Exp Brain Res (2005) 160: 384–393
DOI 10.1007/s00221-004-2017-8

RESEARCH ARTICLES

Denise Y. P. Henriques · Martha Flanders · John F. Soechting

Distortions in the visual perception of shape

Received: 27 January 2004 / Accepted: 17 June 2004 / Published online: 10 September 2004

Abstract It is known that visual illusions lead to a distorted perception of the length and orientation of lines, but it is not clear how these illusions affect the appreciation of the shape of closed forms. In this study two experiments were performed to characterize distortions in the visual perception of the shape of quadrilaterals and the extent to which these distortions were similar to the distortions of haptically sensed shapes. In the first experiment human subjects were presented with two quadrilaterals side by side on a computer monitor. One was a reference shape; the other was rotated and distorted relative to the first. The subjects used the computer mouse to adjust the corners of the distorted quadrilateral to match the shape of the target quadrilateral. They made consistent errors on this task: the adjusted quadrilateral was about 2% wider and about 2% shorter than the veridical shape. Furthermore, subjects adjusted the inner angles of the quadrilateral to make them closer to 90°. The first type of error was also present in a second experiment in which, in a two-alternative forced-choice paradigm, subjects viewed a reference shape and were asked to indicate which of two transiently presented quadrilaterals was closest to the target shape. The width/height errors and the inner angle errors were comparable to those described previously when subjects felt the outline of a quadrilateral and then drew its reproduction in the absence of vision, suggesting that the distortion occurs in the process of remembering the shape.

Keywords Visual illusions · Humans · Length perception · Angle perception · Quadrilateral shape

D. Y. P. Henriques · M. Flanders · J. F. Soechting (✉)
Department of Neuroscience, University of Minnesota,
6-145 Jackson Hall, 321 Church St. SE,
Minneapolis, MN 55455, USA
e-mail: soech001@umn.edu
Tel.: +1-612-6257961
Fax: +1-612-6265009

Introduction

The properties of various sensory systems and the manner in which sensory information is processed centrally introduce distortions in the perception of our surroundings. Perception is usually the result of multisensory integration and each of the sensory systems generally introduces characteristic and unique distortions. Thus there is the potential for conflicting information from various sensory systems. Nevertheless, we do not perceive such conflict and instead experience a unified event.

In some instances such a unified perception comes about because one sensory modality dominates whenever it is present. For example, the perception of body orientation in space is subserved by vestibular, somatosensory, and visual inputs (Nashner and McCollum 1985). It appears that vision, when it is present, dominates vestibular and somatosensory information about spatial orientation and motion in space (Berthoz et al. 1975; Thilo and Gresty 2002; Young et al. 1973). In other instances, visual information may serve to recalibrate or modify input from other sensory modalities. One example is provided by alterations in the auditory map of space (Knudsen 1985; Knudsen and Knudsen 1989). This may be true as well for the kinesthetic perception of hand trajectory. For example, Flanagan and Rao (1995) altered a visual display such that straight hand paths were displayed as curved. Subjects subsequently modified their hand trajectories to produce curved paths that were straight on the visual display (see also Goodbody and Wolpert 1999).

In a recent study we characterized the distortions in subjects' haptic sense of the form of simple geometric objects (Henriques et al. 2004). Specifically, subjects followed along the edges of quadrilaterals without vision of the shape or of the arm and then reproduced the sensed shape by means of an arm movement in free space. Among the consistent distortions that we found, the most marked one was a distortion in the aspect ratio (the ratio of height to width) of the shapes, regardless of the orientation of the shape. Distortions have also been reported in the visual perception of the relative lengths of lines with different orientations (Avery and Day 1969; Butler 1983; Taylor 2001). However, it is not clear whether the haptic shape distortions that we found were congruent with the visual line illusions that have been described.

To resolve this question we performed two experiments in which we asked subjects to make visual judgements of the similarity of shapes presented in different orientations. In one experiment subjects adjusted the sides of one quadrilateral using a computer mouse in an attempt to match the shape of a reference quadrilateral. In the second experiment we presented subjects with a reference shape and asked them to indicate which of two briefly presented quadrilaterals was closest in shape to the reference.

Methods

Subjects

A total of 21 human subjects (12 men, 9 women; aged 20–59 years) with no history of sensory, perceptual, or motor disorders participated in the two experiments. Seven of these subjects participated in experiment I, while 18 performed experiment II; four subjects participated in both. All gave informed consent, and all procedures were approved by the Institutional Review Board of the University of Minnesota.

Experiment I: effect of orientation on the visual perception of the shape of quadrilaterals

We tested how well subjects assimilate visual shape information by having them modify the contours of one quadrilateral to match those of another. Using a custom-written program (LabVIEW, National Instruments) we presented the outlines of two quadrilaterals simultaneously, side-by-side on a 21-in. flat panel monitor. The centers of the two quadrilaterals were separated by 18 cm (22° visual angle), far enough apart so that both shapes could not be foveated simultaneously. The orientation of the quadrilateral on the right varied relative to the one on the left. Furthermore the shape of the right quadrilateral was presented in a distorted form: its corners were each randomly displaced by an average of 0.7 cm from the undistorted locations of the target shape. Using a computer mouse subjects moved the corners of this right quadrilateral-the adjustable shape-to match the shape of the target quadrilateral on the left.

The adjustable quadrilateral was presented in one of six orientations rotated 0°, 60°, 120°, 180°, 240°, or 300° from the orientation of the target quadrilateral. To define the orientation of both shapes, one of the lines of the adjustable quadrilateral, the anchor line, and its corresponding line in the target quadrilateral were drawn in red. The remaining lines were drawn in black on a gray background. A colored dot was placed in each corner and the corresponding dots for the two shapes had the same color.

