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Representation of Object Size in the Somatosensory System

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Abstract

In this study we investigate the haptic perception of object size. We report the results from four psychophysical experiments. In the first, we ask subjects to discriminate the size of objects that vary in surface curvature and compliance while changing contact force. We show that objects exhibit size constancy such that perception of object size using haptics does not change with changes in contact force. Based on these results, we hypothesize that size perception depends on the degree of spread between the digits at initial contact with objects. In the second experiment, we test this hypothesis by having subjects continuously contact an object that changes dynamically in size. We show that size perception takes into account the compliance of the object. In the third and fourth experiments we attempt to separate the individual contributions of proprioceptive and cutaneous input. In the third, we test the ability of subjects to perceive object size after altering the sensitivity of cutaneous receptors with adapting vibratory stimuli. The results from this experiment suggest that initial contact is signaled by the cutaneous slowly adapting type 1 afferents (SA1) and/or the rapidly adapting afferents (RA). In the last experiment, we block cutaneous input at the site of contact by anesthetizing the digital nerves and show that proprioceptive information alone provides only a rough estimate of object size. We conclude that the perception of object size depends on inputs from SA1 and possibly RA afferents, combined with inputs from proprioceptive afferents that signal the spread between digits.

INTRODUCTION

Tactile object recognition involves the perception of an object's size, shape, and texture. Whereas the local two-dimensional form and texture of the object surface are conveyed to the CNS by cutaneous mechanoreceptive afferents that innervate the skin (Johnson and Hsiao 1992), the global size and shape of the object must be conveyed by combined inputs from both cutaneous mechanoreceptors that carry information about the local surface features at the points of contact and proprioceptors that carry information about where those points of contact lie in three-dimensional space. Here we investigate the psychophysics of object size perception, which to date has received only limited attention.

At a first approximation, the size of an object grasped by the hand depends solely on proprioceptive information from joint, muscle spindle, and skin afferents (Burke et al. 1988) signaling the distance between the digits; for large objects the fingers are spread apart widely and for small objects the fingers are close together. However, cutaneous information from

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mechanoreceptors must also play a role because object size perception requires contact between the hand and the object; simply changing the positions of the fingers in space does not produce the sensation of an object changing in size. Moreover, the problem of size perception is complex if one considers that objects show size constancy. Although Gepshtein and Banks (2003) showed that the perception of object size is independent of the way that the object is oriented in space, it is unclear how or whether object size is affected by changes in contact area or force. When objects are grasped with different forces, the contact area of the skin changes and the spread between the digits changes slightly due to the compliance of the fingerpads. The spread between the fingers decreases even more when soft compliant objects are grasped. Understanding what happens to the perceived size of objects under these conditions is a fundamental question we address in this study.

Here we investigate haptic size perception in the absence of visual cues, which were shown in previous studies to have substantial effects on how objects are perceived tactually (Gepshtein and Banks 2003; Heller et al. 1999; Jenmalm and Johansson 1997; Patchay et al. 2003; Safstrom and Edin 2004; Santello and Soechting 1997; Schultz and Petersik 1994). The aim of the first set of experiments is to investigate whether objects show size constancy with changes in contact force. We hypothesized that the perceived size of an object should be unaffected by changes in intrinsic properties of the object, such as its compliance, and by changes in extrinsic factors, such as grasp force. To test this hypothesis, subjects are asked to judge the size of objects that vary in shape and compliance with varying contact forces. Objects are also presented to the subjects with and without cutaneous cues that have been shown to provide information about the compliance of objects (Srinivasan and LaMotte 1995). These experiments allowed us to test whether the slowly adapting type 1 afferents, which have been shown to encode surface compliance (Srinivasan and LaMotte 1995), play a role in size perception.

The aim of the second set of experiments is to determine how the cutaneous inputs are integrated with proprioceptive inputs. In these experiments, we alter the cutaneous inputs by using vibratory adaptation or a digital nerve block. We hypothesize that if size perception is based on the spread between the fingers at the moment when cutaneous input activity reaches a specific level, then decreasing the sensitivity of these afferents should result in objects feeling smaller. Similarly, we hypothesize that objects should also feel smaller in the anesthetized condition because subjects should grasp objects with an even greater grip force in the absence of cutaneous feedback. A subset of the results from these experiments was previously published in abstract form (Berryman et al. 2004).

METHODS

We performed four psychophysical experiments, summarized in Table 1. Below we first describe the subjects who participated in all of the studies. Then we describe the object simulator that was used to generate objects of varying sizes, the experimental methods that were specific to each experiment, and the psychophysical methods that were used. Finally, we describe how the data were analyzed. In all of the experiments, subjects estimated the size of objects by grasping two parallel plates between their index finger and thumb.

Five healthy subjects (four males and one female, including one of the authors), ranging in age from 23 to 32 yr, participated in four psychophysical experiments. All subjects reported that they had normal sensations from their hands. All experiments were performed in compliance with the rules and regulations of the Human Institutional Review Board of the Johns Hopkins University.

Object simulator

To mimic objects of varying sizes and properties in *experiments 1, 2, and 3*, we developed an object simulator that allowed us to dynamically simulate objects of varying size and surface properties (Fig. 1A). The stimulus consisted of two independent, interchangeable plates (b1 and b2, Fig. 1A) that simulated the parallel surfaces of an object. The positions of the plates were changed using two horizontally mounted linear stepper motors (NEMA 17-frame stepper motors mounted on KV Ultra-Compact shuttle stages with IB462 drives) that were controlled by a computer running Labview software and Microsoft Visual C++ (a1 and a2, Fig. 1A). The motors, each with a bidirectional repeatability rating of $\pm 3 \mu\text{m}$, were mounted on a horizontal beam that rotated around its central axis to position the stimulus plates at a location where subjects could comfortably grasp the plates between the thumb and index finger (d, Fig. 1A). Each plate support was connected to a force sensor with a maximum rating of 1814.4 g (Strain Measurement Devices, model S215-4) that detected contact forces applied by the fingers during grasping (c1 and c2, Fig. 1A). We simulated objects with varying surface properties and different sizes by manually changing the plates and by varying the spacing between the plates.

