95% confidence regions for the mean corner positions (over eight cycles) of the last trial without vision (light gray) and the last adaptation trial (dark gray). For all subjects ($n = 24$), changes in position observed at the two corners differed substantially [$t(23) = 15.46$, $P < 0.0001$]. When subjects adjusted their hand position at the feedback location [$t(23) = 17.42$, $P < 0.0001$] no significant positional change could be observed at the opposite corner [$t(23) = 0.89$, $P = 0.3836$]. Mean ($\pm$SE) positional changes were 9.0 ± 0.6 cm for the feedback location (which corresponds to overcompensations because the diagonal visual-display shifts were 7.07 cm) and 0.5 ± 0.5 cm for the opposite corner.

Although these results indicate that localized remapping did not produce the translation of the complete forms (consistent with the idea of a global realignment of vision and proprioception) they do not indicate strictly local adaptation either. Whereas subjects adapted the location of the corner at which false feedback was provided, at the same time they preserved the orientation of the edges adjacent to the point of remapping. We calculated the angle between the two edges defining the corner at which false feedback was provided. The data of
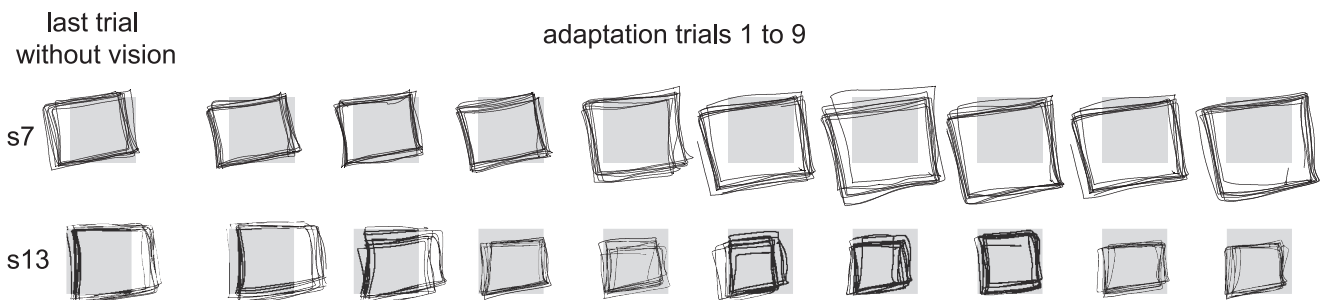
last trial without vision   adaptation trials 1 to 9

FIG. 3.   Hand paths for 2 individual subjects (s7 and s13, whose data are presented in Fig. 2) for adaptation trials 1 to 9 (*experiment* 1). Squares traced before these adaptation trials (last trial without visual feedback of the hand) are shown on the *left*, and serve as baseline.
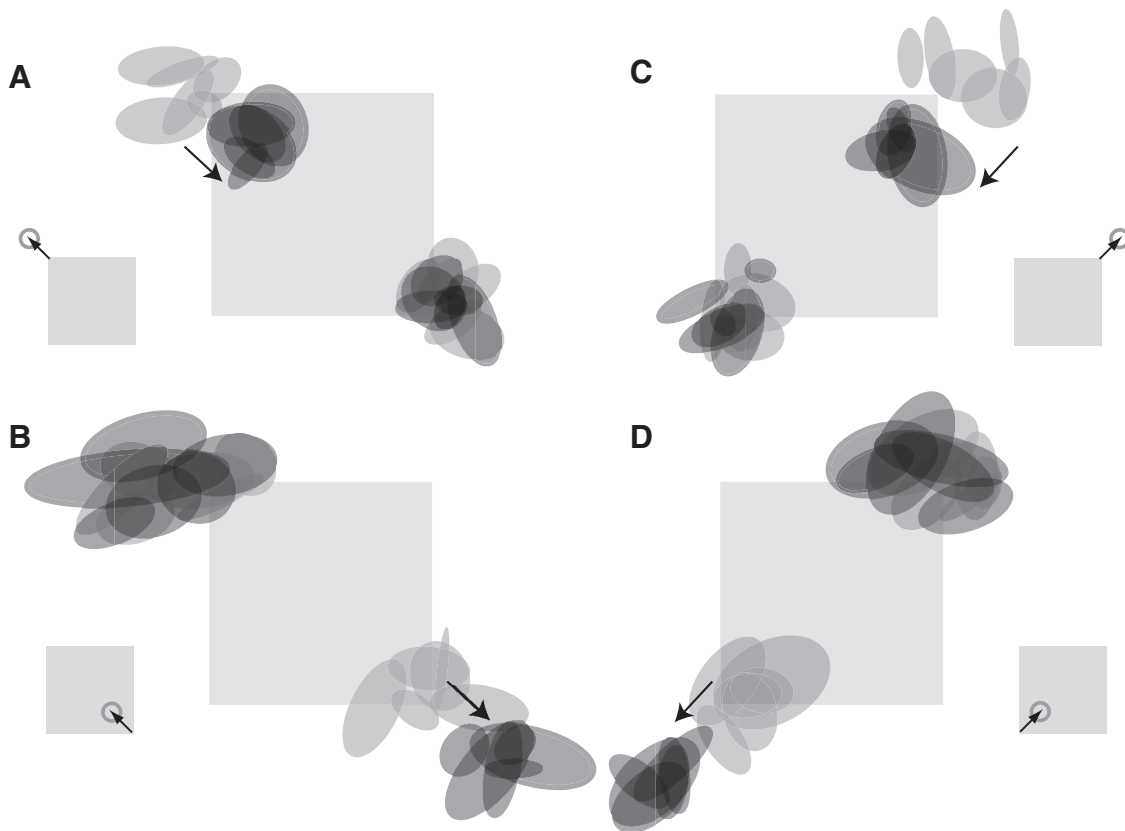
FIG. 4. *A–D* correspond respectively to Fig. 2, *A–D* (*experiment* 1). For each subject, 95% confidence ellipses for the mean hand positions (over 8 cycles) at 2 points: at the corner where subjects received false visual feedback and at the opposite corner. Light gray ellipses correspond to the corner endpoints on the last trial performed without any visual feedback. Dark gray ellipses show endpoint variability observed on the last adaptation trial.