Figure 1 depicts the 12 target-quadrilaterals (left and middle columns) that were used. Six of the target-quadrilaterals had one line oriented along either the horizontal or vertical axis (left column). For five of these shapes this cardinal-line was also the anchor line (dashed line). The other six quadrilaterals had the same shapes as the first six but were rotated by 120° relative to the first six (middle column). The individual lines of the target quadrilaterals were 1.9–12.1 cm long, and perimeters were always 30 cm. The relative angles between the lines ranged from 38 to 148°.

Figure 1 also shows the other five rotated forms of quadrilateral #1 (right column). When first presented, the corners of the adjustable quadrilateral were each shifted between 0 and 2.4 cm (mean=0.5 cm along the x- and y-axes) from the matching corners of the target reference. This display set-up is shown in Fig. 2A. The circles and gray lines show the ranges over which the corners were displaced from the correct locations (x's), producing an adjustable quadrilateral, rotated 240° from the orientation of the target quadrilateral. The corners of the anchor line (dashed line) were shifted only along its length (gray lines) and could only be moved along this same axis, so that subjects could adjust the length of the anchor line but not its orientation. Both quadrilaterals were continuously

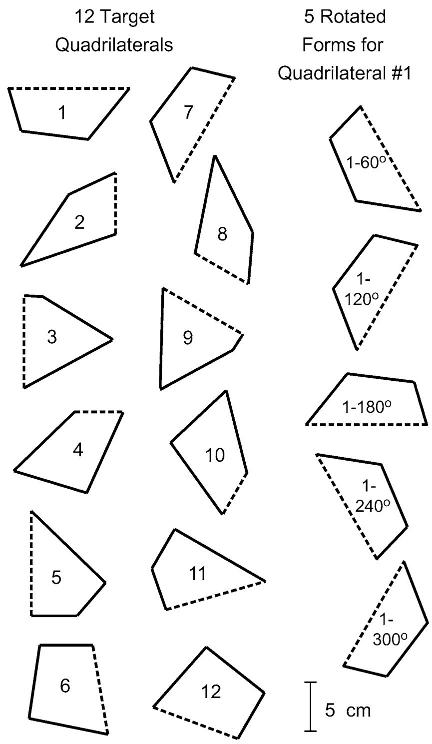


Fig. 1 Target quadrilaterals used in experiment 1. The *left two columns* depict the 12 shapes that were presented in undistorted form as “target” quadrilaterals. Shapes 7–12 are identical to shapes 1–6, but have been rotated by 120°. Each target shape had a perimeter of 30 cm. The distorted quadrilaterals were also presented in one of five rotated orientations, as shown in the *right-most column* for shape #1. The dotted lines were presented on the computer monitor as a solid line of a distinct color to provide unambiguous information about the relative rotation between the target and the distorted quadrilateral

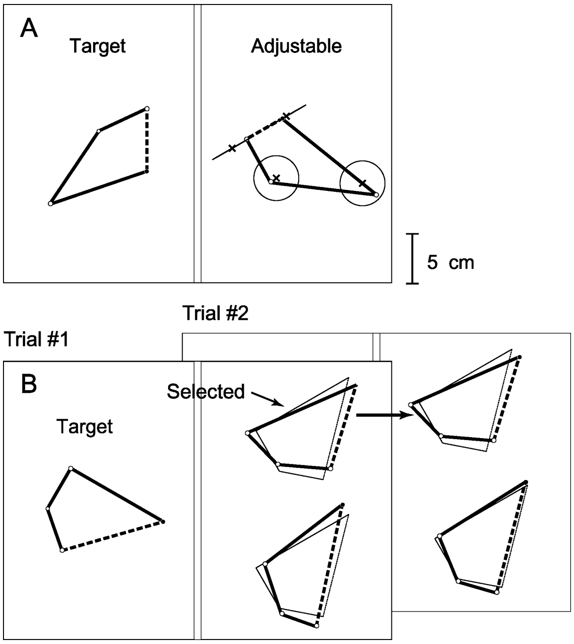


Fig. 2 Schematic of the visual display in the two experiments. **A** In experiment 1 the target and the adjustable quadrilateral were displayed statically side by side. One line (*dashed*) was presented in a different color to indicate the orientation of each shape. On the adjustable quadrilateral, the length of this line, but not its orientation, could be changed, as indicated by the *light gray line*. The locations of the other two corners could be changed arbitrarily. The *x*'s mark the corners of the undistorted shape and the *circles* (or *lines*) indicate the range of distortions used in the experiment. **B** In experiment 2 the target was presented statically, but the two distorted ("contending") quadrilaterals were presented briefly, first one at a time and then together, one above the other. Subjects selected the shape they felt corresponded most closely to the target shape. On the next trial, the selected shape did not change (*arrow*), but the distortion of the other shape was decreased. Veridical shapes are shown in *light gray*

visible so that subjects could make frequent comparisons by shifting their gaze from one to the other.

Subjects altered the shape of the adjustable quadrilaterals by clicking on one of the corner dots with the PC mouse and dragging it into the desired location. Once they felt that the quadrilateral they were adjusting matched the shape of the target quadrilateral, they clicked an "accept" button, which ended the trial and began the next. Each of the 12 target quadrilaterals was paired three times with each of the six rotated forms of the adjustable quadrilateral for a total of 216 trials. The experiment took about 2–3 h to complete, and it was divided into several sessions across one or 2 days to prevent fatigue and boredom.

We measured the location, length, and orientation of the lines, and the relative angles between the lines of the adjusted quadrilaterals. We then compared the extent to which the orientation, length, and inner angles of these adjusted lines differed from the lines of the target quadrilateral. In analyzing these errors we first computed the extent to which they depended on the amount of initial distortion in that parameter and corrected for that effect. For length errors we also corrected for any small differences between the perimeter of the target quadrilateral and the adjusted one. We then decomposed the remaining errors into two components: one that depended on the type of shape and one that depended on the orientation of the shape (Henriques et al. 2004). We computed the shape-dependent errors by calculating the average length of each segment and the average internal angle over all six rotations. The orientation-dependent errors were obtained by subtracting the shape dependent error. We conducted additional statistical tests (analyses of variance and *t* test) to determine whether these systematic errors varied with the orientation, length and inner angle of the target quadrilateral.

