

Somatosensory Comparison during Haptic Tracing

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Active sensing involves memory retrieval and updating as well as mechanisms that trigger corrections to the ongoing exploratory movement. The present study examined this process in a task where human subjects moved the index fingertip clockwise around the circumference of a virtual sphere created by a robotic device. The fingertip pressed into the sphere during the movement, and the subjects were to report slight differences in sphere size (or surface curvature), which occurred from trial to trial. During each 2- to 3-s trial, subjects gradually adjusted their speed and pressure according to the current surface curvature, achieving a consistent level of contact force in the last half of the exploration. The results demonstrate that subjects were gradually accumulating haptic information about curvature and, at the same time, gradually changing the motor commands for the movement. When subjects encountered an unexpected transition in curvature (from circular to flat), they reacted by abruptly decreasing contact force at a latency of about 50 ms. This short latency indicates that spinally mediated corrections are engaged during this task. The results support the hypothesis that during haptic exploration, the neural comparison between expected and actual somatosensory feedback takes places at multiple levels, including the spinal cord.

Keywords: corticospinal system, forward model, long-latency reflex, sensory filtering, spinal reflex

Introduction

Intuition suggests that haptic exploratory movements involve some sort of comparison between what is expected and what is actually felt. For instance, when one runs a hand along a surface, deviations from the expected shape or texture (e.g., a button or a flaw in the fabric) provide information. Although this sort of exploration is an essential aspect of neural processing, we have only a rudimentary understanding of its mechanism.

Numerous recent investigations have focused on the process of forming these expectations, that is, the learning and storing of information about the physical properties of objects: metrics such as shape and texture but also basic mechanical parameters such as inertia and viscosity. Some studies have sought to define types of learning (e.g., “internal model learning,” Thoroughman and Shadmehr 2000; Franklin et al. 2007) or have theorized about the mechanism (e.g., “forward model functions,” Haruno et al. 2001). Others have described the serial nature of the exploratory processes that lead to a haptic perception of the shape of an unseen object, such as a face or a rectangle (Henriques et al. 2004; Soechting et al. 2006). Romo and colleagues (Romo and Salinas 2003; Romo et al. 2004) showed that somatosensory perception essentially involves a comparative interaction between ongoing activity in one cortical region and new activity in another cortical area.

In conjunction with these cortical processes of expectation and comparison, subcortical and perhaps even spinal circuits appear to perform similar computations. The elusive concept of “efference copy” or “corollary discharge” has widespread popularity in studies of animal sensation and movement, despite the fact that the evidence for this sort of mechanism is often indirect (reviewed by Crapse and Sommer 2008). Wolpert and colleagues (Shergill et al. 2003) have provided human behavioral evidence, and other studies suggest that the primate cerebellum may be involved (Ebner and Pasalar 2008; Shadmehr and Krakauer 2008). However, the clearest example of efference copy is the subtractive interaction that occurs in a brainstem nucleus in some species of electric fish (Bell 1982). In this electrosensory system, an expectation signal derived from the animal’s own electric field production is compared with the actual electrosensory signal. This process of neural comparison/cancellation results in an increased sensitivity to unexpected distortions in the electric field (which correspond to unexpected objects in the environment).

In designing the present study, we wondered if an analogous subtraction process might occur in the dorsal horn of the spinal cord of humans. If so, we would expect that during an exploratory movement an unexpected sensation would produce an error signal. The reaction would be subtractive in nature and would occur at a spinal reflex latency. In this paper, we will provide a description of this process in the context of an active sensing task: human subjects feeling along a curved surface, with the entire arm, especially the fingertip, and occasionally reacting to an unexpected change in curvature.

Materials and Methods

Setup and Subjects

Subjects were seated facing a PHANTOM Premium 3.0 Haptic Device (SensAble Technologies, Inc.). The extended right index fingertip was strapped into a “finger sled” such that the fingertip was free to move in the 83.8 × 58.4 × 40.6-cm robot workspace, unless it encountered a virtual surface (see Fig. 1). We programmed the robot to provide a pattern of resistance to movement that created a virtual sphere near the center of the workspace. As indicated by the shapes in Figures 1 and 2, the sphere was nearly complete; it actually had a flat base, programmed as a horizontal plane at the bottom. The virtual sphere was occasionally smoothly joined with a virtual cylinder, extending to the right.

This lightweight robot basically transduces the 3D position of a point at the tip of the finger sled (see Fig. 1, lower panels). Position data are input to a computer program that commands the robot’s motors to produce a specific force when the fingertip is at a particular position. This force was programmed to be perpendicular to the virtual surface, and it was proportional to the amount by which the fingertip penetrated the surface. In order to keep the virtual surfaces contained within the 3D robot workspace, the positional boundaries for transition from free movement to resistive force were formulated as a sphere and a tangent cylinder. However, as shown in Figure 1 (and Fig. 2) and discussed below, subjects generally traced circles (and occasionally