subjects s1–s6 and s13–s18 were regrouped because for these two groups strictly local adaptation would have resulted in increasing the angle at the feedback corner. Similarly, we pooled the data for subjects s7–s12 and s19–s24, for which an angular decrease would have been expected. Comparing the angles before and after adaptation did not reveal any effect of adaptation on this variable [adaptation epoch × group interaction effect: $F(22,1) = 0.76$, $P = 0.3920$; group effect: $F(22,1) = 2.36$, $P = 0.1390$; adaptation epoch effect: $F(22,1) = 0.54$, $P = 0.4701$]. For subjects s1–s6 and s13–s18, mean angles were $91.5 \pm 1.2348°$ before and $91.7 \pm 1.6772°$ after adaptation. Means for s7–s12 and s19–s24 were respectively 89.5 ± 2.0330 and $87.5 \pm 1.7508°$ before and after adaptation.

We also tested how subjects adapted their hand paths when they received false feedback successively at each corner of the square. Figure 5, *A* and *B* shows data for subjects s1–s6 and s13–s18, respectively (see also Table 1, *A* and *C*). In both figures each column shows the data for the last trial of each set. (Thus in Fig. 5, *A* and *B*, the traces in *columns i* and *ii* are the same as those plotted respectively in gray and black in Fig. 2, *A* and *C*.) It is interesting to note that the traces the subjects produced after they had received altered feedback at only one side of the square (the two left corners in Fig. 5*A* and the two right corners in Fig. 5*B*) resembled rectangles rather than squares (see *column iii* in Fig. 5, *A* and *B*) as subjects compressed movement along the frontal axis.

Experiment 2 consisted of two sessions on separate days, each including three phases: a preliminary adaptation phase

(that was essentially a replication of *experiment* 1), a perception task, and a transfer test (see METHODS). Consistent with our previous observations (see Fig. 5*A*, *column iii*) restricting the feedback to the left edge of the square in the adaptation phase of Session 1 induced a compression of movements along the frontal axis as subjects locally updated their hand position. As a result, by the end of Session 1 adaptation phase, subjects traced narrow rectangles rather than squares. Comparing the last trial performed without vision and the last adaptation trial showed that adaptation produced different positional changes along the frontal axis for the two sides of the square [$t(11) = 9.59$, $P < 0.0001$]. Subjects appreciably shifted their hand trajectories at the left edge [$t(11) = 9.59$, $P < 0.0001$], whereas the changes observed for the right side of the square were not statistically reliable [$t(11) = 1.90$, $P = 0.0834$]. Mean ($\pm$SE) group positional changes were 5.3 ± 0.7 cm for the left edge and 1.0 ± 0.4 cm for the right.