Experiment II: using transient cues in shape discrimination

In Experiment I subjects had unlimited time to make the visual comparison and could conceivably make use of all of the available cues (i.e., they could have performed a separate analysis of the length and orientation of each of the lines). It is known that our sense of parameters that contribute to the overall perception of the shape of a quadrilateral, such as the relative length, internal angle, and orientation of each side, may not be internally consistent (Fasse et al. 2000). Thus the results of the first experiment need not have reflected shape perception in a global sense. The second experiment was designed to force subjects to focus on more global aspects of the shape by limiting the viewing time.

We used a two-alternative forced choice design in which subjects had to compare briefly flashed shapes with a target shape that was present throughout the trial. Thus subjects were asked to indicate which of two distorted quadrilaterals (the "contending quadrilaterals"), presented briefly, most closely resembled the target quadrilateral. For one block of 30 trials the target quadrilaterals were presented on the left side of the flat screen, while the two contending quadrilaterals were arranged vertically on the right side of the screen (Fig. 2B). In another block of 30 trials the locations of the quadrilaterals were switched, with the target quadrilateral on the right and the contending ones on the left. The order of the blocks was counterbalanced across subjects. The centers of the two halves of the display were separated by 18 cm. While the target quadrilateral was continuously visible, the contending quadrilaterals were first presented one at a time, for 1 s each, and then simultaneously for another 1 s. The subject chose the contending quadrilateral that he/she thought most resembled the target quadrilateral by clicking on the location of the selected shape with the PC mouse.

In each block the target quadrilaterals were five of the 12 target quadrilaterals in experiment I, presented in random order. As in experiment I, the orientation of the contending quadrilaterals could differ from that of the target. The contending quadrilaterals were rotated either 0°, 60°, 120°, 180°, 240°, or 300° from the orientation of target shape, and all quadrilaterals had a red anchor line and colored corners for reference.

For each trial the shapes of the contending quadrilaterals were stretched along the cardinal axes of the screen but in opposite directions. One quadrilateral was contracted along the vertical axis and expanded along the horizontal axis by the same amount, so that it was shorter and wider than the target shape although its area was the same. The other quadrilateral was expanded vertically and contracted horizontally, and therefore it was taller and narrower. The order of presentation (wider on top or bottom) was randomized from trial to trial. The first trial for each set began with one of the contending quadrilaterals stretched 1.3 horizontally and contracted by 1/1.3 vertically (e.g., short-wide). The other one was scaled by a factor of 0.8 horizontally and by 1/0.8 vertically (e.g., narrow-tall) compared to the veridical shape.

For the 29 trials that followed the amount by which each quadrilateral was scaled (expanded-contracted, or contracted-expanded) along the horizontal and vertical axes was adjusted using a two-alternative forced-choice (2-AFC) adaptive staircase algorithm (Kesten 1958; for a review see Treutwein 1995). In this way the quadrilateral that was not selected (as being similar to the target quadrilateral) was presented in the next trial as less distorted (i.e., the amount by which it was expanded-contracted decreased). The distortion of the selected quadrilateral was left unchanged. This is illustrated in Fig. 2B; the contending quadrilaterals on the first trial are both distorted by equal amounts, with the top one shorter/wider and the bottom one taller/narrower. If subject chose the top one as most resembling the target quadrilateral, the stretching-contracting dimensions would be presented again in the second trial, but the bottom quadrilateral would be less narrow and tall to better resemble the target shape. For easier comparison the second trial in Fig. 2B features the same quadrilateral as the first trial. However, this was not the case in the actual experiment. In each trial, the target-quadrilateral (one of five) and the amount of rotation of the contending quadrilaterals were chosen at random.

Each time the subject altered his/her response from one type of distorted quadrilateral to the other (short-wide to tall-narrow and vice versa), the amount by which we expanded-and-contracted or scaled the quadrilateral was also decreased (see also Henriques and Soechting 2003). Reducing the step size after each reversal ensured that subjects were tested more frequently on scaled shapes closer to their perception of the target quadrilateral. Depending on subjects' responses, the scaled shape for either quadrilateral might approach a scaling factor of one, becoming identical to each other, or even cross 1.0 (switching its axes for expansion/contraction). If the subject responds consistently, the 2-AFC staircase should converge toward the subject's shape bias.

Results

Experiment I

Subjects took a mean of 38.9±20.0 s to move the corners of the adjustable quadrilateral to match the target quadrilateral. They were a bit quicker when the adjustable quadrilateral had the same orientation as the target quadrilateral (34.7 s) than when the shapes were oriented differently (39.7 s). Within this group of five different orientations there were no significant differences in processing time ($F_{(4,1056)}$=0.82, P=0.51). In experiments in which subjects are asked to make judgements about objects it is known that the reaction time is proportional to the amount by which one object is rotated relative to the other (see Georgopoulos et al. 1989; Shepard and Metzler 1971), an effect that has been attributed to a process of mental rotation. Presumably our subjects also used such a strategy, but it was not reflected in the trial lengths since our task required the subjects to make multiple comparisons between the two quadrilaterals to adjust each of the four corners.