For *experiment 4*, a size-matching apparatus was used to allow subjects to estimate the perceived size of objects (Fig. 1C). The spring-loaded parallel sliding plates of the size-matching apparatus were grasped between the thumb and index finger and squeezed together until their separation matched the perceived size of a reference object. The sliding plates were connected to a potentiometer that gave a voltage output proportional to the spread between the plates.

EXPERIMENT 1: EFFECT OF VARYING OBJECT SURFACE COMPLIANCE, CONTACT AREA, AND APPLIED FORCE—

The aim of this experiment was to determine whether objects show size constancy by determining whether perception is affected by surface material, contact area, and contact force. In *experiments 1, 2, and 3*, subjects were seated in a dark room directly in front of the object simulator (Fig. 1A). A monitor that displayed visual cues to guide the subjects was located to the left of center. A molded arm holder was positioned to comfortably cradle the outstretched forearm. The arm and fingers remained free so that the subject could easily reach forward to grasp the stimulus object. A curtain with a hole positioned to allow the subject to contact the stimulus object was placed between the subject and the object simulator to prevent the subject from seeing the stimulus. To eliminate auditory cues, the motor-driven object simulator never moved directly from one position to another; instead, the motors always moved past the final stimulus position by a random amount before returning to the correct position. In addition, subjects wore headphones that delivered white masking noise throughout the experiments. The subjects did not receive any feedback on their performance during the experiments.

In *experiment 1*, subjects performed a subjective magnitude-estimation task in which they reported a number that was proportional to the size of each stimulus. Before the start of each experiment, subjects were instructed to select a number to represent the size of the reference object. They were told to use that reference number as a guide to describe the size of the stimulus object. For example, if the perceived size of the stimulus object was twice the size of the reference object, they were asked to report a number that was twice that of the reference number. Each experimental session consisted of a single task and lasted for <1 h.

Before each trial began, subjects held a rectangular metal block that served as a reference object between the thumb and index finger of the right hand (Step 1, Fig. 1B). The reference object was 56 mm in length. While the subject waited for a visual cue on the monitor, the experimenter slid the appropriate stimulus object plates into position on the object simulator (Step 2, Fig. 1B). Two types of stimulus object plates were used in this experiment: compliant rubber object plates (e, Fig. 1) and rigid object plates of varying area, which we call contact area object plates

(f, Fig. 1). There were five sets of compliant rubber object plates; four pairs were made of foam rubber and one pair was made of metal. The foam rubber objects were created to span the hardness range for foam rubber, from soft to hard. These objects had durometer ratings of 50, 70, 80, and 90 on the shore OO scale, which is the international standard for measuring the hardness of foam rubber. The most compliant rubber object was as soft as a racquet ball (durometer rating of 50), the intermediate compliant rubber objects felt like a rubber band (durometer rating of 70), a pencil eraser (durometer rating of 80), or a tire tread (durometer rating of 90), and the least compliant rubber object was as hard as solid metal (durometer rating of 98). These surfaces allowed us to change the spread between the fingers independent of contact force. In addition, there were five sets of rigid contact area object plates; all five pairs were machined with protruding half-spheres of diameter 2, 4, 6, 8, and 10 mm to indent different areas of the fingerpads (f, Fig. 1). These surfaces allowed us to change contact area independent of contact force.

After the interchangeable plates were locked into the plate supports on the object simulator, the motors moved them outward to generate the appropriate object size for the trial (Step 3, Fig. 1B). When the plates reached their final position, a start/stop indicator light on the monitor was illuminated to signal the start of the trial. The subjects moved their right hand to grasp the stimulus object and squeezed it with their thumb and index finger (Step 4, Fig. 1B). Subjects were required to apply a specific amount of force when squeezing the plates and they received feedback from a force indicator light on the monitor. Each trial tested one of three target forces (250, 500, 750 g), which were calculated by averaging the forces applied by the thumb and index finger. These target forces were chosen to span a range of precision grip forces, from a very light contact to a firm squeeze, without exceeding the maximum grip force (Johansson and Westling 1984). Two force sensors mounted on the plate supports of the object simulator sent force readings from each individual finger to the control computer, and the monitor displayed real-time averaged force information that was used by the subjects to adjust their applied forces. The force indicator light was black when the stimulus object was not being grasped and yellow when the grasp was within the window of target applied force (± 25 g). The indicator light turned green if the force was too low and red if the force was too high. After the subject maintained the target applied force for 1 s, the start/stop indicator light extinguished, prompting the subject to report a subjective magnitude estimate of the size of the object.

The subjects then removed their hand from the stimulus object, grasped the reference object, and waited for the next trial to begin. There were five stimulus object sizes (50, 53, 56, 59, and 62 mm), five stimulus objects (either five compliant rubber objects or five contact area objects), three applied forces, and 12 repetitions of each trial for a total of 900 trials lasting about 1 h.

EXPERIMENT 2: EFFECT OF OBJECT SURFACE CUES AND THE ROLE OF CONTACT—The results of the first experiment (see following text) suggested that size perception is determined by the spread of the digits at the moment of initial contact with the object. The aim of *experiment 2* was to test this hypothesis and to uncover whether tactile surface cues are used in making size judgments. Two types of trials alternated throughout this experiment: the first trial type involved contact with the stimulus object immediately before making a size estimate (contact condition); the second trial type avoided direct contact with the stimulus object before judging size by randomly changing the object size just after grasping (no-initial contact condition). For the contact condition, the plates moved immediately to their final resting position and the subject was visually cued to grasp the plates and report a magnitude estimate as soon as the plates were stationary (as in *experiment 1*). For the no-initial contact condition, the plates first moved to a random starting position before the subject was cued to grasp them. Then, while the subject held the stimulus object securely between the thumb and index finger, the plates moved to three random positions before reaching the final position. These two trial types were randomly interleaved throughout the experiment.

