Approaches to the Study of Haptic Sensing

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Henriques, Denise Y. P. and John F. Soechting. Approaches to the study of haptic sensing. *J Neurophysiol* 93: 3036–3043, 2005; doi:10.1152/jn.00010.2005. This review surveys results from a new approach to the problem of haptic sensing, in which subjects use primarily proximal arm movements to explore the shapes of virtual objects. These shapes are generated using a robotically controlled manipulandum. We begin by summarizing distortions of simple geometric properties (such as the length and orientation of lines) in the haptic perception of space. We then consider the extent to which the sense of more complex shapes (such as quadrilaterals) can be explained by these geometric distortions, i.e., the extent to which the shape of a complex object is synthesized from simpler constituent elements, and some of the sensory cues that may be important in this process. Haptic and visual processing of shapes appear to lead to some similar illusions. However, we argue that the processing of haptic information differs fundamentally from visual processing in that the former requires the integration of information that evolves in time as well as in space.

INTRODUCTION

Haptic sensing, the extraction of information about an object's properties such as its size, shape, and texture by means of exploratory manual movements, is exquisitely linked to object manipulation. In discriminating one object from another, such as finding a key or a coin among a variety of other objects, we tend to move the item, establishing and releasing grasp, changing its orientation, or holding it firmly with some fingers while exploring its contours with other digits (Lederman and Klatzky 1993).

Conversely, grasping and manipulating an object effectively requires tactile cues. For example, an egg is grasped more stably in a 3-digit grasp when the contact points are on the flatter portions of the ellipse (Cutkowsky and Howe 1990). It is easy to convince oneself that behavior conforms to this prediction, with (Goodale et al. 1994) and without vision. It is also well established that during grip, the safety margin (the ratio between the grip force and the load force) is precisely regulated (Johansson 1998; Johansson and Cole 1992; Johansson and Westling 1988). This regulation involves feedback from cutaneous afferents (Birznieks et al. 2001; Johansson et al. 1992). Finally, in a 3-digit grasp, the load force on each digit depends on the precise locations of the points of contact (Baud Bovy and Soechting 2002). Because these are subject to trial-to-trial variability, this observation also argues for the importance of sensory feedback in the control of grasping.

Haptic sensing by means of object manipulation poses a challenging problem in sensorimotor integration. It requires the integration of spatially disparate sensory signals, from cutaneous afferents in the digits and proprioceptors from the proximal as well as the distal arm, with the efferent commands that are in part responsible for the temporal modulation of the sensory signals. It is perhaps in this latter sense that haptic sensing differs most from the processes whereby visual signals lead to the discrimination of objects based on shape and texture. Object recognition based on visual signals, at its simplest level, can be viewed as the spatial analysis of a static image on the retina (Logothetis 1998; Riesenhuber and Poggio 2000), whereas haptic sensing also involves integration of information across time.

Behavioral and psychophysical studies of haptic sense have generally explored this problem by restricting the nature of the exploratory motions. Typically, subjects have been instructed to explore a surface with the extended tip of one digit (cf. Goodwin and Wheat 2004; Lederman and Klatzky 2004; Louw et al. 2002; Robles-De-La-Torre and Hayward 2001). These studies have delineated how well subjects can discriminate some of the dimensions of a surface's contour, such as the height and width of an indentation (Louw et al. 2002), and the radius of curvature of a sphere (Goodwin et al. 1991). They have also identified the potential sensory substrates for discriminating surface properties such as curvature and texture (Blake et al. 1997; Goodwin et al. 1995, 1997). Specifically these studies showed that the discharge of slowly adapting type I (SAI) afferents could discriminate along these dimensions. Slowly adapting type II (SAII) afferents also responded to these stimuli, but provided much coarser resolution.

Hogan and colleagues (Fasse et al. 2000; Hogan et al. 1990) developed a different experimental paradigm that permits the study of haptic sensing on a larger spatial scale. In their studies, subjects grasped the handle of a robotically controlled manipulandum and explored the contours of virtual objects with movements that primarily involved the proximal arm. The forces developed by the robot can simulate viscous and elastic force fields (Shadmehr and Mussa-Ivaldi 1994). In the present application, the contours of an object are simulated by programming the robot such that the forces are zero when the subject's hand is within the contour. When the boundary is penetrated, an elastic restoring force is generated, proportional to the depth of penetration (Fig. 1). A moderate amount of damping is usually added to increase stability. The advantage of this technique is that object shape can be modified adaptively from trial to trial (Henriques and Soechting 2003) and even shapes that are not realizable physically can be simulated (Fasse et al. 2000).