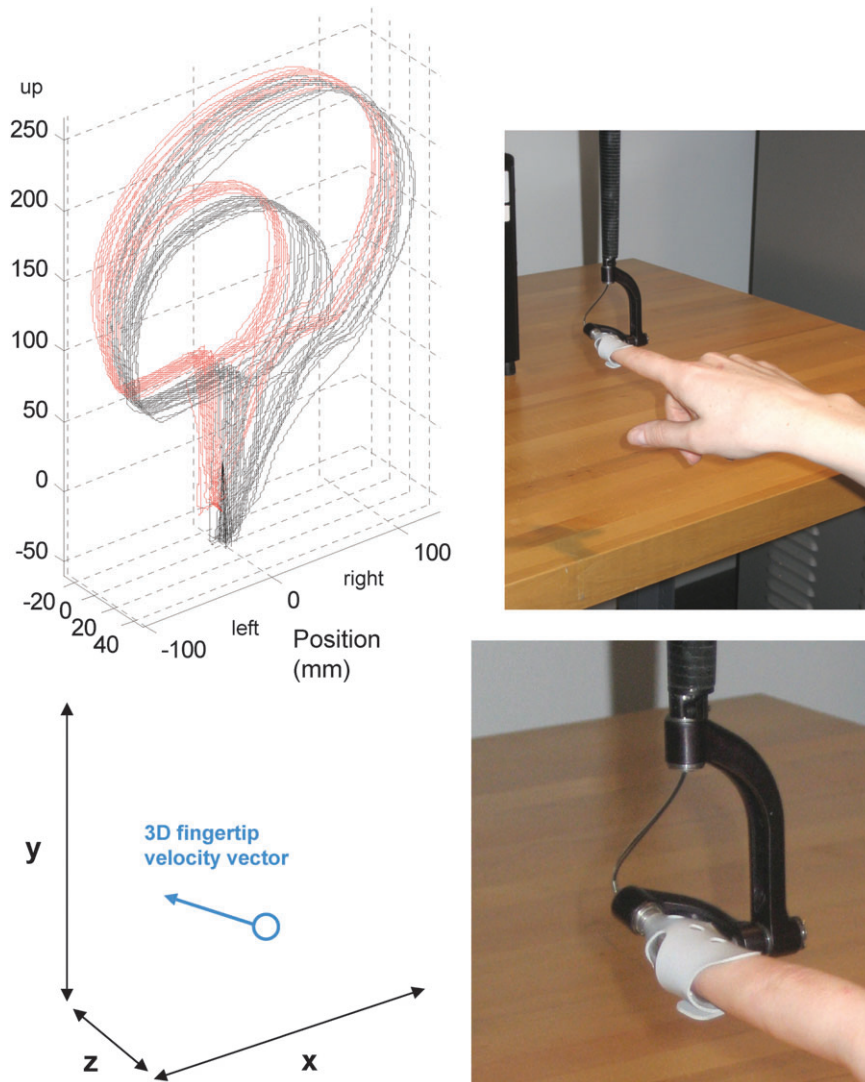


Figure 1. On the top left, the path of the fingertip for 2 sizes (large and small) and 2 subjects (A in black and C in red). On the right, the typical hand and wrist posture, with the index finger strapped into the finger sled attachment at the distal end of the PHANTOM robot arm. Note that the robot was programmed to create a virtual sphere but subjects were instructed to keep the fingertip in a frontal plane. Subject A used a frontal plane slightly closer to her body than did subject C and therefore her traced circles had a slightly smaller radius. On the bottom left, we schematically show the velocity of the point at the tip of the finger sled near the transition from the flat base to the circumference of the virtual sphere. Three-dimensional position, over time, was tracked by the PHANTOM robot and used to control the robot's motors.

tangent lines) in the frontal plane at the edge of the table. Therefore, subjects did not experience the anterior/posterior curvature of the sphere and tangent cylinder. The subjective feeling was one of sliding the fingertip along a smooth surface.

Thus, the virtual spheres were created by causing the robot motors to produce position-dependent forces that resisted movement of the fingertip into the sphere. For all virtual surfaces, the stiffness was set at 1.0 N/mm. The maximum force that the robot can produce is 22 N transiently and 3 N sustained. The maximum force typically used by subjects on the curved part of sphere was about 1–2 N (range of maximum force on any trial = 1.8–3.7 N across subjects). Thus, deformation of the sphere was typically less than 2 mm. We recorded contact force magnitude and direction, as well as the 3D position of the fingertip, at 1-ms intervals.

During the experiment, human subjects were seated facing a table containing the robot (Fig. 1, right). Each trial began with the right-hand resting on the edge of the table at chest height and the elbows supported by the armrests of the chair. Subjects were instructed to keep their eyes closed during each trial and to begin moving upon hearing a computer-generated tone. They were instructed to keep the fingertip in the plane created by the edge of the table (frontal plane)

while tracing around the virtual shape. As indicated by the blue symbols in Figure 2A,B, the fingertip moved straight upward to hit the base and then moved clockwise around the outside of the sphere, pressing in, to trace nearly a full circle. Subjects never received any visual information about the virtual objects.

The subjects were normal, healthy adults (1 male and 4 females), and they gave informed consent before taking part in the experiment. Each subject was seated at a distance where he or she could comfortably trace around the circumference of the largest sphere, thus drawing a circle in the frontal plane. However, circle size could vary somewhat across subjects if some used a frontal plane slightly closer to the body. In Figure 1 (top left), we show large and small circles traced by 2 subjects, and in Table 1, we quantify the sizes of all circles for all subjects. Although we did not attempt to constrain or measure the whole arm posture, we observed that subjects generally kept the back of the hand nearly horizontal (Hore et al. 1992; Gielen et al. 1997). Thus moving the finger sled along the virtual surface felt like hitting the horizontal base with the back of the finger, then moving to the left to round the corner, and then pushing into the virtual sphere first with the right side of the finger, then in the finger pad direction, then with the left side of the finger.