Before the experiment began, the experimenter slid two stimulus object plates into the plate supports of the object simulator. The plates were either compliant rubber object plates or spring cell object plates. The compliant rubber object plates were made of moderately soft foam rubber with a durometer rating of 50. The spring cell object plates were made of the same foam rubber material with a piece of rigid cardboard added on top of the contact surface to disguise cutaneous cues about the compliance of the object. The experiment was conducted once with the compliant rubber plates and a second time with the spring cell object plates. The subject held a metal reference block that separated the thumb and index finger by 56 mm. For a contact condition trial, the subject was cued by the illuminated start/stop indicator light to grasp the plates as soon as they moved to their final position. For a no-initial contact condition trial, the subject was cued to immediately grasp the plates before the plates began moving. For both trial types, after the plates reached their final position, the start/stop indicator light went off, indicating that the subject should report a magnitude estimate. There were five stimulus object sizes (50, 53, 57, 59, and 62 mm), two stimulus objects (either a compliant rubber object or a spring cell object), two contact conditions, and 12 repetitions of each trial for a total of 240 trials lasting about 60 min.

Experiments 3 and 4 were aimed at determining the relative contributions of cutaneous inputs from mechanoreceptive afferents and proprioceptive afferents for the perception of object size. In *experiment 3* we desensitized the cutaneous afferents using a vibrotactile stimulus. In *experiment 4* we blocked the inputs from these afferents completely with an anesthetic block of the digital nerves of digits 1 and 2 (thumb and index finger).

EXPERIMENT 3: EFFECT OF CUTANEOUS ADAPTATION—Before the task began, subjects held a 56-mm-long rectangular metal block between the thumb and index finger of each hand. One block was attached to a minishaker (B&K 4810) and was vibrated along the vertical axis at 30 Hz with an amplitude of 450 μ m, whereas the other block remained stationary. The vibrating block created oscillatory displacement normal to the surfaces of the contacting finger pads to adapt receptors in that hand. The psychophysical experiment began after the subjects grasped the reference objects for 6 min, allowing sufficient time to adapt the afferent receptors (Leung et al. 2005). To eliminate the effects of bimanual grasping (Patchay et al. 2003), subjects were first cued by an indicator light on the monitor to remove both hands from their respective reference objects. Then subjects were shown a color-coded light on the monitor, which indicated whether they should grasp the stimulus object with the adapted hand or with the nonadapted hand. There were equal numbers of trials with each hand and trials were randomly interleaved between the two hands.

After grasping the stimulus object, subjects performed a two-alternative forced choice task and reported whether the stimulus object was bigger or smaller than the nonvibrating reference object that was held in the nonadapted hand. The experimenter recorded the response and continued with the next trial. Between trials, adaptation was maintained by having the subjects return their hands to the two reference objects. There were five object sizes (52, 55, 57, 59, and 62 mm), one stimulus compliance (durometer rating 50), and 12 repetitions for a total of 60 trials lasting for 30 min. This procedure was repeated on the subsequent day with the adapted and nonadapted hands switched. Because there were no significant differences between the results obtained for the two hands, the results for both hands were combined.

EXPERIMENT 4: EFFECT OF BLOCKING CUTANEOUS AND PROPRIOCEPTIVE INPUTS—In *experiment 4*, the experimenter clamped one of eight reference blocks to a stand in front of the subject and cued the subject to perform a method-of-adjustment task. Subjects were required to grasp the stimulus object between the thumb and index finger of their right hand while simultaneously squeezing the plates of the size-matching apparatus with their left hand until the perceived sizes of the two objects were the same. When the subject finished

squeezing the plates, the experimenter recorded the estimated size. The experiment was conducted twice: first with normal sensation in the left hand and a second time with anesthetized fingers in the left hand.

For the trials in which the fingers were anesthetized, an anesthesiologist performed a digital nerve block of the thumb and index finger of the left hand using four injections (two per finger) of 1.5 ml lidocaine (20 mg/ml) into multiple sites around the proximal portion of D1 (thumb) and D2 (index finger). To verify the degree of anesthesia, the distal pads of the two digits were stroked with surfaces of different textures and additional lidocaine injections were given until the subject could no longer distinguish between the surfaces. After a complete block of tactile sensation to the thumb and index finger had been achieved, the experiment began. The subjects were periodically monitored to ensure that they were experiencing no ill effects resulting from the injections. The subjects could not see either hand while performing the experiment; a curtain obscured the right hand grasping the reference object and a cloth was placed over the size-matching apparatus such that the left hand squeezed the plates underneath the cloth. There were eight reference object block sizes (35, 40, 45, 50, 55, 60, 65, and 70 mm), chosen to comfortably span a range of grasp apertures for the thumb and index finger, and 12 repetitions for a total of 96 trials lasting 30 min. The reference blocks were randomly presented during the experiments.

Data analysis

For the subjective magnitude-estimation experiments (*experiments 1* and *2*), magnitude estimates and grip forces were collected. For each subject, size estimates were normalized by dividing individual subjective magnitude estimates by the average of all magnitude estimates given by that subject. The average magnitude estimates for all subjects were calculated by adding the normalized estimates and dividing by the total number of estimates. For *experiment 1*, data were collected and analyzed to track changes in contact area and finger separation when applied force increased. To determine the change in contact area, the surface of the stimulus object was covered in ink. After the thumb and index finger contacted the stimulus object with the appropriate force, the two fingers were pressed onto a sheet of paper, leaving fingerprints that corresponded to the area of contact with the stimulus surface. Contact area imprints were created for all compliances and applied forces and the fingerprints were scanned into a computer. The scanned image of the fingerprints was converted to pixels and the resulting grayscale image was transformed into a solid black and white image using Matlab. Then, the relative areas of the solid black fingerprints were calculated for comparison. To determine the change in finger separation when applied force and object compliance changed, measurements of the distance between the fingers in millimeters were taken from digital photographs of the positions of the thumb and index finger while grasping 62-mm objects of various compliances with different applied forces.