The effect of adaptation in Session 2 also differed between the two sides of the square [$t(11) = 5.25$, $P = 0.0003$]. There was no significant difference in mean hand position between the end of adaptation in Session 1 and the end of adaptation in Session 2, for the left edge [$t(11) = -0.96$, $P = 0.3566$], whereas a difference was seen for the right edge [$t(11) = -9.18$, $P < 0.0001$]. Mean differences in hand positions at the end of adaptation between Sessions 1 and 2 were -0.5 ± 0.3 cm for the left edge and -4.5 ± 0.6 cm for the right. Figure 6*A* shows the hand positions at the corner for the last trial performed with vision (light gray), the last adaptation trial of Session 1 (medium gray), and the last adaption trial of Session 2 (dark gray).
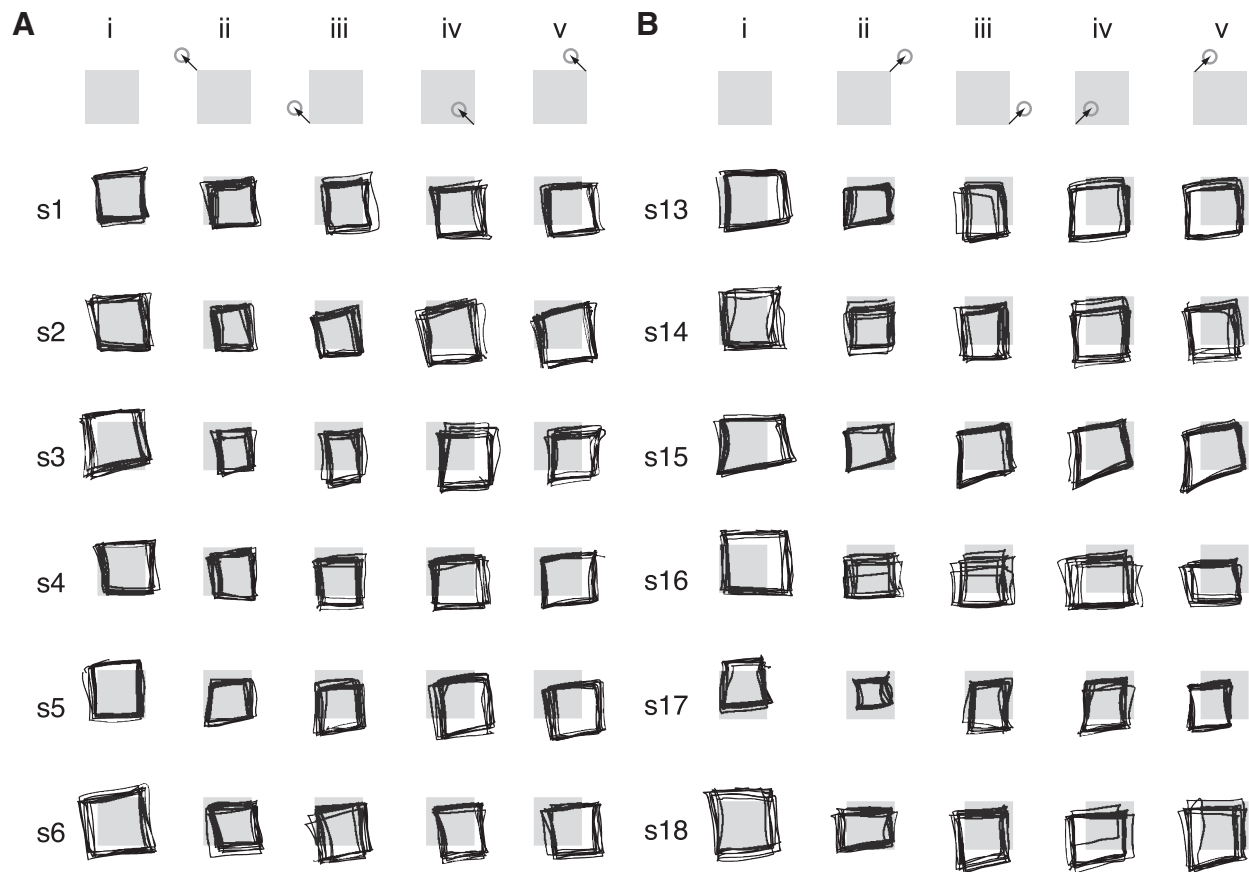
FIG. 5. *A*: hand paths for subjects s1–s6 (*columns i* and *ii* show the paths plotted respectively in gray and black in Fig. 2*A*). *B*: hand paths for subjects s13–s18 (*columns i* and *ii* correspond respectively to the *gray* and *black traces* in Fig. 2*C*, *experiment* 1). *A* and *B*, *top row* indicates the shift applied to the visual feedback of the hand, as well as the location where feedback was provided. Subjects successively received feedback at each corner of the square (*columns ii–v*). One may notice that the traces produced after subjects received feedback at 2 corners of the square (*column iii*) resembled rectangles rather than squares as subjects reduced their movements along the frontal axis.