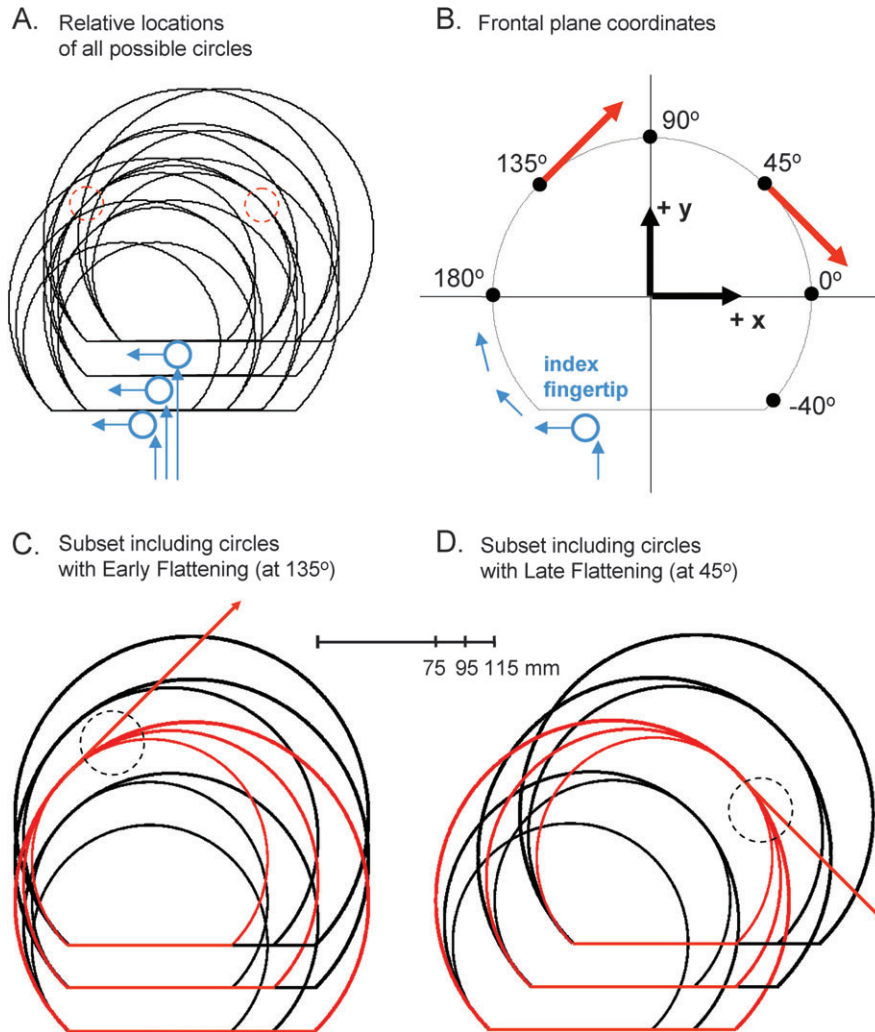


Figure 2. Experimental design. (A) In the main experiment, in each consecutive trial, the subject experienced a virtual sphere programmed to be of an unknown size (small, medium, or large) and to occupy an unknown workspace location; all possible spheres are shown here, projected onto a frontal plane. The fingertip (blue circle) moved up from below, hit a virtual horizontal surface, and then moved around the outside of the sphere, pressing in toward the center. Small, dashed, red circles indicate the spatial locations of possible perturbations. (B) At the 135° and 45° locations, the sphere was occasionally unexpectedly joined to a cylinder, such that the subject's frontal plane tracing transitioned from a circle to a line. In the lower panels (C and D), we show subsets of the circles, with the perturbed circles highlighted in red. Since subjects always traced the circle in the clockwise direction, the perturbation (flattening) at 135° is called "early" and the flattening at 45° is called "late." The locations of flattening are highlighted by dashed circles.

Table 1

The circle size and the movement time used by each subject is quantified using the mean radius and time used to trace the top half of each sphere, in the size unknown condition

Subject	Radius (mm)			Time (ms)		
	Small	Medium	Large	Small	Medium	Large
A	71.9	93	114.7	1014	1241	1483
B	73.6	91.1	110.1	1476	1771	2394
C	73.9	94.6	115.6	1376	1633	1944
D	75.6	93.8	112.3	1054	1229	1578
E	76.4	95.5	114.9	1153	1361	1618

Protocol

The protocol was designed to create a situation where subjects gathered new haptic information during each trial. Beyond the 0° point on the right side of the circle (see Fig. 2B), subjects were allowed to end the exploration and were required to verbally report whether the circle they had just experienced was small, medium, or large in size. The relative sizes were chosen to make the size identification moderately difficult, and as discussed below, the virtual circles were in slightly different spatial locations from trial to trial (see Fig. 2A).

When initially seated, subjects received 7 practice trials. First, they traced a small, a medium, and then a large circle, and in each case, they were told the size. Then, they experienced one trial where the highest point of the sphere was joined with a cylinder, extending to the right. They were told that this sort of surface transition would occasionally happen and that it could happen at any location. They were told that if this happened, they were to continue moving along the surface and then report both the sphere size (small, medium, or large) and the fact that the circular circumference had transitioned into a straight line. Finally, in the last 3 practice trials, we reviewed the 3 sizes: large, medium, and then small.

The main goal of the protocol design was to create a situation where neither the size nor the possibility of a transition to a straight line (a "flattening") would be cued by the starting location of the curved surface. This was achieved by having all 3 sizes and the possibility of flattening follow each starting point. The arrangement of the virtual spheres in many different spatial locations (see Fig. 2A) served this purpose.

As illustrated in Figure 2, flattening could occur at the 135° location ("early flattening") and at the 45° location ("late flattening"). The protocol was designed so that all 3 sizes transitioned to a straight line at the same location in space, thus facilitating size comparisons without

confounding factors such as arm and hand location. Though limiting flattening to a specific spatial location could make this event more predictable, the close proximity of all the spheres in the robot workspace makes this unlikely (small, red dashed circles in Fig. 2A). In the early flattening condition, 81% of the unperturbed trials reached within 40 mm of the point of possible flattening, and all unperturbed trials included locations within 63 mm. Similarly, in the late flattening condition, 78% of unperturbed trials were within 40 mm, and all were within 80 mm. Given that the subjects were engaged in the task of determining circle size, and the low frequency of flattening trials (as discussed below), it seems unlikely that subjects associated the specific point in space with a possibility of flattening.

The main experiment was comprised of 2 blocks. First, there were 294 trials in which the circle size, location, and the occasional flattening varied randomly from trial to trial (the “size unknown” condition). During this block, there were 14 repeats of each unperturbed size/location but only 7 repeats of each of the 6 flattening situations (3 circle sizes × 2 flattening locations). Thus, in the 294-trial block, early flattening (Fig. 2C) occurred in only 7% of the trials and late flattening (Fig. 2D) occurred in only 7% of the trials; in other words, 1 out of 14 trials was ended by early flattening, and for those trials that continued, only 1 out of 13 ended in late flattening.

Cases of early flattening at the 135° location (early in the movement) and late flattening at the 45° location (late in the movement), are illustrated by the red traces in Figure 2B,C, and D. Some of our analysis will focus on the mechanical and neuromuscular events that occurred around the time of the curved to straight surface transition (dashed circles in Fig. 2A,C, and D).

This main block of size unknown trials was followed by 63 trials where there were 7 consecutive trials with each of 9 different virtual objects, for a “size known,” a control condition. The 9 virtual objects included a small, medium, and large sphere, as well as a sphere of each size where the circumference transitioned to a straight line at either the 135° or 45° location.

Analysis

The analysis was focused on comparisons between the size unknown and size known (control) condition and on situations of unexpected early or late flattening compared with the corresponding size unknown conditions where no flattening occurred. We also compared the data from the different circle sizes with see if and how contact force and speed varied with size, in different conditions. In most cases, the particular condition was represented by a 5-trial average of force or speed measurements. This allowed us to exclude the first 2 trials with a new situation or any other outliers. In the size unknown condition, in most cases, we selected the 5 trials that were closest to the mean (judged by correlations between individual trials). However, in the size known condition and for a closer examination of the timing of the response to flattening, we explicitly focused additional analysis on the last 5 of the 7 trials.

The $P < 0.05$ level was used to identify significant differences between circle sizes; it will be highlighted with gray shading when it occurs for at least 10 consecutive data points (Figs 4, 5, and 7). Force and position traces were digitally smoothed with a 2-sided exponential filter, with a time constant of 2 ms. In cases where force or speed data were combined across subjects, they were normalized by adjusting each subject’s mean values (across unperturbed trials) to the grand mean. Speed is the magnitude of the 3D velocity vector.

Results

Gradually Forming a Haptic Percept

The judgment of circle size was reasonably difficult. In the size unknown condition, for trials where subjects moved clockwise all the way around (from 220° to a location beyond the 0° point), their size reports were 81% correct (“no flattening,” Fig. 3). When the circle was interrupted late in the exploration (at 45°), the subjects’ correct response rate was similar, at 70%

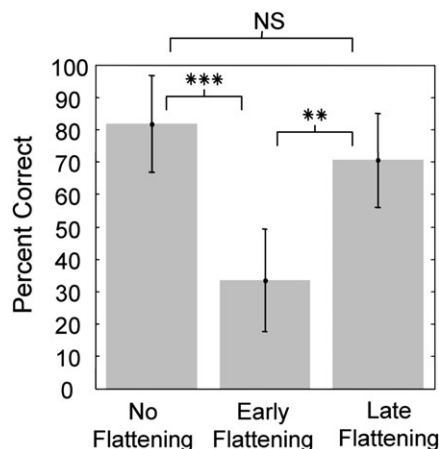


Figure 3. Success rates of the verbal size reports; grand means across all subjects (\pm standard deviation) for the size unknown condition. When subjects traced the entire circle (no flattening), they were correct significantly ($P < 0.001$) more often than when the circular tracing was ended at 135° by early flattening. When subjects traced up until 45° (late flattening), they were also correct significantly ($P < 0.01$) more often than for early flattening. The difference between no flattening and late flattening was not significant (NS, $P > 0.05$).