In the following sections we will review results obtained using this paradigm and discuss unresolved problems and questions. We begin by describing the extent to which haptically sensed space is distorted. We then address the question of
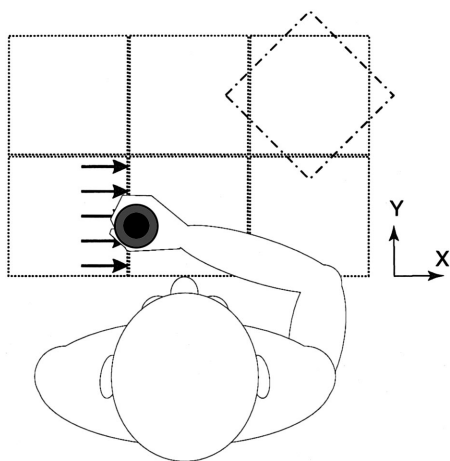
FIG. 1. Boundaries generated by the robot manipulandum. Subjects gripped the handle of the robot arm, which constrained the hand to move in a horizontal plane just above waist level. Robot exerted a force field, shown here by arrows, so that at a boundary, subjects felt a resistance as if they were hitting a wall. Some of the force boundaries ran in the mediolateral (x) direction or the anterior–posterior (y) direction (dotted lines), at the locations shown; these formed a grid spanning 45 × 30 cm centered on the body's midline, 15 cm in front of the subject's torso at the nearest point. Another 24 boundaries ran along the 45° diagonals, 4 of which are illustrated (dotted–dashed lines) in the *top right corner* of the workspace.

how the percept of a complex shape, such as a polygon, might be synthesized from simpler elements such as the lengths and orientation of its constituent elements. Finally, we take up the question of the sensory and motor cues that enter into haptic sensing in this experimental condition.

DISTORTIONS IN HAPTIC SPACE

Figure 2 illustrates some simple ways in which haptically sensed space might be distorted locally, the solid lines depicting a reference square and the dashed lines depicting the sensed shape resulting from various distortions. Because each of these possibilities has been addressed experimentally, we begin by discussing some predictions. In experiments dealing with this problem, subjects were asked to judge the length and orientation of lines, and the angles between intersecting line segments.

A distortion in size along orthogonal directions (horizontal and vertical) is shown on the *left*. Note that such a distortion does not affect either the orientation of the horizontal and vertical lines or the angle between them. However, the orientation of diagonal lines, such as the 45° line connecting the *bottom left* and *top right* corners, will be affected. Conversely, a shear distortion does not change the length of the horizontal and vertical lines, but alters the angle between them. Lengths of diagonals will be altered predictably, however. A rotation (*3rd panel*) represents the geometrically simplest distortion because it affects only the orientation of line segments, but not

their lengths or the angles between them. Finally, haptically sensed space may be warped, in that straight lines are not perceived as straight (*right panel*).

Thus, simple distortions will in general affect the relative lengths of lines, their orientation, and the angles between intersecting lines. Furthermore, one might expect results of psychophysical experiments to reflect a combination of these 4 distortions. Finally, the possibility exists that the distortions in the several parameters (e.g., line length and internal angle) are not consistent with each other and that they are nonuniform over the workspace.