To quantitatively assess the distortions in the traced forms following the two different adaptation conditions (Session 1 vs. Session 2), we calculated an index of "squareness" (see METHODS), for each session and for each subject (Fig. 6*C*; individual data are presented to show bias differences across subjects). The visual feedback condition (Session 1 vs. Session 2, i.e., number of feedback points) had a significant effect on the squareness of the traced shapes [$F(2,22) = 37.63$, $P < 0.0001$]. On the last adaptation trial of Session 1, subjects traced shapes that were considerably narrower than those on the last trial without vision [$t(22) = 7.13$, $P < 0.0001$] (as illustrated in Fig. 6*B*, *top*). At the end of Session 2, the hand paths were roughly square and did not differ from those produced without vision in Session 1 [$t(22) = -0.72$, $P = 0.4818$] (as illustrated in Fig. 6*B*, *bottom*). Mean squareness across subjects for the last trial without vision was 0.041 ± 0.022, for the last adaptation trial in Session 1 was -0.205 ± 0.039, and for the last adaptation trial in Session 2 was 0.066 ± 0.021.

Distortion extends to perception

The foregoing results show that learning a localized remapping produced distortions in subjects' active hand paths. Did adaptation also alter the relationship between visual information and proprioceptive perception of passive limb displacements?

In the vision/proprioception matching task in Session 1 subjects showed perceptual biases that were congruent with the distortions observed in their active tracking (compare Figs. 6*C* and 7*C*). That is, subjects reported that passive hand displacements that followed the edges of a narrow rectangle matched the visual square (mean "squareness threshold" = -0.142 ± 0.039). In contrast, in Session 2 after adaptation to altered visual feedback at all four corners of the square, subjects tended to report that passive hand paths along the edges of slightly wide rectangles matched the target path (Fig. 7*C*). This latter perceptual bias is consistent with that observed in the complete absence of visual information (Fasse et al. 2000; Henriques and Soechting 2003). Mean "squareness threshold" in Session 2 (0.102 ± 0.028) was significantly different from that assessed in Session 1 [$t(11) = 58.17$, $P < 0.0001$]. The relationship that was observed between the active tracking behavior and perception is shown in Fig. 7*D* (Pearson's $r = 0.889$, $P < 0.0001$, for data regrouped over both sessions; for Sessions 1 and 2, respectively, $r = 0.894$, $P < 0.0001$ and $r = 0.385$, $P = 0.217$. The function log (width/height) is roughly linear within the range of values that we observed for the ratio width/height.) This correspondence is also illustrated in Fig. 6*B*, which shows, for a single subject, the adapted active tracking (*black thin traces*) along with the shapes corresponding to the perceptual biases (*gray thick traces*) for Session 1 (*top*) and Session 2 (*bottom*).
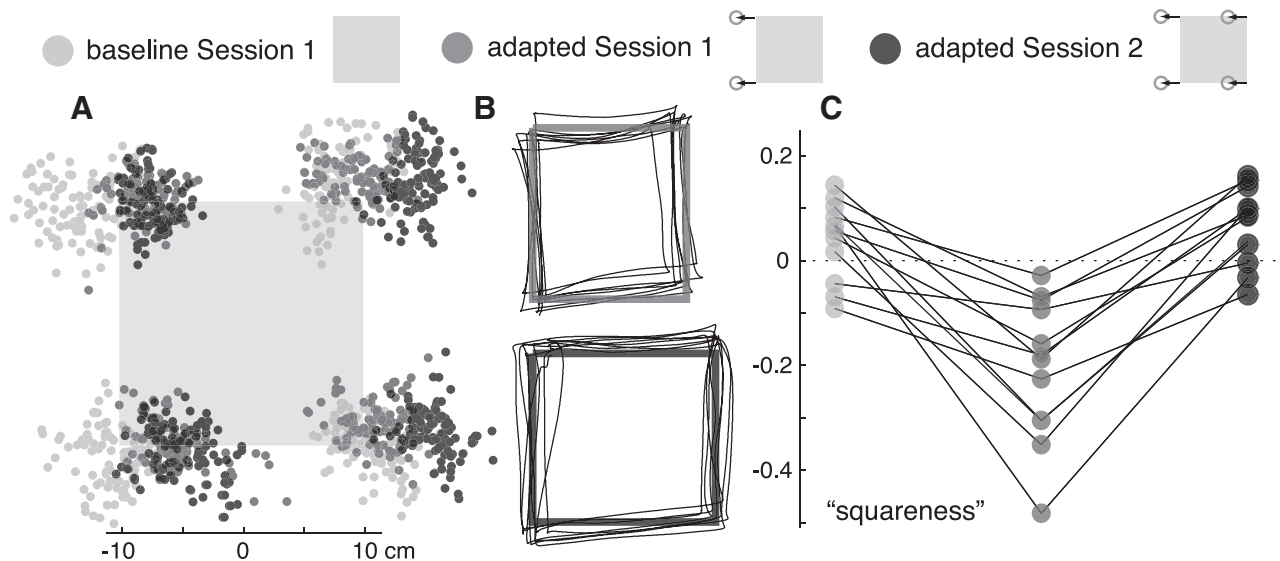
FIG. 6. *Experiment* 2 included 2 sessions each consisting of a preliminary adaptation phase: a perception task and a transfer test. Two sessions differed only in the visual feedback provided during the adaptation phase. In Session 1, subjects received visual feedback of their hand position only on the left side of the square, whereas in Session 2 all 4 corners were remapped. *A*: for all subjects, endpoints are plotted for the last 8-cycle trial performed without vision in Session 1 (light gray) and on the last adaptation trial of each session. By the end of the adaptation phase in Session 1 (medium gray) subjects had adjusted their hand trajectories along the left edge but not on the right side of the square. In contrast, endpoints for Session 2 (dark gray) were shifted for both edges. *B*: traces produced by a single subject on the last trial of the adaptation phases of Sessions 1 and 2. Superimposed squares correspond to the subject's "squareness threshold" (see Fig. 7). *C*: "squareness" measures, log (width/height), of the traces produced by the subjects for the last trial without vision in Session 1 and the last adaptation trial in Sessions 1 and 2. Positive squareness values correspond to "wide" rectangles and negative values to "narrow" rectangles.