(late flattening, Fig. 3). However, when the exploration was interrupted earlier (at 135°), subjects gave correct reports at the chance probability level of 33% (early flattening, Fig. 3). This suggests that information about circle size was gathered during the course of exploration of the circle; the subjects’ knowledge of the true size improved during the movement from the left side to the right side. For the top half of the circle (from 180° to 0°), Table 1 shows the time used and distance covered by each subject. For the 5 subjects, average top half movement times for the small, medium, and large spheres were 1.2, 1.5, and 1.8 s, respectively.

Force Patterns

Subjects tended to use a relatively consistent amount of contact force across the 3 circle sizes when the size was known in advance. However, in the size unknown condition, during the first half of the exploratory movement, contact force was graded with circle size. Using data from a representative subject, these patterns of contact force are shown in 2 different formats in Figures 4A and 5A. In Figure 4B, we also show the control data from the same subject in the size known condition.

In the size unknown condition, there was a significant difference in contact force according to sphere size during the early part of the exploration (gray shaded regions in Figs 4A and 5A) but not during the last half. For the 5 subjects, on average, the transition from a significant difference in contact force across sizes to no difference across sizes occurred at the 73° location (21° standard error). In contrast, in the control trials where the size was known and identical across sequential trials, subjects produced a consistent level of contact force from the very beginning of the circle tracing (Fig. 4B). In this control condition, none of the 5 subjects showed a significant difference across size up to the 135° mark, and 3 of the 5 subjects showed only sporadic, short regions of difference at various later locations (data not shown). This suggests that the motor goal of this task can be viewed as producing a relatively consistent (curvature invariant) level of contact force as soon as the surface type can be sensed.

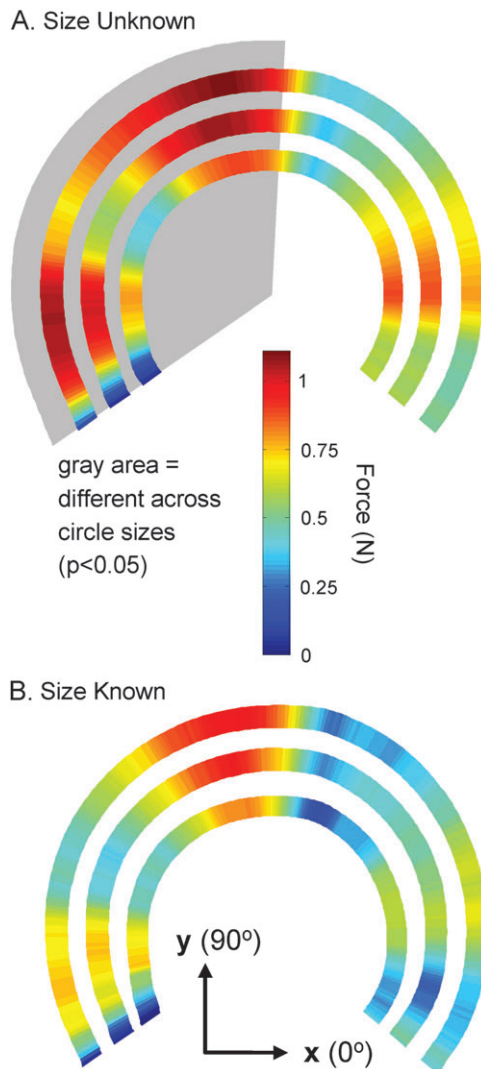


Figure 4. Contact force as a function of position in the size unknown (A) and size known (B), no flattening conditions. Each trace represents an average of repeated trials from a single subject (Subject C) tracing small, medium, or large circles in any workspace location. Contact force (color scale) was a significant function of circle size only in the early part of the size unknown circles (gray region). There was more contact force (red shading) for the large circles and less (green–blue) for the small circles during this part of the trace.

Thus, with experience or with prior knowledge, contact force became curvature invariant. However, there was always a certain waxing and waning of contact force during the exploratory movement. This was true for both the size unknown (Figs 4A and 5A) and the size known (Fig. 4B) conditions. The pattern was similar across subjects (Fig. 5B) and is presumably due to the complex mechanics of these exploratory movements. All subjects pressed most forcefully around 200° and/or 120° (left side) and then again near 10° (right side). In Figures 4A and 5A, data were combined across workspace locations to provide 30 trials for each average. To try to understand the presumably mechanical fluctuations, we also examined the 5-trial averages from different workspace location. There was no consistent effect of workspace location, and thus, the fluctuations are not easily explained by gravity or the left–right reaching posture of the upper arm. The full explanation may also include the biomechanics,

receptor distribution, and haptic control of the hand and index finger.

The subjects' speed also fluctuated with position and sometimes became size related in the second half of the exploration. Figure 5C shows the speed in the same trials as in Figure 5A, with red traces representing small circles and green and blue traces representing medium and large circles, respectively. In contrast to the force data, where there was a significant size difference in the first half of the trial, the speed profiles were not different across sizes until after 135°. Speed also waxed and waned, in a pattern different from contact force, but qualitatively similar across subjects (see Fig. 5D). Its marked difference from the constant speed predicted by the well-known speed/curvature power law (Lacquaniti et al. 1983) emphasizes the fact that this haptic exploratory movement was quite different from a free drawing movement. Instead, speed was always low at the beginning and end and high in the middle, a profile more similar to reaching movements even though the movement times were quite long (up to 3 s). In Figure 5C, notice that in the second part of the trial, this subject adapted by moving significantly faster (gray areas) for large circles (blue) and slower for small circles (red). This was true for 3 of the 5 subjects, and it is consistent with the tendency for speed to be higher for longer distances, in preplanned reaching movements (Buneo et al. 1994).

Thus, the overall pattern of contact force and speed supports the following interpretation: Subjects approached the unknown surface planning to produce a certain (default) action. Due to the elasticity at the haptic interface, moving along the larger sphere mechanically resulted in more contact force than moving along the more tightly curved surface of the smaller sphere. Consonant with the perceptual size reports shown in Figure 3, in the second half of the movement, subjects used accumulated haptic information about circle size to voluntarily adjust the pressure (Figs 4A and 5A) and speed (Fig. 5C) of their motor actions.