For the two-alternative forced choice experiment (*experiment 3*), responses were collected and psychometric curves were plotted to show the proportion of times a stimulus size was judged larger than the standard. For the psychometric plots, the percentage judged larger was plotted on the ordinate and the stimulus object size was plotted on the abscissa. The formula used to describe the psychometric function was $P_c(\xi) = \gamma + (1 - \gamma - \lambda)\Phi(\xi)$, where P_c is the proportion of correct responses, ξ is a measure of the stimulus level, γ is chance performance, and λ is the lapsing rate, which describes nonperfect performance (Strasburger 2001). The function $\Phi(\xi)$ is an S-shaped cumulative normal function equal to the inverse of the Gaussian. The maximum slope of the psychometric curve was calculated at the point of inflection and is given by the inverse of the Gaussian's SD, weighted by a factor of $(1 - \gamma)/\sqrt{2\pi}$. The maximum slope, β' , was determined by the equation $\beta' = [(1 - \gamma)/\sqrt{2\pi}] \times \beta$ with $\sigma = 1/\beta$ being the Gaussian's SD.

The threshold for size discrimination was determined from the psychometric curve by the mean value of the cumulative normal function.

For the method of adjustment experiment (*experiment 4*), the estimated size was plotted against the actual size for the control condition and the anesthetized condition for individual subjects. Significance for all four experiments was calculated using a two-way ANOVA.

RESULTS

Experiment 1: effect of varying object surface compliance, contact area, and applied force

The purpose of this experiment was to determine how size perception is affected by the surface properties of objects and by the forces applied to objects. Figure 2 shows the normalized and averaged subjective magnitude estimates for five subjects grasping five rubber objects with different compliances (Fig. 2, A–C), and five rigid objects with different contact areas (Fig. 2, D–F), using three different contact forces. For all stimulus objects and applied forces, the size estimates are linear and increase with size, showing that subjects can accurately estimate object size when grasping objects with their thumb and index finger. Furthermore, the magnitude estimate curves for the different stimulus conditions are overlapping and show no significant difference in slope.

The individual slopes for each subject along with the means are shown in Fig. 3. For the compliant rubber objects, there is no significant difference between size judgments for different compliances, and the slopes of the averaged magnitude estimate curves are not significantly different for different applied forces ($P = 0.7183, f = 0.34, df = 2$) or different stimuli ($P = 0.1639, f = 2.16, df = 4$). For the rigid objects of varying contact area, there is no significant difference between size judgments for different contact areas, and the slopes of the averaged magnitude estimate curves are not significantly different for different applied forces ($P = 0.5208, f = 0.71, df = 2$) or different stimuli ($P = 0.7795, f = 0.44, df = 4$). These results suggest that applied force, object surface compliance, and area of contact do not affect size perception.

When object compliance changes, contact area and finger separation are affected. Measurements of the contact areas when contacting different compliant rubber object surfaces show that the area of contact increases when the applied force increases for all object compliances (Fig. 4A). There is a significant increase in contact area for all five compliant rubber objects when the applied force increases ($P = 0.0005, f = 112.06, df = 1$). Photographs of finger positions when contacting different compliant rubber objects also show that finger separation decreases when the applied force increases for all object compliances (Fig. 4B). The spread between the fingers when contacting a 62-mm object decreases when either the object compliance increases or when the applied force increases, even when the object size remains constant. There is a significant decrease in finger separation for all five compliant rubber objects when the applied force increases ($P = 0.0258, f = 11.96, df = 1$).

If perceived size depends solely on the distance between the fingertips, we would predict that as surface compliance decreases and applied force increases, the fingers should move closer together and size judgments should decrease. Figure 5A shows finger separation distances when contacting a 62-mm object with different compliances and applied forces. In addition, based on the slopes shown in Fig. 2, we plot the corresponding predicted magnitude estimates that subjects would report if size were based simply on finger spread. The actual size estimates, shown in Fig. 5B, suggest that size perception is independent of the spread between the fingers. A comparison of the data shown in Fig. 5, A and B shows that the actual size estimate for all objects and forces corresponds closely to the predicted size estimate at the maximum average finger spacing (about 60 mm). This size corresponds to the position of initial contact of the

fingers with the objects, independent of contact force, compliance, or shape of the object. These results suggest that the perception of size is based on the spread of the fingers at initial contact.

Experiment 2: effect of object surface cues and the role of contact

If object size is based on finger spread at the moment of initial contact with the object, then what happens when one eliminates initial contact information? In this experiment we studied size perception under two conditions. For the contact condition, subjects performed the same task that they completed in *experiment 1* and judged the size of five compliant objects using any grip force they desired. For the no-initial contact condition, after subjects grasped the stimulus object, we dynamically changed the size of the object to eliminate contact cues by moving the plates smoothly back and forth while the subjects maintained contact with the object. In this condition, although subjects have information about the changes in joint angle, they have no cues about the final size of the object based on initial contact information.

Figure 6A shows the normalized average size estimates for the two contact conditions plotted against object size. Surprisingly, the data illustrate that there is no difference in the subjective size estimates for the two contact conditions. This suggests that our hypothesis of size perception being related simply to finger spread at initial contact is incorrect and that other cues must contribute to the perception of object size.