Transfer to a translated form

After the perception task in both Sessions 1 and 2, we asked subjects again to track the visual target moving along the edges of a square with their unseen arm. The square was identical to that presented during the adaptation phase (and the perceptual task) but was translated to the right (see Fig. 8*A* and METHODS). Figure 8*B* shows the trace produced by a single subject on the complete transfer trial (eight cycles) in Sessions 1 and 2. In Session 1 (*left plot*), the first movement along the ambiguous edge (thick gray line) clearly differed from the traces produced
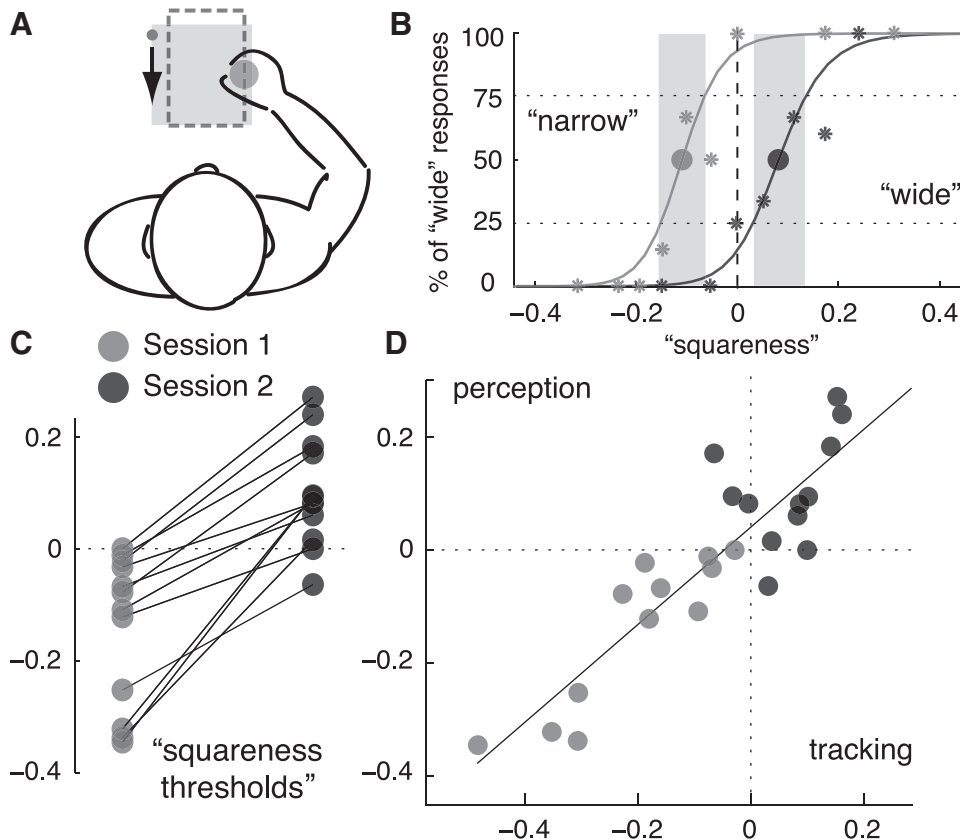