Response to Unexpected Flattening

The mechanical effect of an unexpected flattening was an immediate increase in contact force and decrease in speed. This is shown in Figure 6 using repeated trials from a representative subject (Fig. 6A,C) and results averaged across all subjects (Fig. 6B,D). In these examples, the flattening occurred at 45°, after contact force levels for small (red), medium (green), and large (blue) spheres had started to converge. Flattening corresponds to time zero in these plots. Compared with the control condition of no flattening (black traces), the flattening caused force to increase consistently around the onset of the change in curvature (time zero).

Mechanical considerations indicate that without a modification of the motor command, contact force would have continued to increase due to the increasing spatial distance between the tangent surface and the expected curved path. Focusing on the dashed circle in Figure 2D, at this time, subjects were rounding the right side of the circle and planning to continue pressing down and to the left. Thus, due to the elasticity of the finger, the tangent surface would mechanically cause a force increase. Furthermore, the monosynaptic stretch reflex would be expected to cause a further increase in contact force after about 30 ms (Doemges and Rack 1992; Maluf et al. 2007).

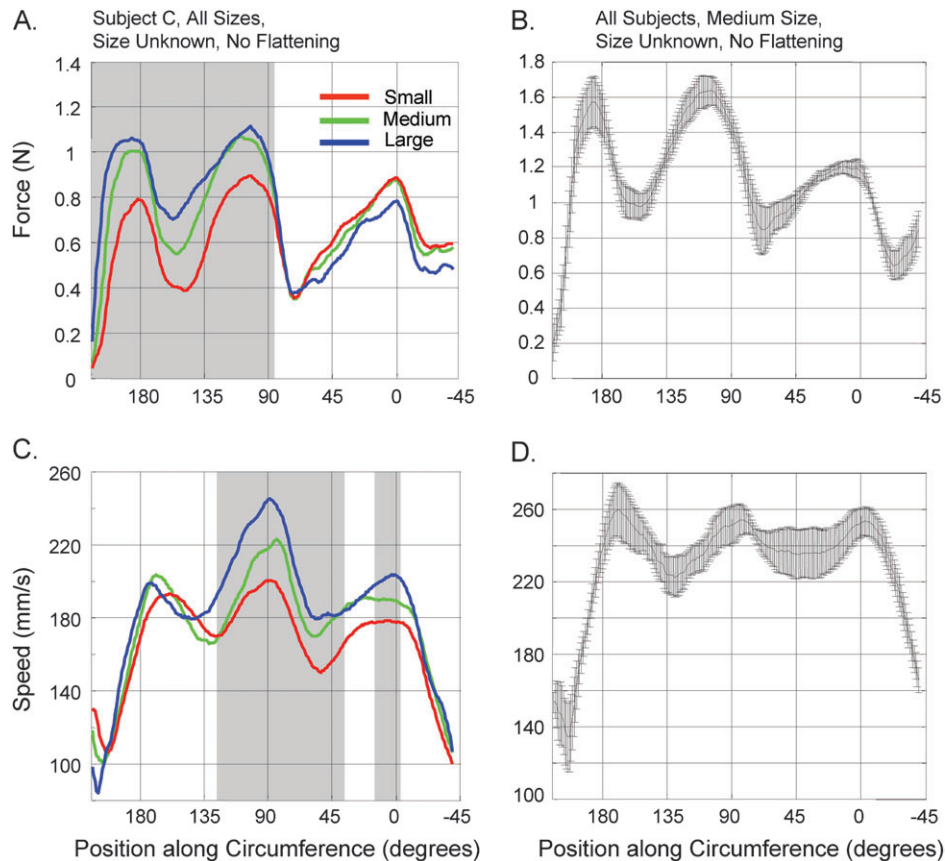


Figure 5. Contact force (A and B) and speed (C and D) as a function of position in the size unknown, no flattening condition. In the left panels, each trace represents an average of 30 trials from Subject C tracing small (red), medium (green), or large (blue) circles in any location. Gray regions highlight significant ($P < 0.05$) differences across circle size. In the right panels, each trace represents the average across the 5 subjects (bars represent standard error) for tracings of the medium circle in the location that served as the control (no flattening) condition for the late flattening. Thus, the time around the 45° position corresponds to the black traces shown in Figure 6B,D.

Thus, contact force would be expected to (mechanically) continue to increase nearly monotonically or (reflexively) increase its rate of rise. However, in a situation where the goal is to continue to produce a consistent level of contact force, the functionally appropriate neural response would be to decrease contact force. As shown in Figure 7, closer examination of contact forces (top) and their derivatives (bottom) around time zero revealed an abrupt decrease in the rate of force increase about 40–50 ms after the onset of the flattening. This was most apparent in the derivative plots (Fig. 7C,D), which peaked at this time and was true for both early (left) and late (right) flattening.

For early flattening, there was also an early size difference in the rate of change of force (Fig. 7C), which may have both a mechanical and a neural interpretation. As illustrated in Figure 2C (dashed circle), due to the smaller difference between the tangent and the expected surface, the tangent line to the large circle (blue traces in Fig. 7) should have created less of a perturbation and would have triggered less of a response than for the small circle (red traces in Fig. 7). In contrast, there is no size difference in the rate of change of force for late flattening. By the time of late flattening (Figs 2D and 7D), the voluntary increase in speed for large circles (in 3 of 5 subjects) may have created a more intense perturbation at the tangent point for these circles and therefore may have counterbalanced the geometrical aspect of the size effect.

To more precisely measure the onset of the abrupt termination of the force increase (the derivative peaks in Fig. 7C,D), using individual trials from each subject, we estimated this latency as the time between zero-crossings of the force double derivatives. Table 2 shows that the latency estimates for each subject and condition ranged from 39 to 73 ms. The longest latencies were observed in the slowest subject (Subject B, cf. Table 1). The grand mean response latency was 51.5 ms \pm 3.7 ms.

Thus, the mechanical force increase was counteracted by a decrease after 50 ms. After 150 ms, the rate of change of force began to return to the preperturbation level (Fig. 7C,D), and the significant difference in force level related to the previous circle size began to disappear (end of gray shaded area in Fig. 7A). Thus, our analysis revealed neural reactions at spinal (50 ms) and well as cortical (150 ms) latencies.