QUANTIFYING HAPTIC SENSITIVITY

Figure 3 illustrates the approach that we (Henriques and Soechting 2003) used to address these questions. Similar procedures were used by Hogan and colleagues (Fasse et al. 2000; Hogan et al. 1990). To determine one of the geometric parameters, subjects moved the manipulandum in the horizontal plane as often as they liked along a haptic boundary that was about 15 cm long. For example, in our study of line orientation, subjects ascertained the direction of tilt of the boundary, clockwise (CW) or counterclockwise (CCW) from the frontal or the sagittal plane, in a 2-alternative forced-choice (2-AFC) procedure (Treutwein 1995). Based on the answer for each trial, the direction and amount of tilt for the next trial were adjusted using a pair of adaptive staircases (Fig. 3*A*). Each
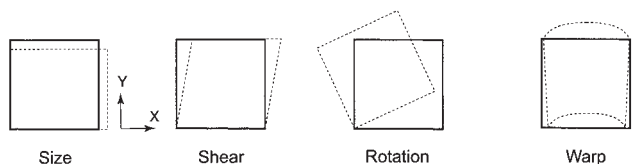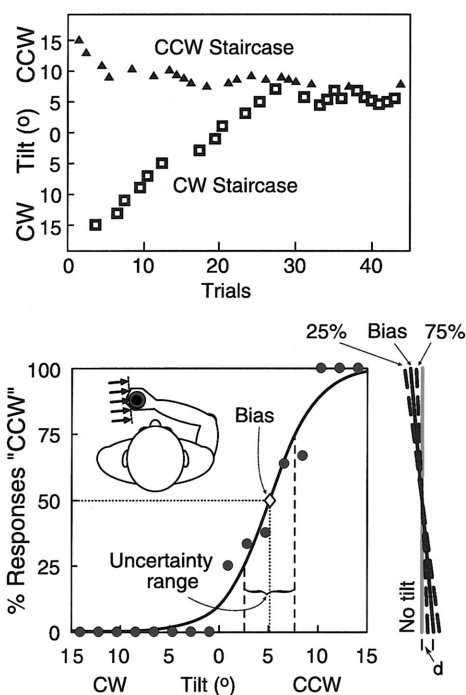

FIG. 2. Distortions of haptic space. Schematic illustrates the various types of distortions in subjects' sense of the length or orientation of lines. Actual shape is shown by solid lines and the sensed shape is depicted by dashed lines.

FIG. 3. One subject's performance detecting the tilt of an anterior–posterior boundary to his immediate left (see *inset* in *bottom panel*). *Top:* tilts presented to the subject varied from trial to trial in a pair of 2-alternative forced-choice adaptive staircases, as shown (triangles for one staircase, squares for the other). *Bottom:* tilts of all the stimuli from both staircases have been sorted into 16 bins, each 2° wide and the filled circles show how likely the subject was to report that tilt as counterclockwise (CCW). A sensitivity function was fitted to these data. Tilt bias (open diamond) is the angle of tilt where the sensitivity curve crosses the 50% line, whereas the 25 and 75% points define the uncertainty range (or difference threshold). For this subject, the bias is 5.1° CCW, and the uncertainty range is 5.0°.

staircase began with a boundary that was clearly tilted in one direction, 15° CCW for one staircase and 15° CW for the other. Trials drawn from the 2 staircases were randomly interleaved and the size of the step was decreased every time the subject's response was inconsistent with the response in the previous trial of that staircase. The 2 staircases converged toward the same tilt angle: the direction judged to be straight ahead (i.e., the one with an equal probability of CW and CCW responses).

To quantify these responses, we fitted a logistic function to the data (Fig. 3*B*) to define the *bias* (the point of 50% probability) and the *uncertainty range* (the difference between the values at which the response probability was 25 and 75%). Bias is therefore a measure of the *accuracy* of the haptic sense and the uncertainty range defines its *precision*. In the illustrated example, the bias was about 5° CCW with an uncertainty range of ±2.5°.

BASIC GEOMETRY

Haptic sensitivity derived from proximal arm movements has been defined for several geometric features: absolute direction, absolute curvature, relative length, relative angle, relative curvature, rate of change of curvature, and circularity.

Absolute direction

On average, subjects perceived contours tilted 2.2° CCW from the frontal plane and 3.2° from the sagittal plane as being cardinal. To determine the dependency of the bias on the location of the contour in the workspace, we tested subjects on 24 contours, each 15 cm long, arranged as in Fig. 1 (dotted lines) so they formed a grid spanning 45 × 30 cm centered on the body's midline (Henriques and Soechting 2003). Tilt biases were largest in the left part of the workspace and smallest in the right part, but did not depend on the distance of the contour from the subject's torso or right shoulder. The uncertainty, which averaged 4.9°, was uniform throughout the workspace. Slightly different results were obtained by Fasse et al. (2000), with an average 2.5° CW bias from the frontal plane and a 6.6° CCW bias from the sagittal plane.

Absolute curvature

The results of experiments in which subjects moved the manipulandum along a curved contour and reported whether it curved inward or outward suggest that haptic space is not warped. As in the tilt experiments, we (Henriques and Soechting 2003) tested a range of locations in the workspace and contours oriented along the mediolateral, anteroposterior, and diagonal directions (see dotted–dashed lines in the *top right* area in Fig. 1). The subjects' curvature biases (the arcs they perceived as straight) were surprisingly small, with an average radius of curvature of 2 m. Curvature biases did not vary with location in the workspace but they did vary with path direction: biases were larger for sideways contours than for diagonal or sagittal ones.