FIG. 7. *A*: in the perception task of *experiment* 2, as subjects were presented with the visual target moving around the square (the arrow indicates the direction of the target's displacement), they had their hand guided by the manipulandum along the edges of a rectangle. Motions of the visual target and those of the hand were synchronous so that when the target reached one corner of the square contour the hand reached the corresponding corner of the proprioceptive rectangle. *B*: an adaptive staircase procedure was used in which subjects reported whether the rectangle they passively traced with their hand was "too narrow" or "too wide" to match the path of the visual target. Narrow rectangles are associated with negative "squareness threshold" values and wide rectangles with positive values. Data from one subject are shown. *C*: subjects' perceptual bias changed with the conditions of the visuomotor adaptation. *D*: biases in subjects' "squareness" perception were closely related to the distortions observed in their active tracking.
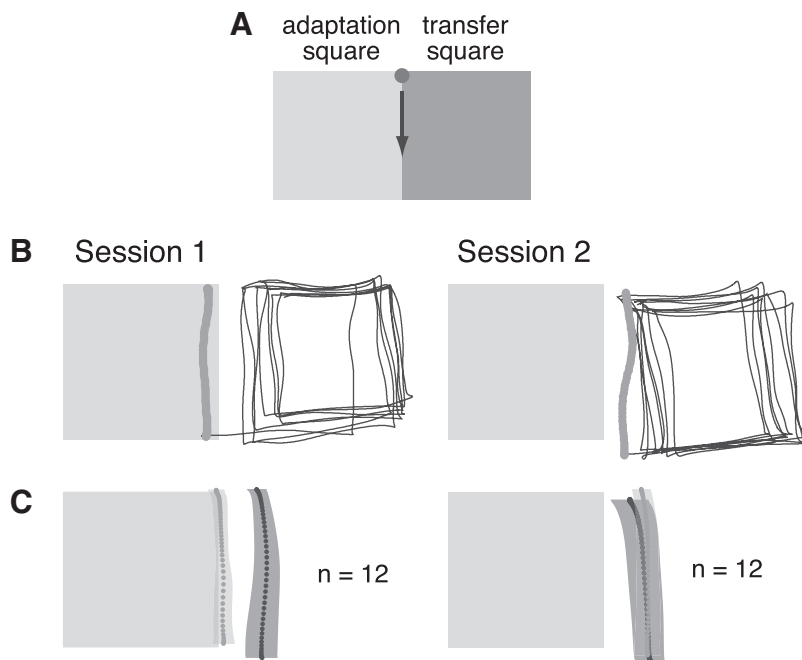
FIG. 8. *A*: after the adaptation phase and the perceptual task, subjects were required to track the target along the edges of a second square (shown in dark gray) contiguous to the first one so that the 2 squares had an edge in common. Arrow indicates the direction of the target displacement. *B*: for Sessions 1 and 2, traces by a single subject for the 8 cycles of the transfer trial. First movement segment is highlighted in gray. *C*: mean frontal axis positions ($\pm$SE) across subjects for the movement segment along the ambiguous edge. For both sessions, the means for the first and second cycles are shown in light and dark gray, respectively.

on the following cycles, even though the path of the visual target was identical. Although the hand path on the first cycle overlapped the visual edge, on the second cycle the subject shifted the hand path rightward. In other words, immediately on recognizing the square, the subject translated it as a whole to the right.

Figure 8*C* presents group data consistent with the illustrative single-subject traces. The *left plot* shows the mean hand path across subjects for the first tracking segment (light gray) for Session 1, along with the mean path for the same edge on the second cycle (dark gray). Significant differences were observed between the position along the frontal axis (axis of visual shift) of the ambiguous edge for the last adaptation trial (mean over eight cycles) and the first and second cycles of the transfer trial [$F(2,22) = 41.28$, $P < 0.0001$]. Although there was no significant difference between the last adaptation trial and the first transfer cycle [$t(22) = -0.45$, $P = 0.6594$], subjects positioned their hand differently on the first and second transfer cycles [$t(22) = -7.64$, $P < 0.0001$]. The mean of the frontal axis positions of the ambiguous edge for the last adaptation trial was 10.1 ± 0.5 cm, for the first transfer cycle was 10.4 ± 0.4 cm, and for the second transfer cycle was 15.8 ± 0.8 cm.