Discussion

In this study, human subjects felt along a curved surface, with the entire arm and especially the fingertip. After about 2 s of exploration, they had to report the circle size. We aimed to create a situation where subjects gradually formed a new percept within each trial, so that we could examine how the motor commands gradually changed. An unexpected change in surface curvature introduced a mechanical increase in contact force. Subjects responded first by decreasing the rate of

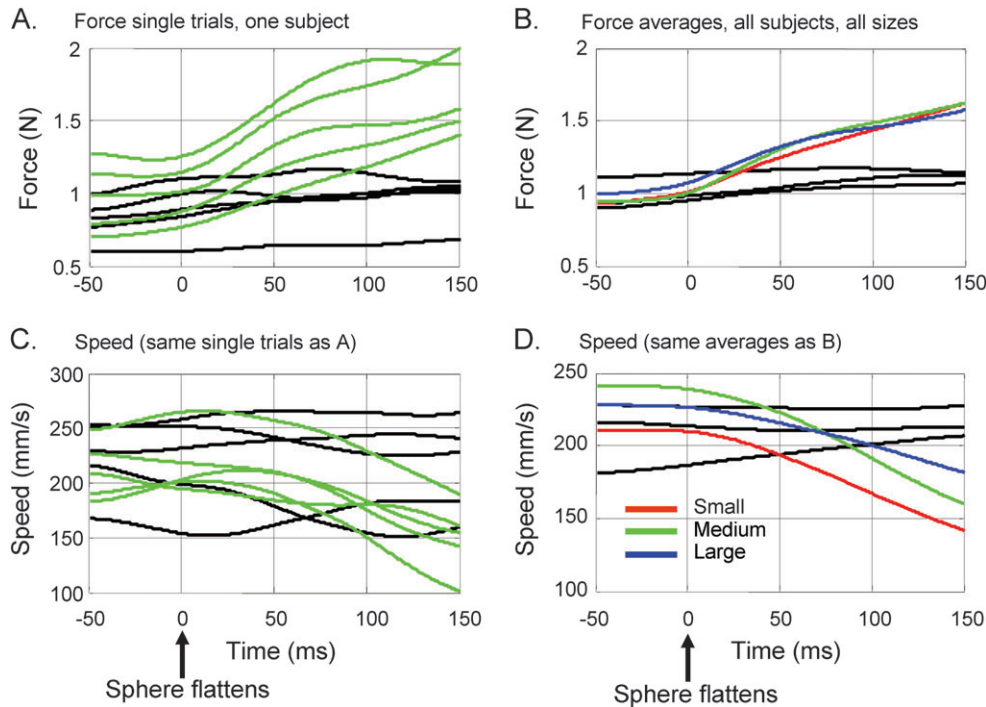


Figure 6. Contact force (A, B) and speed (C, D) changed when the circle unexpectedly flattened at time zero (colored traces) but not in control trials (black traces). In the left panels (A and C), we show 5 medium-sized late flattening trials for Subject E, and in the right panels (B and D), we show grand means across all subjects for small (red), medium (green), and large (blue) late flattening.

increase of contact force at a latency of 50 ms and then by more gradually updating the motor command after 150 ms. Our goal was to use the experimental results to infer the basic steps that the system normally uses to gradually gather somatosensory information while continuously updating motor commands.

Cortical Motor Commands

According to the currently popular view, during this process, arm and hand muscles receive descending motor commands (gray arrows in Fig. 8) that are approximately accurate due to experience. Somatosensory input (Fig. 8, far right) can act as feedback to update the ongoing commands (upper left, loop a). Due to the amount of time required to conduct signals from tactile (cutaneous) receptors and proprio (joint and muscle) receptors to the cortex and then back to the spinal cord, the update would influence a hand movement after about 100 ms (Johansson and Flanagan 2009).

Somatosensory feedback signals also provide learning-related inputs (Fig. 8, loop b) to the inverse model (box), which is defined as a mapping between desired movements and the appropriate forces to produce them. Note that the main input (large gray arrow) to the inverse model is the difference between the current state and the target state. It is well known that cortical motor commands represent the direction between the current and final states not just the final target state (Georgopoulos et al. 1982; Buneo et al. 2002). Thus, even if a preplanned motor response is simply “triggered,” the new motor command should still be tailored to the current state of the system. As discussed below, maintaining a cortical representation of current state may involve more complex, comparison mechanisms.

Brain/Spinal Interactions

The major anatomical circuit for the use of somatosensory feedback is thought to depend on reciprocal connections between cerebral cortical areas, the cerebellum, and perhaps even the basal ganglia (reviewed by Flanders 2009). The spinal cord is generally not included in this thinking. But anatomical considerations militate against this omission. A significant portion of the corticospinal tract terminates in the dorsal horn of the spinal cord, converging with somatosensory input from the dorsal root ganglia. In recent reviews, Lemon and colleagues (Lemon and Griffiths 2005; Lemon 2008) suggested that the function of this convergence is to cancel “expected” somatosensory inputs, that is, those that predictably result from descending motor commands. Classic work suggests that the result of this convergence is conveyed to the cerebellum by the ventral spinocerebellar tract (Lundberg 1971). Furthermore, this hypothetical comparison/cancellation could potentially allow the “unexpected” somatosensory inputs direct access to spinal motor circuits, where they could have a significant role in shaping motor commands.

Support for this hypothesis can be found in the results of a recent stimulation and recording study of the primate cervical spinal cord (Seki et al. 2003, 2009). This study revealed that just prior to voluntary wrist flexion or extension, cutaneous afferent input to spinal interneurons is inhibited. The authors reasoned that this inhibition most likely comes from the descending motor command. In Figure 8, this idea is illustrated by the longest, black arrow, labeled efference copy.

Spinal Mechanisms

Thus, filtered information from cutaneous receptors is potentially available at the level of the spinal cord. In the present