Subjects also erred less in replicating the length and the orientation of the lines, and the inner angle between these lines, when both shapes were in the same orientation. Figure 3 shows the mean absolute values for errors in estimating line length (top), inner angles between lines (middle), and line orientation (bottom) for each orientation of the adjustable quadrilateral. The mean error in line length (over all orientations) was 4.0 mm. When the adjustable shapes were rotated with respect to the target shape, the average error was 4.3 mm (or 1.4% of the length, dark bars), significantly more (open stars, P<0.05) than the error for shapes oriented 0° (2.5 mm or 0.9% of the length, white bars). The absolute error in line length for obliquely oriented shapes was also greater than that seen when the shape was rotated by 180° (filled stars). Mean error in estimating the inner angle between lines was 3.5° when both quadrilaterals had the same orientation and 6.9° when they did not. This difference was also observed for absolute errors in orienting the individual lines, with mean errors of 3.0° and 6.0°, respectively. Over the course of the experiment we did not find trends in any of these errors that would indicate learning.

As a first step in analyzing the subjects' errors we determined the extent to which these errors depended on the initial distortion of the adjustable shape (Fig. 4). We then removed these initial distortion-dependent errors in the perimeter, length, and angles of the quadrilateral from the total error. Our subsequent analysis followed the procedures used previously to analyze distortions in the haptic sense of shape (Henriques et al. 2004). We related the errors in reproducing the lengths and orientations of each of the lines making up the quadrilateral to the lengths and orientations of the respective line of the reference quadrilateral. We performed a similar analysis on the inner angle between pairs of lines.

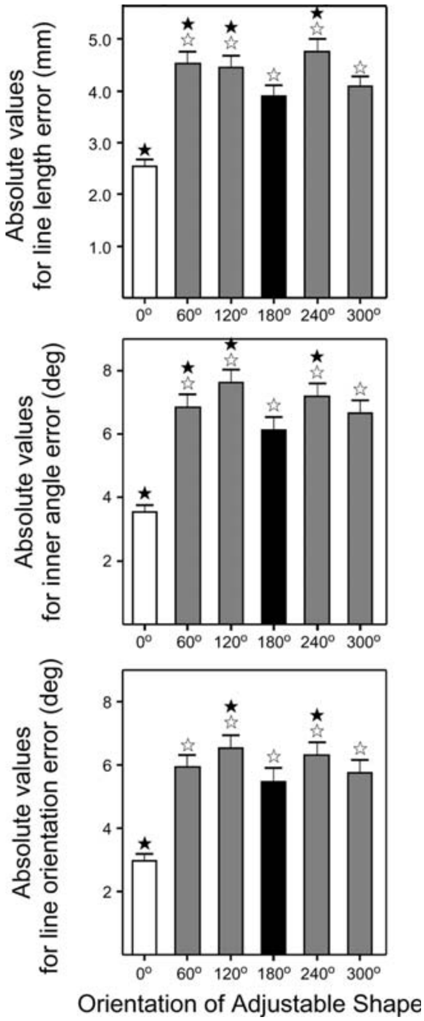


Fig. 3 Effect of relative orientation of target and adjustable quadrilaterals on errors in matching length of individual lines (*top*), inner angles between lines (*middle*) and the orientation of individual lines (*bottom*). Values that differ significantly from those when the adjustable quadrilateral had the same orientation (0°, *white bar*) are indicated by white stars; those that differ signicantly from the errors when the orientations differed by 180° (*black bar*) are indicated by *filled stars*. *Error bars* Standard error of the mean

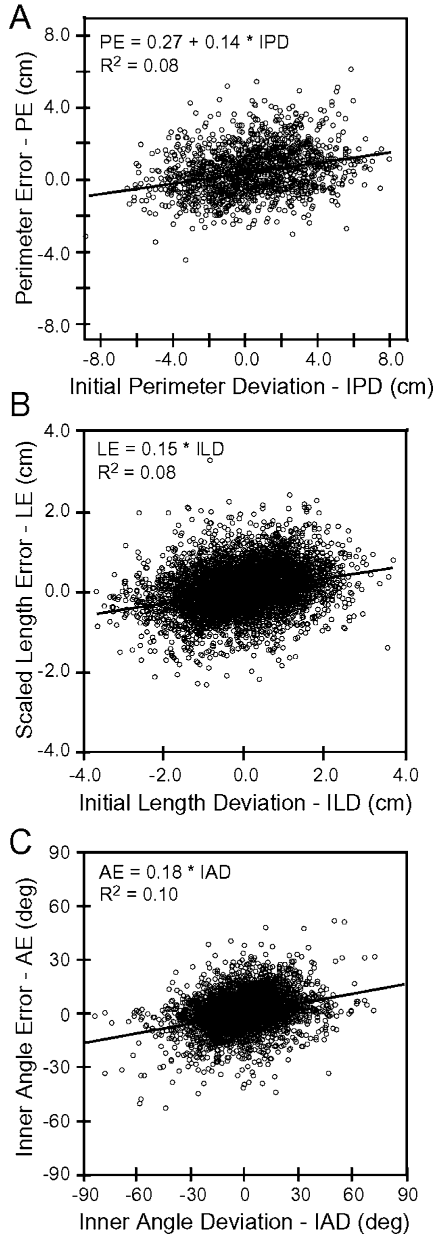


Fig. 4 Influence of the initial distortion of the adjustable quadrilateral on the final perimeter error (**A**), the error in scaled length (**B**), and the errors in the inner angles between adjacent line segments (**C**). Scaled lengths were computed by scaling the lengths of all four segments of the quadrilateral equally so that its perimeter equaled that of the target shape (30 cm). The *plots* show pooled data from all subjects and the *solid lines* depict the regression for each set of parameters. All regressions were significant ($P<0.001$)

Length errors

Although the target quadrilaterals always had a perimeter of 30 cm, displacing the corners of the adjustable quadrilateral changed the size of this shape, so that its initial perimeter ranged between 22 and 38 cm, with an SD of 2.6 cm. On average, subjects were relatively accurate in adjusting the size of this quadrilateral to match the target one (30.4 cm) with the adjusted perimeters ranging from 25 to 36 cm, with an SD of 1.3 cm. This variance in the size of the adjusted quadrilateral was partly the effect of the size of the original, distorted quadrilateral, prior to adjustments (R^2=0.08, P<0.001). That is, subjects tended to make the quadrilateral larger when its original distorted shape was larger than the reference and smaller when its original shape was smaller (Fig. 4A).