There are several possibilities that can explain these results. One explanation is that in the no-initial contact condition, subjects formed an initial estimate of the size of the object and then dynamically tracked the changes in size as the plates moved back and forth. Another explanation is that subjects used other surface-feature cues to make their size judgments. Because *experiment 1* showed that the area of contact does not affect size perception, this suggests that cues related to object shape are unlikely to be used for size perception. However, we propose that surface cues related to texture perception could play a role. Texture perception has been shown to be a multidimensional percept and it is composed of at least three dimensions (Hollins et al. 2000) corresponding to the perception of roughness, hardness, and stickiness. We hypothesize that, of these three dimensions, hardness could play a significant role in size discrimination because the perceived hardness of a surface is directly correlated with object compliance (Srinivasan and LaMotte 1995). To test this notion, we modified the surface of the compliant object without changing its compliance by gluing a hard surface to its exterior and thereby creating a “spring cell”-like object, which felt rigid to the touch, but deformed when squeezed with added contact force. We then tested whether the ability of subjects to perform the task in the no-initial contact condition was a result of dynamic tracking or of information about local surface features.

The results are shown in Fig. 6B, which compares the contact condition with the no-initial contact condition using the spring cell objects. We found that there is a significant difference between the two contact conditions ($P = 0.0184$, $f = 14.79$, $df = 1$). In the no-initial contact condition, subjects underestimate the size of the object by about 0.15 units on the magnitude-estimation scale. This corresponds to a change in finger separation of about 2.0 mm (see Fig. 5A), which is roughly the amount that the fingerpad is indented into the surface. This suggests that the estimates in the no-initial contact condition with the spring cell objects are approximately what one would predict if the estimates had been based on an object with a noncompliant surface. These results rule out cues related to dynamic tracking and suggest that, in addition to initial contact information, local texture information about the compliance of the object also plays a role in size perception.

But how do local texture information and initial contact information provide us with an accurate description of object size? Our working hypothesis is that the perceptual system shows constancy of object size perception despite variations in grasping. For compliant objects in

which the surface is directly touched, the pattern of stimulation on the skin changes as the object is grasped with different contact forces. Subjects then use that information to estimate the size of objects at initial contact. Hard objects create flat spatial skin profiles, whereas compliant objects create skin profiles that are more congruent to the curvature of the fingerpads. In the next two experiments we attempt to tease out the relative contributions of the cutaneous and proprioceptive inputs to size discrimination. In *experiment 3* we alter the sensitivity of the cutaneous input using vibratory adaptation. In *experiment 4* we block all of the cutaneous input using local anesthesia.

Experiment 3: effect of cutaneous adaptation

The purpose of the third experiment was to study the role that cutaneous inputs play in size discrimination by adapting these afferents using low-frequency/high-intensity vibrations. In an earlier study, Lundstrom and Johansson (1986) showed that vibration exposure can cause decreased sensitivity of mechanoreceptors by raising thresholds. Such vibratory stimuli cause the absolute and entrainment thresholds for cutaneous receptors to rise, resulting in decreased sensitivity to tactile stimuli for both rapidly adapting (RA) and slowly adapting type 1 (SA1) afferents (Bensmaia et al. 2005). In *experiment 3*, the frequency of vibration was chosen to be 30 Hz because RAs and SA1s respond to low-frequency mechanical vibrations $\lesssim 100$ Hz (Freeman and Johnson 1982).

Data for this task were divided between responses made when the vibrated hand grasped the stimulus object (vibration data) and responses made when the nonvibrated hand grasped the stimulus object (control data). Psychometric curves were plotted for individual subjects and for the average across all subjects for the control and vibration conditions of this task to show the percentage of stimulus objects judged larger than the reference object. The mean discrimination threshold shifted from 58.87 mm in the control condition to 58.70 mm in the vibration condition. The shift in the threshold of size discrimination for all subjects was not significant ($P = 0.2470$, $f = 1.84$, $df = 1$). Although the threshold remains unaffected by cutaneous adaptation, the mean maximum slope of the psychometric curve for the vibration condition is significantly smaller.

Figure 7 shows the maximum slopes of the psychometric curves for the vibration condition (black bars) and the control condition (gray bars) in the cutaneous adaptation task for all five subjects. The difference in slope between the two conditions is significant ($P = 0.0266$, $f = 11.75$, $df = 1$), where the slopes of the psychometric curves become less steep in the adapted condition. Thus adaptation causes a significant increase in the interquartile range (IQR) of the psychometric function, which is a measure of the spread of the psychometric curve, for the vibration condition ($P = 0.0094$, $f = 21.91$, $df = 1$) and a corresponding decrease in certainty at the point of initial contact. Furthermore, the small shifts in threshold with adaptation result in small changes in size estimates. This agrees with neurophysiological studies showing that adaptation only causes minimal changes in activation thresholds for the cutaneous afferents (Bensmaia et al. 2005). These results suggest that the afferent input signaling initial contact is either the SA1 or RA afferents because both of these afferent types have entrainment and absolute thresholds that are affected by the adapting stimuli (see DISCUSSION for further details).

Experiment 4: effect of blocking cutaneous and inputs

The aim of the fourth experiment was to block cutaneous input at the site of contact without affecting the perception of finger location in space. Although the digital nerve block also eliminated inputs from joint afferents, it did not affect inputs from either the muscle spindles in the forearm or the cutaneous afferents that innervate the back of the hand. Perceived sizes with and without anesthesia are plotted as a function of the actual object size for five individual

subjects (Fig. 8, A–E). For both conditions, size estimates are linear and increase with size, with four of the five subjects (except for Subject E) showing a significant change in perceived size under anesthesia (Subject A: $P = 0.00$, $f = 72.37$, $df = 1$; Subject B: $P = 0.00$, $f = 424.65$, $df = 1$; Subject C: $P = 0.0017$, $f = 24.19$, $df = 1$; Subject D: $P = 0.0125$, $f = 11.12$, $df = 1$; Subject E: $P = 0.2309$, $f = 1.72$, $df = 1$; average of all five subjects: $P = 0.0002$, $f = 54.27$, $df = 1$). This result shows that proprioceptive inputs provide necessary but insufficient information for size perception. Figure 8F shows the mean percentage change in estimated size for the five subjects. Without cutaneous input, there is a 28% change in perceived size across all subjects, which is based purely on proprioceptive input. The largest effects of anesthesia on size perception can be seen in data collected from Subjects A, B, and C, where the mean change in estimated size was 22.37, 51.46, and 44.90%, respectively.