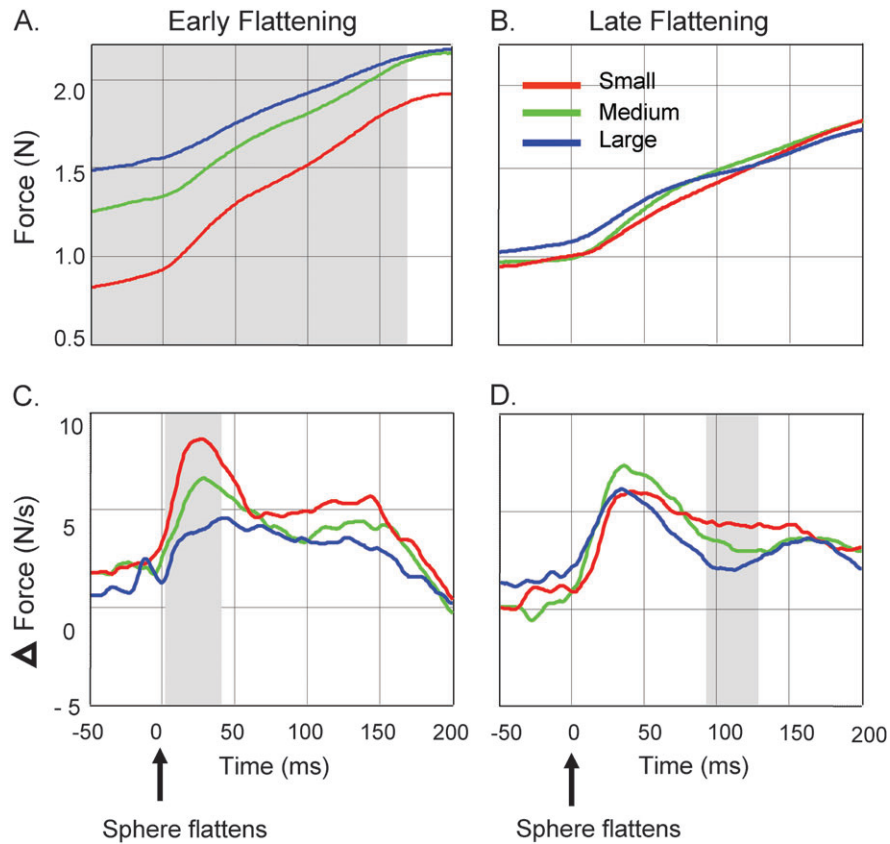


Figure 7. Contact force (A, B) and the time derivative of contact force (C, D) exhibit an abrupt mechanical effect of early (A, C) and late (B, D) flattening, as well as the neuromuscular response to this somatosensory input. Each trace is a grand mean across all subjects for small (red), medium (green), and large (blue) circles.

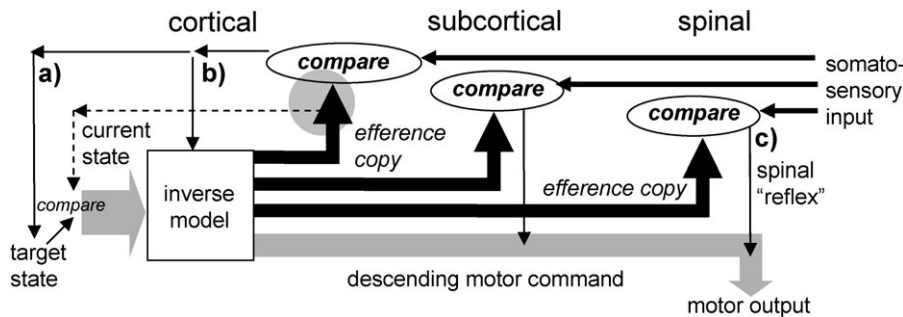


Figure 8. Schematic model of reactions to somatosensory input at the spinal (right), subcortical (middle), and cortical (left) levels. Loop a) is a feedback-based updating of the motor command at the highest level (target state). Loop b) represents the comparison of somatosensory feedback with efference copy used to update the inverse model (square). The gray circle represents forward model operations used to facilitate this comparison and to update the current state. Loop c) is a hypothetical comparison of somatosensory input with efference copy at the level of the spinal cord. This could give rise to functionally appropriate modifications to motor output at spinal reflex latencies.

study, proprioceptive input was also potentially useful. A well-established role of proprioceptive input is in stretch reflexes, which are known to provide short latency (20 ms), direct feedback regulation of the muscle of origin (Fig. 8, loop c). Proprioceptive and cutaneous input has also been shown to produce slightly longer latency (50 ms), functionally organized adjustments to tensions in many muscles (Traub et al. 1980; Rothwell et al. 1982; Johansson and Westling 1984; Cole and Abbs 1988; Soechting and Lacquaniti 1988; Nichols et al. 1999; Ohki et al. 2002). In these cases, the muscle that is stretched is not always the one that exhibits a reflexive contraction; instead an abrupt muscle or skin stretch can give rise to a more complex pattern of excitation and inhibition of various

motoneurons, and cortical circuits may be involved in tailoring these reactions to the task at hand. To what extent do these proprioceptive and cutaneous mechanisms work to automatically correct mismatches between desired and actual contact forces?

Valero-Cuevas (2005) has shown that the direction of force produced at the tip of the index finger is critically dependent upon the balance of tensions in a complex chain of tendons. We propose that these tensions could be automatically adjusted based on filtered sensory inputs, which would signal a misalignment between the desired and actual force direction. A finger force reaction at a latency less of than 60 ms from the mechanical event can be taken as evidence for a spinal (rather

Table 2

Correction latencies (in ms) based on zero-crossings of the force acceleration in individual subjects (5 trial averages)

Subject	Early flattening correction time (ms)			Late flattening correction time (ms)			Mean (standard deviation)
	Small	Medium	Large	Small	Medium	Large	
A	48	53	58	44	48	48	49.8 (4.9)
B	52	54	52	59	73	51	56.8 (8.4)
C	42	52	49	62	50	49	50.6 (6.5)
D	43	39	53	42	56	49	47.0 (6.7)
E	56	41	63	41	57	62	53.3 (9.9)

than a brain) mechanism (Garnett and Stephens 1980). Although stereotypical grab and slip reflexes have been reported previously (e.g., Traub et al. 1980; Cole and Abbs 1988), the results of the present study may be among the first to highlight a more routine, spinal, efference copy comparison mechanism for fine-tuning ongoing fingertip forces.

Somatosensory Comparison at Multiple Levels

The schematic in Figure 8 combines this hypothetical spinal mechanism, with its better-known subcortical and cortical counterparts. In this schematic, the essential function of the somatomotor system is viewed as the comparison between expected and actual somatosensory input, with expectations generated by efference copy signals and comparison-based error signals used to adjust motor output. It is generally accepted that a sensory input-efference copy comparison (Fig. 8, gray circle) is a forward model function of the cortex and/or the cerebellum (Ebner and Pasalar 2008; Shadmehr and Krakauer 2008; Flanders 2009). We now propose that the spinal cord implements a similar comparison (Fig. 8, loop c).

As mentioned above, in order to produce a movement, the cortical-level process issuing new motor commands must take into account the current state of the system (e.g., the hand's current position or velocity) (dashed arrows in Fig. 8). For a movement sequence or an ongoing movement, the transcortical 100-ms somatosensory delay would preclude a reliance on somatosensory feedback to track current state. Historically, in studies of ongoing movements, investigators tended to emphasize segmentation, which was taken to imply either feedforward control with preplanned endpoints (Soechting and Terzuolo 1987; Soechting and Flanders 1992), or discrete updates at least 100 ms after the initial output (Flanagan et al. 2003; Johansson and Flanagan 2009). Feedforward control with preplanned, fixed final-initial postures is also an explanation for the desirability the Donders' law phenomenon for eye movements: a fixed mapping of 2D gaze direction to 3D eye posture prevents the accumulation of eye torsion in a sequence of saccades and therefore simplifies the tracking of final-initial state (Crawford et al. 2003; see also Hore et al. 1992; Gielen et al. 1997).