In terms of hand deviations, the subjects' ability to sense deviations from a straight line is about twice as acute as their ability to sense tilt. The average bias of 2.7° we found in our direction studies meant that the hand deviated 3.6 mm from the cardinal direction at the end of the 15-cm contour. Curvature sense was also more *precise* than direction sense. For curvature

sense, the uncertainty averaged to a 3.1-mm deviation from a straight line, whereas for tilt-it was 6.5 mm.

The accuracy with which curvature can be haptically sensed compares well with results from studies of spatial vision and of motor performance. In our experiment, a sideways arc that felt straight had a peak deviation from a straight line of about 0.7% of the arc length. In studies of visual acuity, subjects presented with a spot moving along a curved path judged one that had a peak deviation of 2.5% of the path length to be straight (Wolpert et al. 1994). (We are not aware of studies of sensitivity to visual displays presented statically.)

Haptically sensed curvature biases were also smaller than the curvature of hand paths during pointing movements. This curvature depends on the direction, location, and speed of the movement, but on average the peak deviation is about 1–3% of the path length (Atkeson and Hollerbach 1985; Klein Breteler et al. 1998; Miall and Haggard 1995; Pellegrini and Flanders 1996; Sergio and Scott 1998; Wolpert et al. 1994). So our findings suggest that haptic sense is acute enough to detect the kind of curvature that occurs in natural hand paths.

Relative length and angle

Fasse and colleagues (2000) assessed the extent to which distortions in size (Fig. 2) affected haptic sense. These investigators asked subjects to discriminate the relative lengths of the sides of rectangles oriented either along the cardinal directions or at 45° to them. They found substantial size distortions, with a rectangle 29% wider than tall being sensed as square. More precisely, by combining results from 2 orientations, they predicted that an ellipse with an aspect ratio of 1.29 and a major axis oriented 17° to the *x*-axis should be sensed as circular. This size distortion depends on the location in the workspace, increasing with distance from the shoulder (Hogan et al. 1990). We found a slightly smaller effect than that reported by Fasse et al. (2000); on average subjects reported an ellipse with an aspect ratio of 1.07 (i.e., a wide ellipse) to be circular, and mistook a circle for a slightly tall ellipse (Henriques and Soechting 2003).

Nonuniform scaling of an object along 2 orthogonal dimensions will also introduce distortions in the orientation of lines and in the relative angles between intersecting lines. Fasse et al. (2000) asked subjects to discriminate between pairs of acute angles, asking subjects to report which of the 2 was larger. They found considerable distortions in this perceptual dimension as well. Importantly, these distortions were incompatible with those predicted from the results of their experiment dealing with judgments of relative length (i.e., the assumption of pure size distortions). It is possible that a combined size and shear distortion (Fig. 2) could account for their data. However, the results on judging tilt (see above) suggest that the amount of shear distortion is modest. Thus, as suggested by Fasse et al. (2000) judgments of lengths and angles are geometrically incompatible with each other.

Relative curvature

We also tested subjects' ability to discriminate the relative curvature of 2 arcs (Henriques and Soechting 2003). In one experiment we presented a contour that was straight on one half (reference) and curved on the other portion of the midline.

In another experiment, the reference arc had a radius of 40 cm. Subjects reported which segment (left or right) was more curved. In this study, on average, the relative curvature bias was about as small (0.24 and 0.11 m^{-1}) as the bias in the estimation of absolute curvature. However, the difference threshold was much larger (2.26 and 2.88 m^{-1}) than it was for the estimation of absolute curvature (1.11 m^{-1}). Subjects were poorer at making comparisons between 2 curves than they were at making an absolute judgment (whether the border curved in or out). With respect to haptic sensitivity for different geometric features, subjects required about the same relative hand displacements to be 75% confident that a path spiraled in rather than out as they did to be confident that one arc was more curved than another, or that an ellipse was wide rather than tall.