Figure 8, A–E shows that for all subjects, the anesthesia curves fall well below the equality line (dotted line), indicating that subjects squeezed the plates of the size-matching apparatus more closely together than necessary with their anesthetized fingers when estimating object size. Although the actual separation between the plates of the size-matching apparatus is smaller with anesthesia, the perception of the separation is actually much larger because of the distortion illusion produced by the digital nerve block. All subjects reported that their fingers felt swollen, which is consistent with reports that anesthesia increases perceived size by 60–70% (Gandevia and Phegan 1999). Even though subjects squeezed the plates more closely together, the illusory doubling of finger size and uncertainty about where the fingers contacted the object suggest that subjects actually perceived the separation between their fingers to be larger. Thus with anesthesia, subjects judged object sizes to be larger than without anesthesia.

DISCUSSION

The aim of this study was to determine how proprioceptive and cutaneous information are combined to produce the perception of object size. *Experiment 1* investigated the roles of object surface properties and grip forces on the perception of object size. Results showed that the area of contact, object compliance, and applied forces alone do not affect size perception. These results support the initial hypothesis that objects show size and shape constancy and that perception of object size is determined by the spread between the fingers at the moment of initial surface contact. This is a reasonable assertion because objects generally do not change size depending on how they are grasped (Gepshtein and Banks 2003). In *experiment 2* we tested this hypothesis by eliminating initial contact information and asking the subjects to discriminate the size of an object that dynamically changed size. We found that subjects could discriminate size without initial contact information; however, their ability was impaired if information about the surface compliance of the object was eliminated. Based on this study, we modified our hypothesis to account for the importance of surface compliance cues for size discrimination.

Role of cutaneous afferents in size perception

The results suggest that size perception occurs in two steps: first, cutaneous afferents signal skin contact and detect object surface properties and, second, proprioceptive afferents signal finger spread. Here we provide evidence that SA1 and RA afferents play major roles in the first phase of object size perception. Rapidly adapting (RA) afferents are ideally suited for indicating the point of initial contact with the object surface. Studies of grip adjustment have shown that only RA afferents respond well during the period when the coefficient of friction is being sensed and have latencies short enough for the reflexive changes that accompany a sudden change in load force (Johansson and Westling 1987). On the other hand, slowly adapting (SA1) afferents provide the CNS with a high-quality neural image of the spatial structure of objects contacting the skin, and neurophysiological studies in monkeys (Srinivasan

and LaMotte 1995) suggest that these cutaneous afferents are responsible for coding object compliance at the moment of contact between the fingers and the object surface.

SA1 afferents are responsible for fine form and texture perception (for a review see Johnson 2001). Psychophysical and neurophysiological studies of form processing have shown that only these afferents provide a neural representation of spatial form and curvature (Blake et al. 1997; Hsiao et al. 1996; LaMotte and Srinivasan 1996). Studies of texture perception also suggest that these afferents are important for roughness and softness perception (Johnson et al. 2002; Srinivasan and LaMotte 1995). Of particular relevance to this study are the human studies of the neural mechanisms of tactual softness discrimination by Srinivasan and LaMotte (1995), in which they showed differences between the responses of RA and SA1 afferents to changes in compliance. In additional neurophysiology studies in monkeys, Srinivasan and LaMotte (1996) showed that SA1 afferents are well modulated by surfaces of different compliance while RA afferents are not.

When the finger is pressed into a compliant object, skin deformation is encoded by both SA1 and RA mechanoreceptors, which convey information about the mechanical stimulus to create an image of the skin's surface (Phillips and Johnson 1981; Westling and Johansson 1987). An object indented into the skin presents regions of maximum pressure corresponding to changes in curvature, and the indentation is nonlinearly related to the force (Pawluk and Howe 1999; Serina et al. 1998). Studies show that objects with higher curvatures produce higher stresses and strains at receptor sites without an increase in contact force (Srinivasan and LaMotte 1991). In addition, humans can scale the perceived magnitude of curvature and indentation when spherical shapes are indented into the fingerpad (Goodwin and Wheat 1992). The responses of cutaneous mechanoreceptors depend on the object's pattern of physical properties, such as compliance and texture, as well as the applied force, orientation, and velocity (LaMotte and Srinivasan 1996). Here we demonstrate that only compliance plays a role in object size perception.

The applied force when contacting an object depends on feedforward, predictive neural control mechanisms that are based on internal representations of the physical properties of objects (Johansson and Cole 1994). Flanagan and Wing (1997) showed that fingertip forces predict the mass, mass distribution, shape, and complex loads that result from viscous and spring properties of the object. Internal representations of both the expected consequences of the actions ("corollary discharge") and the motor commands ("efference copy") are needed to apply an appropriate amount of force to the object contact surfaces. In manipulative tasks, subjects incorporate important predictable object properties into the internal models of their own motor systems (Johansson and Cole 1992). When subjects lift predictable objects, they can easily adapt to object features critical for grasp stability. Studies have shown this with reference to surface friction (Johansson and Westling 1984), weight (Johansson and Westling 1988), and object shape (Jenmalm and Johansson 1997; Jenmalm et al. 2000). A result of *experiment 1* is that force and consequently motor commands play no role in object size perception.

Although we have no evidence that shows that PC afferents do not play a role in object size perception, results from *experiment 3* suggest that PCs may not be as important in this process. In *experiment 3* we show that adaptation of cutaneous RA and SA1 receptors degraded the ability of subjects to accurately determine object size. Studies on vibratory adaptation of cutaneous mechanoreceptive afferents introduced a two-channel theory of flutter vibration, suggesting that detection of vibration is mediated by two channels: the Pacinian channel responds preferentially to high frequencies and the non-Pacinian, or RA, channel responds to low frequencies (Mountcastle et al. 1967; Talbot et al. 1968; Verrillo 1968). Because adaptation occurs independently within these two systems (Gescheider et al. 1979; Hollins et al. 1990;

Verrillo and Gescheider 1977), we were able to selectively adapt the non-Pacinian channels (RA and SA1 afferents) by using a low adapting frequency. Psychophysical studies of vibrotactile adaptation have also shown that under certain conditions, extended exposure to a vibratory stimulus enhances discrimination of amplitude and frequency (Delemos and Hollins 1996; Goble and Hollins 1994).