With their more complex mechanics, feedforward control of sequences of arm or hand movements might be even more prone to error accumulation. However, it appears that the sensorimotor system is inherently designed, through comparison operations, to continuously keep track of its own current state. In eye movement control, the current gaze direction/eye posture is constantly represented by the locus of activity in the superior colliculus and the pattern of activity in the motor nuclei. For arm and hand movement, where outcomes are less

certain, a similar goal may be achieved through the widespread use of efference copy comparisons with somatosensory input to maintain an accurate representation of the current state of the motor system.

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References

- Bell CC. 1982. Properties of a modifiable efference copy in an electric fish. *J Neurophysiol.* 47:1043-1056.
- Buneo CA, Jarvis MR, Batista AP, Andersen RA. 2002. Direct visuomotor transformations for reaching. *Nature.* 416:632-636.
- Buneo CA, Soechting JF, Flanders M. 1994. Patterns of muscle activation for reaching: the representation of distance and time. *J Neurophysiol.* 71:1546-1558.
- Cole KJ, Abbs JH. 1988. Grip force adjustments evoked by load force perturbations of a grasped object. *J Neurophysiol.* 60:1513-1522.
- Crapse TB, Sommer MA. 2008. Corollary discharge across the animal kingdom. *Nat Rev Neurosci.* 9:587-600.
- Crawford JD, Martinez-Trujillo JC, Klier EM. 2003. Neural control of three-dimensional eye and head movements. *Curr Opin Neurobiol.* 13:655-662.
- Doemges F, Rack PM. 1992. Changes in the stretch reflex of the human first dorsal interosseous muscle during different tasks. *J Physiol.* 447:563-573.
- Ebner TJ, Pasalar S. 2008. Cerebellum predicts the future motor state. *Cerebellum.* 7:583-588.
- Flanagan JR, Vetter P, Johansson RS, Wolpert DM. 2003. Prediction precedes control in motor learning. *Curr Biol.* 13:146-150.
- Flanders M. 2009. Voluntary movement. In: Binder MD, Hirokawa N, Windhorst U, editors. *Encyclopedia of neuroscience.* Berlin (Germany): Springer. p. 4371-4375.
- Franklin DW, So U, Burdet E, Kawato M. 2007. Visual feedback is not necessary for the learning of novel dynamics. *PLoS One.* 2(12):e1336.
- Garnett R, Stephens JA. 1980. The reflex response of single motor units in human first dorsal interosseous muscle following cutaneous afferent stimulation. *J Physiol (Lond).* 303:351-364.
- Gielen CC, Vrijenhoek EJ, Flash T, Neggers SF. 1997. Arm position constraints during pointing and reaching in 3-D space. *J Neurophysiol.* 78:660-673.
- Georgopoulos AP, Kalaska JF, Caminiti R, Massey JT. 1982. On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J Neurosci.* 2:1527-1537.
- Haruno M, Wolpert DM, Kawato M. 2001. Mosaic model for sensorimotor learning and control. *Neural Comput.* 13:2201-2220.

- Henriques DY, Flanders M, Soechting JF. 2004. Haptic synthesis of shapes and sequences. *J Neurophysiol.* 91:1808-1821.
- Hore J, Watts S, Vilis T. 1992. Constraints on arm position when pointing in three dimensions: Donders' law and the Fick gimbal strategy. *J Neurophysiol.* 68:374-383.
- Johansson RS, Flanagan JR. 2009. Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nat Rev Neurosci.* 10:345-359.
- Johansson RS, Westling G. 1984. Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Exp Brain Res.* 56:550-564.
- Lacquaniti F, Terzuolo C, Viviani P. 1983. The law relating the kinematic and figural aspects of drawing movements. *Acta Psychol.* 54:115-130.
- Lemon RN. 2008. Descending pathways in motor control. *Annu Rev Neurosci.* 31:195-218.
- Lemon RN, Griffiths J. 2005. Comparing the function of the cortico-spinal system in different species: organizational differences for motor specialization? *Muscle Nerve.* 32:261-279.
- Lundberg A. 1971. Function of the ventral spinocerebellar tract. A new hypothesis. *Exp Brain Res.* 12:317-330.
- Maluf KS, Barry BK, Riley ZA, Enoka RM. 2007. Reflex responsiveness of a human hand muscle when controlling isometric force and joint position. *Clin Neurophysiol.* 118:2063-2071.
- Nichols TR, Cope TC, Abelew TA. 1999. Rapid spinal mechanisms of motor coordination. *Exerc Sport Sci Rev.* 27:255-284.
- Ohki Y, Edin BB, Johansson RS. 2002. Predictions specify reactive control of individual digits in manipulation. *J Neurosci.* 22:600-610.
- Romo R, Hernández A, Zainos A. 2004. Neuronal correlates of a perceptual decision in ventral premotor cortex. *Neuron.* 41:165-173.
- Romo R, Salinas E. 2003. Flutter discrimination: neural codes, perception, memory and decision making. *Nat Rev Neurosci.* 4:203-218.
- Rothwell JC, Traub MM, Day BL, Obeso JA, Thomas PK, Marsden CD. 1982. Manual motor performance in a deafferented man. *Brain.* 105:515-542.
- Seki K, Perlmutter SI, Fetz EE. 2003. Sensory input to primate spinal cord is presynaptically inhibited during voluntary movement. *Nat Neurosci.* 6:1309-1316.
- Seki K, Perlmutter SI, Fetz EE. 2009. Task-dependent modulation of primary afferent depolarization in cervical spinal cord of monkeys performing an instructed delay task. *J Neurophysiol.* 102:85-99.
- Shadmehr R, Krakauer JW. 2008. A computational neuroanatomy for motor control. *Exp Brain Res.* 185:359-381.
- Shergill SS, Bays PM, Frith CD, Wolpert DM. 2003. Two eyes for an eye: the neuroscience of force escalation. *Science.* 301(5630):187.
- Soechting JF, Flanders M. 1992. Organization of sequential typing movements. *J Neurophysiol.* 67:1275-1290.
- Soechting JF, Lacquaniti F. 1988. Quantitative evaluation of the electromyographic responses to multidirectional load perturbations of the human arm. *J Neurophysiol.* 59:1296-1313.
- Soechting JF, Song W, Flanders M. 2006. Haptic feature extraction. *Cereb Cortex.* 16:1168-1180.
- Soechting JF, Terzuolo CA. 1987. Organization of arm movements. Motion is segmented. *Neuroscience.* 23:39-51.
- Thoroughman KA, Shadmehr R. 2000. Learning of action through adaptive combination of motor primitives. *Nature.* 407:742-747.
- Traub MM, Rothwell JC, Marsden CD. 1980. A grab reflex in the human hand. *Brain.* 103:869-884.
- Valero-Cuevas FJ. 2005. An integrative approach to the biomechanical function and neuromuscular control of the fingers. *J Biomech.* 38:673-684.