To compare length errors for the individual lines making up the quadrilaterals, in the remaining analyses we first corrected for these perimeter errors by scaling each segment equally so that the length of the adjusted perimeter equaled that of the target shape. In this way we computed errors in estimating line length by subtracting the lengths of these scaled lines from the lengths of the corresponding lines of the reference quadrilateral (scaled length errors).

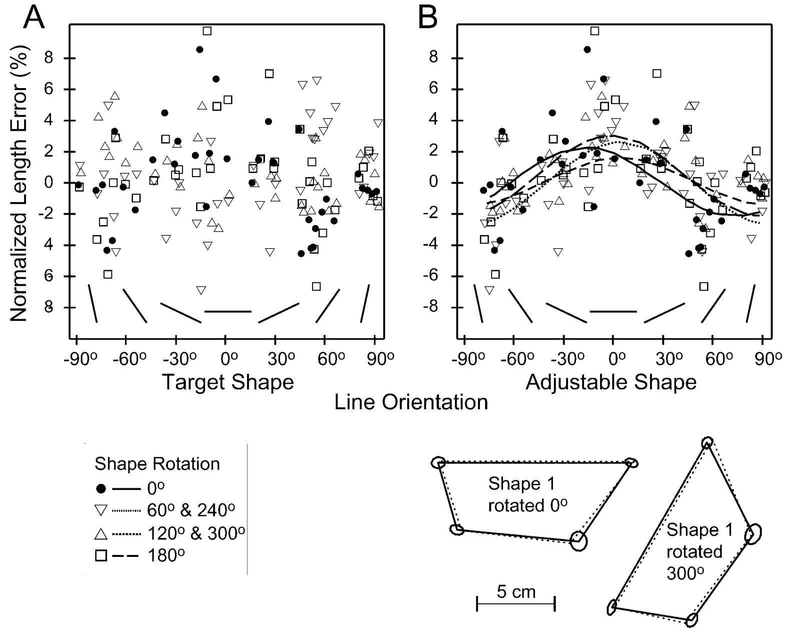


Fig. 5 Normalized length error as a function of the orientation of the line in the target shape (**A**) and in the adjustable shape (**B**). The different symbols denote the relative orientation between the target shape and the adjustable shape. *Each data point* depicts average results for one line segment. Normalized length error did not depend on line orientation in the target shape, but it varied significantly with the line's orientation in the adjustable shape, as indicated by the sinusoidal fits. *Bottom panel* Mean results for shape # 1 in two orientations (0° and 300°). *Solid lines* Adjusted shape; *dotted lines* target shape. Ellipses in the four corners depict the 68% confidence limits

Unsigned scaled length errors were small, with the average only 0.4 cm, or about 5.7% of the target line length. As with errors in adjusting the overall size of the quadrilateral, scaled length errors were influenced by the initial length of that line in the original adjustable quadrilateral. Scaled lengths of individual lines were as much as 3.9 cm smaller or larger than the length of the target line. Figure 4B shows how scaled length errors varied with the difference in the line length of the original adjustable quadrilateral and the corresponding length of the target quadrilateral.

We also measured whether the length of the target line influenced subjects' estimate of its length. Subjects' errors in adjusting line length were not influenced by the length of the target line (R^2=0.00). Thus there were no shape-dependent errors for line length.

Next we assessed orientation-dependent errors by determining whether the orientation of the line to be matched (target shape) or the line to be adjusted (adjustable shape) influenced subjects' estimates of line length. For example, did subjects adjust the corners of the adjustable quadrilaterals so that the resulting lines were longer when the corresponding target lines were oriented horizontally compared to when they were oriented along a diagonal? Adjusted length errors were plotted as a function of the line orientations of the target quadrilateral (Fig. 5A) and as a function of what would be the accurate orientation of the lines forming the adjustable quadrilaterals (Fig. 5B). Since different lines had different lengths, we normalized the adjusted length error by the length of the target line, i.e., errors are plotted as a percentage of the accurate length. (Positive values indicate that subjects adjusted the line's length so that it was longer than the correct length.) Length errors did not vary with the line orientation of the target shape, implying that subjects did no worse trying to adjust lines to match horizontal lines than vertical lines or lines along the diagonal. However, subjects did make systematic errors that depended on the orientation of the lines forming the adjustable quadrilateral. Length errors varied approximately sinusoidally with line orientation (P<0.001 for all quadrilateral orientations, as shown in Fig. 5B). Subjects adjusted the corners so that the lengths of vertical lines were underestimated while horizontal lines were overestimated. Accordingly, the adjusted shape was shorter and wider than the reference shape.

To characterize this trend more precisely, we fitted a sinusoid to the data for each orientation of the adjustable shapes, and computed the phase and amplitude. Neither the depth of modulation (range 3.0 to 5.1%) nor the phase (−18.2° to 4.1°) depended on the orientation of the adjustable shape. Surprisingly, this was true even when the adjustable shape had the same orientation as the target shape (0°) or when it was presented upside-down (180°). Thus adjusted quadrilaterals were wider horizontally with respect to the screen, as illustrated by the two examples shown at the bottom of Fig. 5B (solid lines). The target quadrilaterals are shown in the dashed lines for comparison. These two target quadrilaterals are the same shape, but have different rotations: 0° and 300°. Notice that in both instances the adjusted quadrilaterals are wider than the veridical ones.