Recently, we showed (Bensmaia et al. 2005) that peripheral SA1, RA, and PC afferents in monkeys show significant threshold changes in response to an adapting stimulus. Whereas SA1 and RA afferents show small shifts in sensitivity of about 100 μm , the PC afferents show much smaller shifts of only a few micrometers. In *experiment 3* we find that adaptation has small, insignificant effects on absolute size perception (on the order of 100–200 μm). Because the force produced at the moment of initial contact was large enough to exceed even the elevated thresholds of adapted RA and SA1 afferents, adaptation did not produce significant changes in size discrimination thresholds.

In Bensmaia et al. (2005) we show that the adapting stimulus causes a shift in both the absolute (I_0) and entrainment (I_1) thresholds in monkeys. Further, we show that with the adapting stimulus, the shifts for both RA and SA1 afferents are close to additive (equal change in I_0 and I_1), although the shifts for SA1 afferents may represent a combination of additive and multiplicative ($I_0/I_1 = \text{constant}$). An additive shift implies that while the threshold increases, the change in sensitivity, which is the intensity needed to go from I_0 to I_1 , remains unchanged. In contrast, multiplicative changes result in a change in sensitivity such that a greater change in intensity is needed to activate the afferent fiber and, consequently, there is more uncertainty about when the finger has contacted the object. Thus the data from *experiment 3* support the notion that SA1 and RA afferents play a role in size perception and that PC afferents do not.

Previous studies point to a role for SA2 afferents in the second phase of size perception. Edin and Johansson (1995) showed that skin strain sensed by SA2 receptors on the back of the hand and near joints produces perceived joint movement and, without skin strain, movement cannot be perceived. In addition, Gandevia and McCloskey (1976) showed that when the extensor and flexor muscles are disconnected from the distal phalanx of the middle finger, substantial joint angle sense remains. In this study the receptors on the back of the hand were not affected by the anesthetic and subjects reported that with anesthetic they had normal perception of joint position and the movements of their index finger and thumb. Thus we hypothesize that either RA and/or SA1 and SA2 cutaneous afferents each play a role in object size perception.

Role of proprioceptive afferents in size perception

In *experiment 4* we show that without cutaneous input, subjects have a rough but reliable sense of object size. In addition to the SA2 afferents discussed above, there are four proprioceptive afferent types that may play a role in size perception: two kinds of muscle spindle afferents, Golgi tendon organs, and joint receptors. Muscle spindle afferents in the extrinsic muscles of the hand may play a role (Wessberg and Vallbo 1995) because they are important for signaling muscle length, velocity, and joint angle; Golgi tendon organs probably do not because they are responsible for signaling muscle tension (Jones 1996). Joint receptors have been associated with coding the positions of joints near their extremes (Ferrell and Smith 1989). The available data suggest that information about finger spread is derived from either SA2 receptors or muscle spindle afferents.

In *experiment 4*, subjects squeezed the plates of the size-matching apparatus much closer together than we initially expected—a result that we attributed to the effects of the digital nerve block. Subjects under anesthesia reported that their fingers felt swollen and they had a distorted perception that objects felt larger. Experiments by Gandevia and Phegan (1999) also revealed that anesthesia significantly alters sensory inputs and changes “haptic” or “tactile” perception.

When afferent input is altered, the perceived size of body parts changes rapidly and subjects note a large increase in perceived body size. For example, when the thumb was anesthetized by a digital nerve block, the mean increase in perceived area of the thumb was around 60%. A control experiment in which the same volume of saline was injected produced no change in perceived size of the thumb. Gandevia and Phegan (1999) suggested that the increase in perceived body size could be related to the unmasking of inputs to primary somatosensory cortical cells. When afferent input is removed by anesthesia, the spontaneous firing rate increases and the receptive fields of cortical cells representing areas around the anesthetized area enlarge (Calford and Tweedale 1991).

Working model of object size perception

Our working hypothesis is that when judging the size of objects, central mechanisms combine inputs from SA1 and RA afferents that signal initial contact with information about the spread between the fingers from SA2 afferents and muscle spindle afferents to estimate the size of rigid objects. When judging the size of compliant objects, the central mechanisms take into account the compliance of the object and use inputs from the SA1 afferents to estimate the distance between where the finger is presently contacting the object and where the point of initial contact would be if the fingers were not indented into the object. Then, this distance is added to the spread between the fingers to give an estimate of object size. This compensation factor must be performed unconsciously.

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Fig. 1.

Object simulator (*top view*) and experimental procedure. *A*: stepper motors (a1 and a2) mounted on a horizontal beam (d) move the independent, interchangeable plates (b1 and b2) along the horizontal axis to simulate objects of different sizes. Two sets of plates, compliant plates (e, *side view* and *front view*) and surface area plates (f, *side view* and *front view*), were used to simulate objects of varying tactile properties. Spring cell plates (g, *side view* and *front view*) were used in *experiment 2* to test the importance of surface cues in size perception. Force sensors (c1 and c2) mounted on the interchangeable plate supports detected forces applied by the thumb and index finger. *B*: steps in *experiment 1*. Object simulator is shown in various stages during the experiment. Circle in the *top left corner* shows the hand grasping the reference

object (56 mm) while the subject waits for the cue to start the experiment. Computer in the *top right corner* shows the visual cues; the top circle is the start/stop indicator light and the bottom circle is the force indicator light. *B, Step 1*: experimental setup before the trial begins. Start/stop indicator light is off and the force indicator light is black (the stimulus object plates are not mounted to the device in this figure). *B, Step 2*: experimenter slides the stimulus object plates into the supports and starts the experiment. *B, Step 3*: motors move the stimulus object plates outward to their final position. *B, Step 4*: start/stop light is illuminated, signaling the subject to grasp the stimulus object. Subjects squeeze until the force indicator light turns yellow, indicating that the required amount of force is being applied. When the start/stop light goes off, subjects remove their hand and the next trial begins. *C*: description of *experiment 4*. While grasping one of 8 reference blocks with their unanesthetized hand, subjects squeeze the spring-loaded sliding plates of the size-matching apparatus with the thumb and index finger of their anesthetized hand. After matching the perceived size of the reference block with the size-matching apparatus, the estimated size is recorded, a new reference block is clamped in place, and the next trial begins.