Results for the same transfer test in Session 2 (in which subjects adapted to visual feedback provided at all four corners) offer a different picture: from the very first cycle around the transfer square subjects shifted their hand rightward relative to the visual target (Fig. 8, *B* and *C*, *right plots*). No significant differences were seen between the mean hand positions for the last adaptation trial, the first transfer cycle, and the second transfer cycle [$F(2,22) = 1.26$, $P = 0.3028$]. Mean frontal-axis positions of the ambiguous edge were 9.6 ± 0.3, 11.0 ± 0.6, and 10.5 ± 1.0 cm, for the last adaptation trial, the first transfer cycle, and the second transfer cycle, respectively. It is worth noting that in Session 2 subjects likely remembered the contiguous (transfer) square they encountered in Session 1. In contrast, in Session 1 most subjects were clearly surprised

when the target unexpectedly turned right, instead of left, for the first time to initiate the second edge of the second (transfer) square.

Also interesting was the comparison between the complete shapes traced in the two transfer tests. Indeed, surprisingly the hand paths for the second and subsequent cycles in Session 1 transfer test trial and the complete transfer trial in Session 2 had comparable squareness. The mean squareness index over seven cycles in Session 1 was -0.017 ± 0.042 and over eight cycles in Session 2 was -0.004 ± 0.038 [$t(11) = -0.57$, $P = 0.5832$]. Indeed, between the first and second cycles in Session 1 readjustment in hand position extended to the right side of the transfer square. Mean frontal positions for the first and second cycles were 31.0 ± 1.0 and 35.31 ± 1.1 cm, respectively [$t(11) = -7.35$, $P < 0.0001$].

DISCUSSION

Using a manual tracking task, we tested how the tracing of a form would be affected by the introduction of a visual bias for an isolated point along its contour (not visible to the subjects). Would subjects translate their entire hand paths (i.e., adapt the location of the form) or, instead, would their adjustments remain local and apply to parts of the traced shape only (i.e., alter its shape)? The patterns of adaptation that we observed were inconsistent with the idea of a global realignment of visual and proprioceptive spaces because the subjects did not adapt to the localized remapping by globally shifting their entire hand paths. Instead, after adaptation, they traced distorted forms. However, the distortions induced in the hand paths did not reflect strictly local adaptation either. Indeed, when tracking the target around the circle, some subjects adapted by stretching their circular hand paths into ellipses (which would be consistent with local adaptation), but others globally rescaled their circular hand paths. Also, in the square tracking, had adaptation been restricted to the point of feedback, the directions of the edges of the square-shaped forms

would have been altered. In contrast, whereas they adjusted their hand position at the feedback location, the subjects preserved the direction of their movements, thus modifying the amplitude of their strokes. As a consequence, the forms they traced were sometimes dramatically altered in size (expanded or contracted) and/or proportion relative to the visual template (e.g., subjects tracing rectangles rather than squares). That is, whereas different subjects could respond differently to the localized perturbation, some by global scaling, others by x/y gain changes—a heterogeneity that we do not explain—all subjects in the square tracking exhibited the same propensity not to modify the direction of their movements.

Using a measure of visuoproprioceptive matching, we found that these distortions also extended to the perception of passive limb displacements (subjects matching proprioceptive rectangles with a visual square). However, these distortions did not transfer when, after adaptation, subjects had to track the visual target moving along the contour of the same "form/object" but translated to the right of their workspace (transfer test in Session 1 of *experiment* 2).

Our conclusion differs from that of Bedford. Why? The most obvious candidate is that we used a different task—we used tracking rather than pointing. Pointing consists of positioning (transport and stabilization) of a body segment relative to a stationary visual target (topokinesis; see e.g., Paillard 1971). In contrast, tracking a visual target moving along a recognizable form/object involves different spatial information processing: that is, operations on intraobject space and the extraction of perceptive invariances, supporting the identification and recognition of the form/object (morphokinesis; see e.g., Paillard 1971).