Inner angle errors

Subjects systematically erred when reproducing the angles between the intersecting lines. First, their errors in estimating the inner angles varied with the amount by which the inner angle had been distorted initially in the adjustable quadrilateral (Fig. 4C), as they did for length errors. The correlation between inner angle error and the initial deviation of the inner angle was significant (P<0.001), with a positive slope that had about the same value as the dependence of the perimeter and scaled length

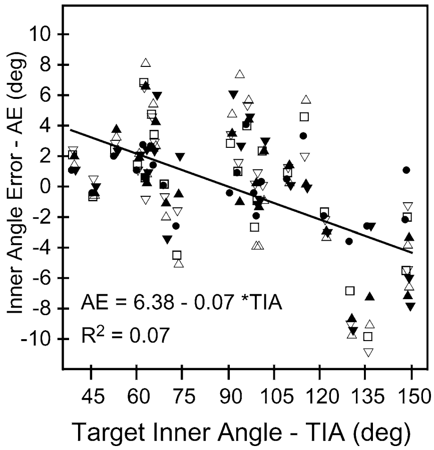


Fig. 6 Dependence of errors in the inner angles between adjacent line segments on the target inner angle. Solid line Results of a regression analysis on the data (P<0.001). The various symbols denote the relative orientation between the target and adjustable quadrilateral, as in Fig. 5

errors on their respective initial distortions. Inner angle errors also depended on the value of the respective target inner angle, as shown in Fig. 6. Subjects on average overestimated the inner angles of the quadrilateral when the angles were acute, but underestimated them when they were greater than 100°.

Line orientation errors

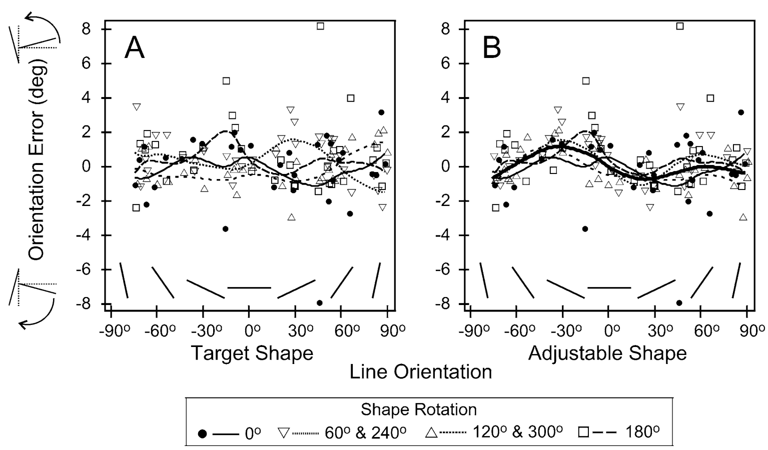
Finally, we assessed the extent to which errors in reproducing the orientation of the individual segments depended on the orientation of the target line and that of the adjusted line. To quantify this effect we first subtracted shape-dependent errors in line orientation, that is, the mean orientation errors for the same segment for all six rotated forms, for each subject. The remaining error and its dependence on line orientation is plotted in Fig. 7, the convention for defining orientation error being indicated by the diagrams to the left of the plot in Fig. 7A. In Fig. 7, the lines show fits to the data, grouped according to the amount by which the adjustable shape had been rotated. As with the length errors plotted in Fig. 5, orientation errors varied consistently with the orientation of the adjusted line, and did not appear to depend on the amount of shape rotation (Fig. 7B) However, there were no consistent trends when the results were plotted as a function of the orientation of the target line (Fig. 7A). On average, orientation errors were largest in the CCW direction for adjusted lines oriented around −30°. Small CW errors were found for lines oriented about 15° from the mediolateral direction. Inaccuracies in adjusting line orientation did not vary with the length of the line (R^2=0.00, P>0.05).

Experiment II

In contrast to the first experiment, in which the two quadrilaterals used in the comparison were always in view, this was not the case in the second experiment. As we described above, the most pronounced result in the first experiment was that subjects adjusted the length of the lines of the adjustable quadrilateral so that it was about 2% shorter and wider than veridical (Fig. 5B). In the second experiment we focused on this phenomenon by presenting subjects transiently with two contending quadrilaterals and asking them to determine which of the two best matched the reference quadrilateral (which was present throughout the trial). The two contending shapes differed in their aspect ratios (Fig. 2B). One was stretched along the horizontal and contracted along the vertical whereas the other one was contracted along the horizontal and stretched along the vertical. A staircase procedure was used to adjust the two aspect ratios (see Methods).

The results for a typical subject are shown in Fig. 8A. In one block of trials, the static target quadrilateral was on the left and in the other block it was on the right. Each block began with two contending quadrilaterals, one stretched by a scale factor of 1.3 along the horizontal, and the other contracted by a factor of 0.8. The plots show how the scale factors of the two contending quadrilaterals varied across the 30 forced-choice matches, the scaled quadrilateral selected as best matching the target (i.e., scale factor=1.0) being indicated by the filled circle. This subject's choices

Fig. 7 Dependence of the error in orienting individual lines on the line's veridical orientation in the target shape (**A**) and in the adjustable shape (**B**). Different symbols denote the rotation of the adjustable shape relative to the target shape. The *lines* interpolating the data are the results of a smoothing fit; *heavier solid line* the fit to all of the data. Note that the peaks and troughs for different rotations are aligned in **B**, but they do not coincide in **A**