In summary, experiments dealing with subjects' ability to extract simple geometric features from exploratory arm movements suggest that the major source of distortion is one of relative size. In this tangential–radial distortion, lines radiating from the body (roughly along the *y*-axis) are judged to be longer than lines of the same length in the perpendicular direction. Shear and warp distortions appear to be small as does the rotation away from the cardinal directions (a few degrees). Furthermore, it appears that measures of various geometric properties such as lengths and angles are not geometrically congruent with each other. However, it needs to be recognized that these conclusions rest on a limited set of observations. For example, it is not known whether judgments of relative length are affected by the angle between the 2 line segments.

However, it is clear that absolute judgments (such as straightness and tilt) are more precise than are relative judgments, such as the lengths of 2 lines or the size of 2 angles (Fasse et al. 2000; Vosin et al. 2002a). Subjects sensed absolute curvature more precisely than they sensed relative curvature (Louw et al. 2000). Subjects sensed absolute tilt better than they sensed differences in tilt (Appelle and Gravetter 1985; Kappers 1999; Kappers and Koenderink 1999). We suspect that this dichotomy arises from the need, in haptic perception, to integrate sensory and motor signals over time. In making a relative judgment, this evolving signal would need to be compared to one stored in working memory and derived from a preceding movement. We will take up this point in more detail later.

HAPTIC SYNTHESIS OF COMPLEX SHAPES

It seems reasonable that the shapes of complex objects are synthesized from the sense of the properties of simpler constituent elements, such as the lengths, orientations, and curvatures of simpler elements making up the shape. If so, the distortions described above should be reflected in subjects' judgments when they are presented with complex shapes, such as quadrilaterals. Our work on this topic (Henriques et al. 2004) provided evidence in favor of this supposition, but also showed that additional factors come into play.

We presented subjects with 5 quadrilaterals, whose internal angles varied from 45 to 145° and whose sides made up anywhere from 10 to 40% of the length of the approximately 50-cm perimeter. Each of the 5 quadrilaterals was presented to the subject in 6 different orientations in the horizontal plane, for a total of 30 contours (see Fig. 4 for two examples). With eyes closed, subjects traced the contours of the quadrilateral,

moving along the boundaries until they were satisfied that they felt confident to reproduce the shape, which they did in one of 2 ways. In one experiment, they drew the remembered quadrilateral with the same manipulandum but without the force field (so that they had fully free motion in the horizontal plane), also with their eyes shut (*left panels,* Fig. 4). In the other experiment, they reproduced the same shapes on a vertical touch screen, and they were allowed to see their finger and their rendition of the shape's outline. By comparing reproductions made with the touch screen to those made with the manipulandum, we could see how performance was influenced by motor recall versus visual feedback.

Subjects made systematic errors on these tasks, some of which were consistent with the distortions of basic geometric features described in the previous section. On average, the overall size tended to be 15% larger when the subjects used the manipulandum to reproduce the shape and 31% smaller when they used the touch screen. The reproductions reflected the nonuniform distortions in length described above. Using the manipulandum, subjects exaggerated the length of segments in the *x*-direction (*left panels,* Fig. 4), but did the opposite on the touch screen, stretching the shapes in the *y*-direction (*right panels,* Fig. 4). There were also errors in orienting the individual segments that were in part consistent with the distortions in scale: lines reproduced using the manipulandum tended to be oriented closer to the *x*-direction. The difference in the results from the 2 modes of reproduction may in part reflect the influence of visual feedback when subjects used the touch screen. A visual illusion (horizontal–vertical illusion) affects the perception of relative line lengths in the frontal plane, vertical lines being perceived as longer than horizontal lines of the same length (Lederman and Taylor 1969).

Other errors were the same whether subjects drew with the manipulandum or on the screen and did not depend on the quadrilateral's orientation. Subjects drew short segments of the quadrilateral too long (in proportion to the overall perimeter) and long segments too short. As a result, the drawn shape was more nearly equilateral than the traced shape. They also reproduced internal angles between segments as being closer to right angles than they really were and they tended to make the
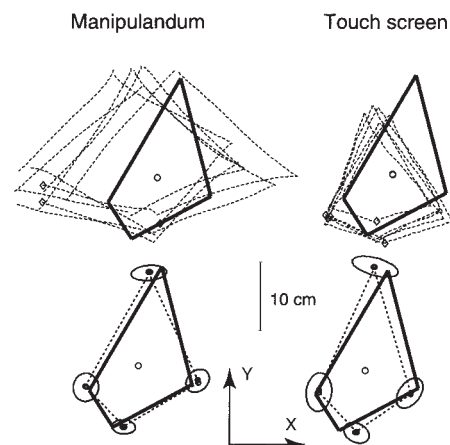