After adaptation, hand position adjustment at the location of feedback did not result in the translation of the entire form. Moreover, the observed distortions reflected independent processing of spatial attributes in the form/object visual template (Smeets et al. 2002): the location of the corners and the tilt and length of the edges. The nature of the spatial information used in reaching movement has been largely debated. According to one view, the final egocentric position of the endpoint (position coding: Bizzi et al. 1984; Desmurget and Prablanc 1997; Feldman 1966; Flanders et al. 1992; Rosenbaum et al. 1995; Van den Dobbelsteen et al. 2001) is crucial, whereas according to another view, the direction and distance of the target relative to the starting position are the most relevant (vector coding: Atkeson and Hollerbach 1985; Bock and Eckmiller 1986; Ghez et al. 1997; Rossetti et al. 1995; Vindras and Viviani 1998; Vindras et al. 2005). However, it seems that, depending on the task and the available information, subjects may flexibly switch between the different types of spatial coding (e.g., Grave et al. 2004). In the present experiments, although the subjects may have used postural information to adjust the position of their hand at the location of false visual feedback (starts of the trials), the induced distortions (in which subjects preserved the tilts of the edges but altered their lengths) reflected independent processing of movement direction and amplitude, consistent with vector coding (Vindras et al. 2005).

When tested for transfer of adaptation to an adjacent workspace location, on recognition of the squared visual target path (after the initial cycle along the transfer square, Session 1 of *experiment* 2) subjects shifted their entire hand paths. That is, high-level identification of the second (transfer) square induced

its complete translation in space. Whereas in the adaptation phase subjects distorted the squared form into a rectangle, in the transfer test they shifted it, unaltered in its intrinsic spatial properties ("squareness"). These results may be related to the idea of distinct processing of form/object position and form/object shape (Paillard 1971). For instance, it has been shown that when forms are drawn continuously without vision, their position drifts but their shape is preserved (Brown and Rosenbaum 2001; Brown et al. 2003; Verschueren et al. 1999; Zelaznik and Lantero 1996). In addition, our results present some similarities with research that demonstrates presaccadic compression of visual space: the perceived locations of objects shift toward the saccade goal just before saccades (Dassonville et al. 1995; Honda 1993; Lappe et al. 2000; Morrone et al. 1997; Ross et al. 1997). Interestingly, Matsumiya and Uchikawa (2001) reported that, although distances between separate objects are compressed, the apparent width of a single object remains unaltered by this phenomenon. That is, whereas presaccadic compression of visual space shifts the apparent location of an object, it does not distort its shape, and thus does not affect its recognition.

In our study, why did subjects translate only the form/object in the transfer test? One conjecture may be as follows. Because the contour of the form was never visible as a whole, the subjects had to mentally reconstruct it from the visual target path. Thus one may speculate that, in the initial adaptation trials, the subjects may have processed the different parts of the form (i.e., its edges) separately. On initial exposure to the new tracking task, the attentional load imposed by solving the sensory-feedback mismatch (e.g., Blouin et al. 1993; Ingram et al. 2000; Miall and Cole 2007; Rossetti 1998) may have hindered the spatial integration of the movement sequence into a coherent form/object. This in turn may have contributed to motor correction to be applied to hand path components only, rather than to the form as a whole. In the absence of any further sensory error signal and without any change in the task conditions, subjects may have simply maintained this schema throughout the whole adaptation period. In contrast, on initiation of the transfer test, the subjects were by then very familiar with the visual contour traced by the target and so they may have relied to a greater extent on internal cues to guide their movements (Gowen and Miall 2006). Driven by the internal representation of the form/object, the subjects would have been more concerned with maintaining the overall shape of the traced contour (e.g., the relative distance between the corners of the square), as they would if they were drawing the form from memory rather than truly tracking the moving target.

Finally, even though the mechanisms involved in prism adaptation and those recruited by learning in virtual-reality environments may fundamentally differ (Redding and Wallace 2006; Redding et al. 2005) it would be worth exploring possible parallels. Several studies have demonstrated that prism adaptation involves the cerebellum (e.g., Baizer et al. 1999; Martin et al. 1996; Morton and Bastian 2004; Stein and Glickstein 1992; Weiner et al. 1983). There is also a growing body of evidence supporting the idea that the parietal and premotor areas may play an important role in visuomotor adaptation (Kurata and Hoshi 1999). In particular, whereas slow developing adaptive sensory changes may depend on cerebellar mechanisms, functional neuroimaging (e.g., Clower et al. 1996; Inoue et al. 1997, 2000), lesion studies (e.g., Gréa

et al. 2002; Newport and Jackson 2006; Newport et al. 2006; Pisella et al. 2000, 2004; Rode et al. 1998/1999; Rossetti et al. 1998), and transcranial magnetic stimulation experiments (Desmurget et al. 1999) suggest involvement of the posterior parietal cortex for more high-level cognitive strategies (also see Newport and Jackson 2006). Because our results also point to the idea of adaptation processes at multiple levels, it would be interesting to determine which anatomico-functional distinctions may be identified and associated with the contrasting patterns of adaptation and generalization we observed in the present study.

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