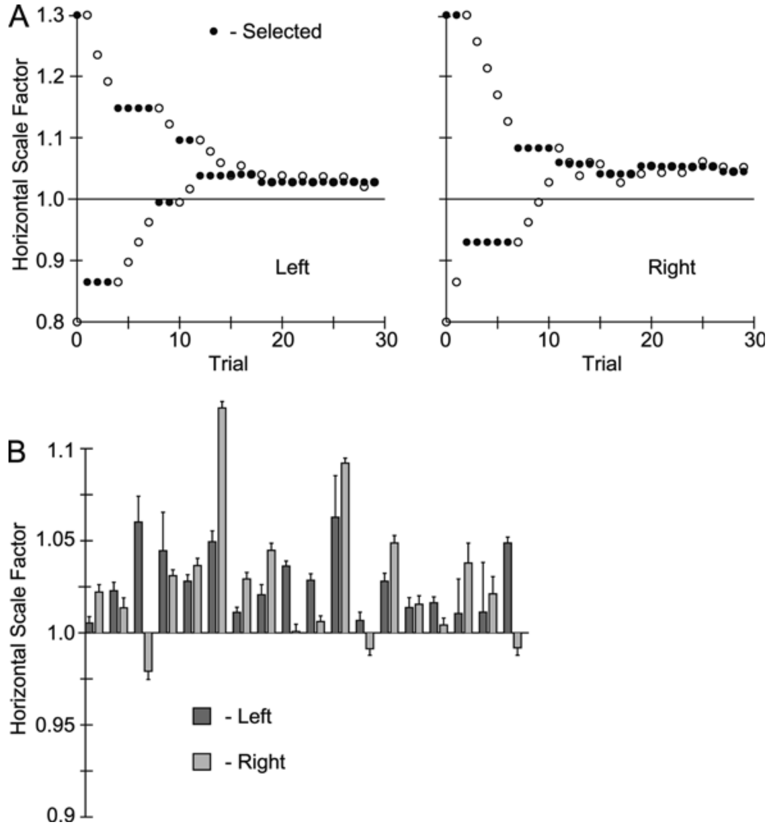


Fig. 8 Results of a two-alternative forced choice experiment in which two distorted shapes were displayed transiently. **A** Results from one subject for all trials in which the static (reference) quadrilateral was on the left (*left panel*) or on the right (*right panel*). The extent to which the horizontal dimension of the distorted quadrilaterals was altered is indicated on the ordinate. The contending shape that was selected is indicated by the *filled circle*. Note that in both instances the choices converge on a scale factor greater than 1.0. **B** Average values (±1 SD) of the choices each of the 18 subjects. These values were computed from the distortions on the contending quadrilaterals on the last three trials

converged to a value of 1.028 for the left and a value of 1.049 for the right. On average, subjects' responses converged onto quadrilaterals with a scale factor of 1.028 (i.e., a width scaled up by 2.8% and a height shrunk by the same amount). Results for each of the subjects are shown in Fig. 8B. Statistically, the side on which the transient quadrilaterals were presented (left or right) had no effect ($F_{(1,252)}$=0.79). However, the scale factor differed reliably from 1.0 (t=16.79, P<0.001).

Discussion

Subjects made consistent errors in matching the shapes of visually presented quadrilaterals and we identified several different sources of these errors. When they used the computer mouse to adjust the distorted shape, on average they undercompensated by about 15% for the magnitude of the initial distortion (Fig. 4). The size of this effect was similar for errors in the perimeter of the shape, in the length of individual segments and in the inner angles between adjacent segments. Other errors depended on the orientation of the adjustable shape (Figs. 5, 7). Horizontal lines tended to be stretched and vertical lines tended to be shortened by about 2%. It is significant that these errors did not depend on the orientation of the adjustable shape relative to the reference shape (Fig. 5). There were also errors in adjusting the inner angles between adjacent segments. Acute angles tended to be set as less acute and obtuse angles as less obtuse, i.e., there was a trend towards right angles. The second experiment, in which distorted quadrilaterals were presented transiently, replicated the horizontal/vertical distortion in length (Fig. 8).

As noted, the errors appeared to be aligned with the cardinal directions of the subjective vertical and horizontal. This finding is congruent with a large body of data on visual and haptic illusions. One example is provided by the horizontal/vertical illusion (see below). Performance is also poorer at defining oblique orientations than at defining the horizontal or the vertical (see Kappers and Koenderik 1999; Luyat et al. 2001). Finally, right angles appear to be privileged, especially when the sides are oriented horizontally and vertically (Ferrante et al. 1995).

To a large extent the visual distortions in shape reported here mirror errors in reproducing haptically sensed quadrilaterals (Henriques et al. 2004). In those experiments subjects used their arm to trace the outline of a quadrilateral with their eyes closed and then drew the remembered shape, also with their eyes closed. The tracing and reproduction were performed in the horizontal plane. As in the present experiments, subjects overestimated the length of lines oriented mediolaterally by about 2%, and they underestimated the length of lines perpendicular to this direction, thus drawing a shape that was shorter and wider than the target shape. As was the case in the present experiment, acute inner angles tended to be overestimated, and obtuse ones tended to be underestimated. Furthermore, the complex pattern of errors in line orientation in the present experiment (Fig. 7) is similar to the pattern found when shape was sensed haptically, although the peaks in the present experiment were shifted by about 30° relative to those reported by Henriques et al. (2004).

Other experimenters have also reported similarities in visual and in haptic illusions, but this is not true in every case. For example, the horizontal/vertical illusion for line length is similar in the haptic and in the visual domain (Taylor 2001), as are oblique effects in sensing line orientation (Gentaz et al. 2001). However, these investigators found quantitative differences in the effect for the two modalities. Differences were also found in the processing of symmetric shapes using vision or haptic sensation (Ballesteros et al. 1998). Finally some visual illusions can also be elicited haptically, but others can not (Suzuki and Arashida 1992).

A distorted perception can arise from errors in sensory processing but it can also arise as this sensory information is stored in short-term memory for subsequent recall. We believe that this latter stage accounts for many of the errors that we have described here. Our reasoning is based on the results described in Figs. 5 and 7. Errors in adjusting the lengths and orientations of each of the sides of the quadrilateral depended on the orientation of that line in the adjustable shape. However, they did not depend on the amount by which the adjustable shape had been rotated relative to the reference shape. This was true even when the adjustable shape and the reference shape were displayed in the same orientation. This is not what one would expect if the errors reflected a visual distortion of spatial perception. In that case there should have been no error when the adjustable shape had the same orientation as the reference shape since both would be distorted visually in the same manner. By the same token, a visual distortion should produce a maximal effect for a rotation of 90°.