FIG. 4. Haptic sensing of the shape of quadrilaterals. *Traces* show results of 5 trials from one subject (*top*) and average results from all subjects (*bottom*). Heavy lines depict the traced quadrilaterals and the dotted lines show the subjects' reproductions made using the manipulandum (*left side*) or on a touch screen (*right side*). Circles mark the centroids of the traced shapes. Ellipses represent 68% confidence intervals for segment endpoints.

reproduced shapes more symmetrical. Thus, the perception or memory of multisegment shapes is regularized—more equiangular and equilateral than the real shape—whether tested with the manipulandum or the touch screen. To quantify this aspect, we computed the length ratio of the shortest to the longest line in each quadrilateral. The average ratios for manipulandum drawings (0.50) and touch screen drawings (0.46) were larger than the actual ratios in the traced shape (0.41). The same was true for the ratio of the smallest to the largest angle in each quadrilateral. Average ratios for manipulandum drawings (0.52) and touch screen drawings (0.54) were larger than those for the traced quadrilaterals (0.48).

SENSORY CUES IN HAPTIC SENSING

In addition to the cognitive factors we have just mentioned, sensory cues of cutaneous and proprioceptive origins affect haptic sensing. In a recent experiment, Voisin et al. (2002a) asked subjects to discriminate angles by tracing their outlines with the index finger and the arm extended. These authors found a discrimination threshold (uncertainty) of slightly less than 5° and then repeated the experiment removing tactile cues (by anesthetizing the finger), proprioceptive cues from the arm (by keeping the arm still while reproducing its path by moving the object relative to the finger), or both (Voisin et al. 2002b). When either tactile or proprioceptive cues were removed, the discrimination threshold approximately doubled. When both cues were removed, subjects were unable to perform the task.

Robles-De-La-Torre and Hayward (2001) showed that force cues can override geometric cues during haptic exploration. In their experiments, subjects explored surfaces with an extended index finger, identifying bumps or troughs with a Gaussian profile, 0.3 cm deep and 4 cm wide. They simulated force cues through a manipulandum and found they could induce illusory changes in contour by manipulating the tangential force, a force resisting the motion producing an illusory bump and one assisting the motion producing an illusory depression.

To the contrary, forces normal to the contour do not appear to alter haptic sensing under our experimental conditions, i.e., when subjects explore virtual boundaries with whole arm movements. First, we assessed whether the direction of force affected haptic acuity by determining the extent to which tilt and curvature biases depended on the direction from which the subjects approached a contour. Of the 24 cardinal contours in Fig. 1, 9 pairs of contours (dotted lines, forming the inner walls of the grids) coincided spatially, and differed only in the direction of force. For instance, consider the sagitally oriented contour the subject is exploring in Fig. 1. In one set of trials, subjects approached the contour from the right, and so had to *push,* exerting force away from their arms, whereas on another set of trials subjects approached the same contour from the left and so had to *pull.* The direction of force had no significant effect on the bias or uncertainty in the sense of direction of curvature.

In many everyday actions we let our surroundings partially guide our motion, such as when we slide a hand along a wall searching for a light switch or when we draw on a blackboard. This type of behavior is called *compliant motion* because its control can take advantage of the compliance of the arm (Mussa-Ivaldi et al. 1985). Specifically, we do not need to plan motion that is perfectly on the surface and in fact, motions

exerted in free space are not (Soechting and Terzuolo 1987). For example, the 2 loops of a "figure 8" are generally drawn in 2 different planes. However, as long as a force is exerted against the surface during a drawing movement, the motion will conform to the plane of the surface, given a compliant arm.

Conceivably, normal force cues could be used in the haptic sensing of curvature. In this scenario, deviations from a planned trajectory along a constraint would generate variations in the normal component of the force and these variations could be used to identify the curvature of the contour. More generally, because subjects are able to discriminate variations in compliance (Hogan et al. 1990; Jones and Hunter 1989, 1990), surface compliance could introduce a bias in the haptic perception of curvature. To investigate this possibility, we varied the stiffness of the contour as subjects determined whether it curved in or out (Song et al. 2004). Stiffness was either constant, largest in the middle of the contour or largest at the ends, varying by a factor of 2 from 20 to 40 N/cm. We found that this parameter did not influence the bias in the judgment of what constituted a straight contour. Furthermore, the normal forces exerted by the subject against the contour were either constant or varied linearly and this pattern was not influenced by the contour's compliance.