Fig. 2.

Normalized magnitude estimates averaged across all subjects. Five subjects provided magnitude estimates of the sizes of different objects presented by the object simulator shown in Fig. 1A. Abscissas of all graphs represent actual object sizes (52, 55, 57, 59, and 63 mm). Ordinates represent the normalized average magnitude estimates for all subjects. Graphs A, B, and C show the average magnitude estimates for the 5 compliant surface objects (50 is the softest foam rubber, 90 is the hardest foam rubber, and 98 is metal). Each graph shows results for a different applied grip force (250, 500, and 750 g). Graphs D, E, and F show the average magnitude estimates for each of the 5 contact area objects (2 mm is the smallest contact area; 10 mm is the largest contact area). Each graph shows results for a different applied grip force (250, 500, and 750 g).

Fig. 3.

Normalized magnitude estimates for individual subjects. Ordinates of all graphs represent the slopes of the magnitude estimates shown in Fig. 2. Abscissas of graphs A, B, and C represent the compliance rating of the tactile objects. Abscissas of graphs D, E, and F represent the contact area of the tactile objects. Each of these graphs shows results for a different applied grip force (250, 500, and 750 g). Dashed lines represent data from individual subjects and the solid lines represent the mean across all subjects.

Fig. 4.

Effect of contact area and finger separation on applied force. Abscissas represent the compliance rating of the tactile objects. *A*: average contact area when a small force is applied (250 g) and a large force is applied (750 g) across all object sizes (52, 55, 57, 59, and 62 mm). Area of contact is greater when the applied force is greater for all stimuli. *B*: average finger separation when a small force is applied (250 g) and a large force is applied (750 g) for all object sizes (52, 55, 57, 59, and 62 mm). Average finger separation is smaller when the applied force is greater for all stimuli.

Fig. 5.

Difference between actual finger separation distance and normalized and predicted magnitude estimates when a 62-mm object with varying compliances is grasped with 3 different forces. Abscissas of both graphs represent the combined force applied by the thumb and index finger when grasping the object with 3 forces (250, 500, and 750 g). *A*: *left ordinate* represents the average finger separation distance; *right ordinate* is the predicted magnitude estimate based on the finger separation estimated from the data in Fig. 2. Each dotted line shows the results for a stimulus object with a different durometer rating. Solid line represents the mean average finger separation. *B*: ordinate represents the normalized magnitude estimate averaged across all subjects. Each dotted line shows the results for a stimulus object with a specific durometer rating. Solid line represents the mean normalized average magnitude estimate.

Fig. 6.

Normalized magnitude estimates for the compliant rubber stimulus object and the spring cell stimulus object. For both graphs, stimulus object size is plotted on the abscissa and the normalized average magnitude estimate across all subjects is plotted on the ordinate. *A*: difference between size estimates for the contact condition and the no-initial contact condition is not significant for the compliant rubber stimulus objects of different sizes. *B*: difference between the contact condition and the no-initial contact condition is significant for all sizes of the spring cell stimulus object.

Fig. 7.

Change in the slopes of psychometric functions caused by cutaneous adaptation. Psychometric curves were plotted for 5 individual subjects and for the average across all subjects for control (no adaptation) and the cutaneous adaptation condition (30-Hz adapting frequency). Slopes of each of the psychometric functions were calculated and plotted for comparison. Slopes of the psychometric functions are significantly steeper for the control condition, indicating that cutaneous adaptation causes a decrease in the accuracy of the size estimations.

Fig. 8.

Individual subject results for size-matching task with anesthesia and without anesthesia. A–E: abscissas represent the actual size of the object and the ordinates represent the subjects' estimated matching size. For all subjects, the anesthesia curve falls well below the dotted equality line, indicating that the subjects squeezed the plates of the size-matching apparatus more closely together than necessary with their anesthetized fingers when estimating object size. With anesthesia, subjects judged object sizes to be larger than without anesthesia. Each graph shows the estimated sizes reported by a single subject. F: mean change in estimated size between the control condition and the anesthetized condition was plotted for each of the 5 subjects. Abscissa represents the subject (A–E) and the ordinate represents the mean change in estimated size, calculated from the individual subject data. All subjects show a significant

change in size estimation as a result of anesthesia and the average change across all subjects is 28%.

TABLE 1

Experimental designs

Experiment	Description	Number of Subjects	Method	Equipment	Stimuli	Sizes
1	Effect of varying object surface compliance, contact area, and applied force	5	SME	Object simulator	Five sets of compliant rubber object plates and five sets of contact area object plates	50, 53, 56, 59, and 62 mm
2	Effect of object surface cues and the role of contact	5	SME	Object simulator	One set of compliant rubber object plates and one set of spring cell object plates	50, 53, 57, 59, and 62 mm
3	Effect of cutaneous adaptation	5	2AFC	Object simulator and vibrating reference object	One set of compliant rubber object plates	52, 55, 57, 59, and 62 mm
4	Effect of blocking cutaneous and proprioceptive inputs	5	MOA	Size-matching apparatus	Eight plastic blocks of varying sizes	35, 40, 45, 50, 55, 60, 65, and 70 mm

SME, subjective magnitude estimation; MOA, method of adjustment; 2AFC, two-alternative forced choice.