Since the reference and the adjustable shapes were spatially segregated in our experiments, it is reasonable to assume that subjects shifted their gaze back and forth between the two shapes, i.e., they were not foveated simultaneously. Such shifts in spatial attention have been described in tasks requiring subjects to copy a visually presented pattern (Ballard et al. 1992; Pelz et al. 2001). Accordingly, the tasks implicit in the present experiments as well as in the experiments dealing with haptic perception (Henriques et al. 2004) required subjects to store a percept of the shape in memory and then to reproduce it either by means of an arm movement (in the haptic task), or by adjusting a visually presented shape to match the one in memory (in experiment 1) or making a judgment concerning which of two transiently presented shapes most closely matched the one in memory (experiment 2).

Distortions in spatial representations in working memory have been described previously. For example, McIntyre and colleagues (1997, 1998) investigated errors in pointing to memorized targets by imposing variable delay times between the presentation of the target and the arm movement. They found that the nature of the pointing errors changed gradually with time. In a similar vein, saccadic errors to remembered targets evolve over time (Gnadt et al. 1991). Thus, since the distortions observed in our recent studies were independent of sensory modality, and since subjects were required to hold shape information in short-term memory, this may have been the major source of the distortions we observed.

Acknowledgements This work was supported by NIH grant NS15018. We thank J. Thompson for programming the visual displays.

References

Avery GC, Day RH (1969) Basis of the horizontal-vertical illusion. J Exp Psychol 81:376–380

Ballard DH, Hayhoe MM, Li F, Whitehead SD (1992) Hand-eye coordination during sequential tasks. Philos Trans R Soc Lond B Biol Sci 337:331–338

Ballesteros S, Millar S, Reales JM (1998) Symmetry in haptic and visual shape perception. Percept Psychophys 60:389–404

Berthoz A, Pavard B, Young LR (1975) Perception of linear horizontal self-motion induced by peripheral vision (linear vection). Exp Brain Res 23:471–489

Butler DL (1983) Effect of orientation on judgments of line length. Percept Mot Skills 57:1015–1020

Fasse ED, Hogan N, Kay BA, Mussa-Ivaldi FA (2000) Haptic interaction with virtual objects. Biol Cybern 82:69–83

Ferrante D, Gerbino W, Rock I (1995) Retinal vs. environmental orientation in the perception of the right angle. Acta Psychol 88:25–32

Flanagan JR, Rao AK (1995) Trajectory adaptation to a nonlinear visuomotor transformation: evidence of motion planning in visually perceived space. J Neurophysiol 74:2174–2178

Gentaz E, Luyat M, Cian C, Hatwell Y, Barraud PA, Raphael C (2001) The reproduction of vertical and oblique orientations in the visual, haptic and somato-vestibular systems. Q J Exp Psychol A 54:513–526

Georgopoulos AP, Lurito JT, Petrides M, Schwartz AB, Massey JT (1989) Mental rotation of the neuronal population vector. Science 243:234–246

Gnadt JW, Bracewell RM, Andersen RA (1991) Sensorimotor transformation during eye movements to remembered visual targets. Vision Res 31:693–715

Goodbody SJ, Wolpert DM (1999) The effect of visuomotor displacements on arm movement paths. Exp Brain Res 127:213–223

Henriques DY, Soechting JF (2003) Bias and sensitivity in the haptic perception of geometry. Exp Brain Res 150:95–108

Henriques DY, Flanders M, Soechting JF (2004) Haptic synthesis of shapes and sequences. J Neurophysiol 91:1808–1821

Kappers AM, Koenderink JJ (1999) Haptic perception of spatial relations. Perception 28:781–795

Kesten H (1958) Accelerated stochastic approximation. Ann Math Stat 29:41–59

Knudsen EI (1985) Experience alters the spatial tuning of auditory units in the optic tectum during a sensitive period in the barn owl. J Neurosci 5:3094–3109

Knudsen EI, Knudsen PF (1989) Vision calibrates sound localization in developing barn owls. J Neurosci 9:3306–3313

Luyat M, Gentaz E, Corte TR, Guerraz M (2001) Reference frames and haptic perception of orientation: body and head tilt effects on the oblique effect. Percept Psychophys 63:541–554

McIntyre J, Stratta F, Lacquaniti F (1997) Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space. J Neurophysiol 78:1601–1018

McIntyre J, Stratta F, Lacquaniti F (1998) Short-term memory for reaching to visual targets: psychophysical evidence for body-centered reference frames. J Neurosci 18:8423–8435

Nashner LM, McCollum G (1985) The organization of human postural movements. A formal basis and experimental synthesis. Behav Brain Sci 8:135–172
Pelz J, Hayhoe M, Loeber R (2001) The coordination of eye, head and hand movements in a natural task. Exp Brain Res 139:266–277
Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects. Science 171:701–703
Suzuki K, Arashida R (1992) Geometrical haptic illusions revisited: haptic illusions compared with visual illusions. Percept Psychophys 52:329–335
Taylor CM (2001) Visual and haptic perception of the horizontal-vertical illusion. Percept Mot Skills 92:167–170
Thilo KV, Gresty MA (2002) Visual motion stimulation, but not visually induced perception of self-motion, biases the perceived direction of verticality. Brain Res Cogn Brain Res 14:258–263
Treutwein B (1995) Adaptive psychophysical procedures. Vision Res 35:2503–2522
Young LR, Dichgans J, Murphy R, Brandt T (1973) Interaction of optokinetic and vestibular stimuli in motion perception. Acta Otolaryngol (Stockh) 76:24–31