In unconstrained limb motions, the speed of the hand varies with the local curvature of its path: we slow down on tight curves and speed up on more gradual curves and straightaways. This observation has been formalized as the "two-thirds power law" relating speed and curvature (Lacquaniti et al. 1983; Viviani and Cenzato 1985). It holds even when subjects track moving targets; performance is degraded if the target motion does not conform to this relation (de'Sperati and Viviani 1997; Viviani et al. 1987). In fact, this covariation between speed and curvature is maintained qualitatively when subjects trace unknown and unseen curvilinear closed contours (unpublished observations). Thus, it seems plausible that subjects might use patterns in the sensed temporal variations in speed to deduce curvature.

We recently tested this supposition (Soechting and Poizner 2005) by programming the robot manipulandum to transport the hand passively along elliptical contours. The eccentricity of the ellipse varied from trial to trial, and subjects reported whether the ellipse was wide or narrow in a 2-AFC staircase procedure. Thus the task was to determine the motion that was perceptually equivalent to a circle. Because the curvature of circular motion is constant, a circle would normally be drawn at a constant speed. This was indeed the case in one block of trials. However, in 2 other blocks of trials, the motion of the manipulandum was changed so that a wide or narrow ellipse would be generated at a constant speed. The corresponding motion for a circle was nonuniform, being either faster on the sides (see Fig. 5) or faster on the top and bottom arcs. If subjects based their judgments of circularity purely on speed, ellipses traced at constant speed would be reported as being circular. (If they used a combination of position and speed cues, their report would be somewhere in between those predictions based on position and speed cues.) However, contrary to this supposition, the speed profile did not affect the circularity bias (Fig. 5), suggesting that temporal variations in speed are not used in haptic sensing.

At the conclusion of the experiment, we also interviewed the subjects about their experience. Some of them reported that the
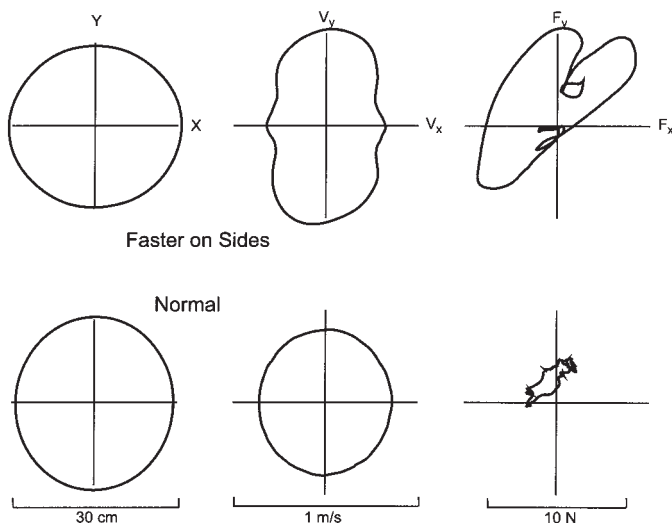
FIG. 5. Haptic sensing of circularity under different movement conditions. Speed conformed to the 2/3 power law (*bottom*) and was distorted so that an ellipse with an aspect ratio of 3/2 was traced at constant speed. *Traces* in the *left panels* depict the *x–y* hand paths reported by the subject as being circular, whereas those in the middle panel show the corresponding variations in speed. Forces generated by the subject in resistance to the imposed motion are shown in the *rightmost panels.*

ellipses seemed to be tilted, with the major axis at a substantial angle with the *x*- or *y*-directions. Their reports exceeded distortions in tilt described in an earlier section. In the experiments in which speed was manipulated, we recorded the forces on the manipulandum as well as the motions of the hand (see Fig. 5). When the motion was in accordance with the two-thirds power law, the forces were small (*bottom panel,* Fig. 5). However, when the speed profile was distorted, forces were much larger (*top right,* Fig. 5), with an asymmetrical profile, tilted away from the cardinal axes. Thus, the results of this experiment (and others described above) are compatible with the idea that force cues do have a significant influence on haptic perception of shape.

COMPARISONS WITH VISUAL ILLUSIONS

Many of the distortions in haptic sensing are replicated by visual illusions. For example, the haptic distortions in size are replicated in the visual domain in the form of the horizontal–vertical illusion. We (Henriques et al. 2005) found distortions similar to those described above for haptic exploration when subjects were visually presented with 2 quadrilaterals side by side and asked to adjust one to make it identical to the reference shape. Similar effects were also found in a discrimination task in which subjects were asked to judge which of 2 quadrilaterals, briefly presented visually, most closely resembled a reference shape. Specifically, in both tasks, subjects stretched the quadrilaterals along the horizontal dimension, by about 2%, and shortened them in the vertical direction by a similar amount. Furthermore, some of the common visual illusions, such as the Müller–Lyer illusion, can also be evoked in the haptic domain (Suzuki and Arashida 1992) but others cannot. Gentaz and Hatwell (2004) argued that the discrepancy arises from the nature of exploratory movements in haptic perception, i.e., given the sequential nature of manual movements, a shape that produces a visual illusion may not be experienced in the same context in the haptic domain.

Based on the similarity of distortions in visual and haptic space, one might be tempted to argue that the processing of visual and haptic information has the same neural substrates. The neural substrates for the processing of haptic information have not been well delineated, although it most likely occurs in parietal cortex (see Goodwin and Wheat 2004 for a review). To the contrary, inferior temporal cortex (IT) has been implicated in visual object recognition and discrimination. Activity of neurons in IT discriminates between the shapes of visually presented objects, even between abstract geometrical shapes (Logothetis 1998). This does not exclude a participation of parietal cortical areas in visual shape processing because parietal lobe lesions do result in deficits, such as constructional apraxia, that require visual processing of shapes (Andersen 1987).

It is also possible that the correspondence between visual and haptic distortions in space comes about because one sensory modality serves to calibrate the other. Examples of this are provided by visually induced alterations in the auditory map of space (Knudsen 1985; Knudsen and Knudsen 1989) and visually induced alterations in the trajectories of limb movements (Flanagan and Rao 1995; Goodbody and Wolpert 1999).

TEMPORAL ASPECTS OF HAPTIC PERCEPTION

One fundamental difference between visual and haptic processing of information about shape is that, whereas the former may involve the spatial integration of static information, the latter of necessity involves the integration of information that evolves in time. The temporal order of stimuli does make a difference in haptic perception (Henriques et al. 2004). We had subjects trace 3 straight sides of an open shape in a fixed order, and then reproduce the shape with the manipulandum. We determined whether the length and orientation of one segment affected the reproduction of other preceding and subsequent segments. The results suggest that the length and angle of one segment influence the reproduction of later but not of earlier segments.

More generally, the sequential nature of haptic processing implies that the information must be stored in working memory for later retrieval. The process of storing the information in working memory, by itself, may introduce distortions in the representation of a shape. Such distortions have been demonstrated in tasks in which subjects made limb movements (McIntyre et al. 1997, 1998) or saccades (Gnadt et al. 1991) to remembered target locations.

Little is known about the neural correlates of haptic sensing but recent work by Romo, Salinas, and colleagues (Romo and Salinas 2001, 2003; Romo et al. 2002) is directly relevant to this question. They studied a task in which monkeys were required to discriminate the frequency of 2 vibratory stimuli presented in succession. They found that neurons in primary somatosensory cortex showed no evidence of a mnemonic representation; instead they responded only to the stimulus currently presented. In contrast, activity in secondary somatosensory cortex (S2) and in prefontal cortex depended on the frequency of both stimuli during the second stimulus period, thus providing a substrate for the comparisons needed for frequency discrimination. Averbeck et al. (2002, 2003) studied a task in which monkeys copied simple geometric shapes

presented visually and found task-related activity in prefontal cortex that encoded each of the segments in an overlapping fashion.

In summary, haptic sensing poses interesting questions because it involves the integration of a variety of sensory and motor signals over space and time. Technological advances have greatly facilitated behavorial studies of haptic sensing by permitting one to create virtual shapes that can be modified adaptively (see also Robles-De-La-Torre and Hayward 2001). From our review of recent work on this topic it should be clear that, although some pieces of this puzzle are beginning to come together, there are still many open questions. Furthermore, the neural processes that underlie haptic sensing are practically unexplored. It would appear that the behavioral studies described here could be adapted to electrophysiological investigations in behaving primates.

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