SENSORY SIGNALS IN NEURAL POPULATIONS
UNDERLYING TACTILE PERCEPTION AND
MANIPULATION

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Abstract For humans to manipulate an object successfully, the motor control system must have accurate information about parameters such as the shape of the stimulus, its position of contact on the skin, and the magnitude and direction of contact force. The same information is required for perception during haptic exploration of an object. Much of these data are relayed by the mechanoreceptive afferents innervating the glabrous skin of the digits. Single afferent responses are modulated by all the relevant stimulus parameters. Thus, only in complete population reconstructions is it clear how each of the parameters can be signaled to the brain independently when many are changing simultaneously, as occurs in most normal movements or haptic exploration. Modeling population responses reveals how resolution is affected by neural noise and intrinsic properties of the population such as the pattern and density of innervation and the covariance of response variability.

INTRODUCTION

Primates, an order which includes humans, apes and monkeys, are the only animals in which hands have evolved, and this has played a significant part in their evolutionary success (Napier 1980). In our daily lives we explore and manipulate a wide range of objects, and there are myriad examples of our dependence on manual dexterity and of our reliance on tactile perception of these objects. As illustrations, we can palpate an avocado to determine if it is ripe, scan our fingers over a surface to assess its roughness, lift an object to estimate its weight, do up our shoe laces, separate a peanut from its shell, pick a cherry, or write a message.

Hand function is a vast field that we do not attempt to cover in breadth; rather in this review we focus on a crucial component, namely the cutaneous neural signals from the digits, which are vital to tactile perception and manipulation. We place particular emphasis on the importance of neural population analyses.
THE SPECTRUM OF HAND FUNCTION

The repertoire of hand movements used by humans in their everyday lives is extensive. In the majority of cases the movement comprises several components commencing with a reaching phase and culminating in manipulation or haptic exploration of the object (Jeannerod et al. 1998).

There is a continuous spectrum of hand function. At the one extreme, the object is grasped and manipulated and the main objective is to accomplish the task; a simple example is lifting a cup of coffee off a table. Here the sensory signals from the digits are used by the motor control system to effect the task. However, even at this extreme, sensory perception plays a role and the person is certainly aware of whether the cup is light or heavy and whether the handle is highly curved or not. At the other extreme, the object is explored with the fingertips and the main objective is sensory perception; a simple example is determining how smooth the surface of the object is. Here the sensory signals from the digits are the source for conscious sensory perception and cognition, but they are also important for the motor control system to enable effective scanning of the surface, particularly if its shape is complex.

Although, in general, vision plays a significant part in manipulation, there is abundant evidence that somatosensory feedback is essential. Mott & Sherrington (1895) sectioned the dorsal roots in monkeys and dramatically illustrated the dependence of all phases of upper limb movements on somatosensory feedback despite the fact that vision was unaffected. There are now several reports in the literature of patients with large fiber sensory neuropathies, and in these patients hand function is severely compromised (Sanes et al. 1985). Even in the presence of vision, the case report of Rothwell et al. (1982) states that “...he could no longer execute certain manual tasks; thus he was unable to do up his shirt buttons or manipulate a pen properly.” More specifically, when feedback from the glabrous skin of the digits is eliminated by blocking the digital nerves in humans, manipulation is impaired (Johansson & Westling 1984, Monzee et al. 2003). In the reverse direction, precise manipulation is possible without vision. For instance, many tasks like doing up a button or switching on a light in the dark are done without vision; also blind people are dexterous.

Grasp and Manipulation

We cover only those aspects of grasp and manipulation that relate directly to tactile feedback—for a broad review see Johansson (1996). For experimental convenience and tractable analysis, the “manipulation” in most studies is highly simplified. Twodigit (thumb and forefinger) grasp and lift tasks are used extensively (Gordon & Duff 1999, Westling & Johansson 1984), but there have also been studies of multidigit grasp and lift tasks (Reilmann et al. 2001) and a variety of tasks involving movements more complex than simple lifts (Flanagan & Wing 1997, Gysin et al. 2003).
When an object is gripped between the thumb and index finger and lifted off a table (Figure 1A), there are several key stimulus parameters, as detailed below. Relaying information about these parameters to the CNS is crucial, whether it be for feedback correction during the task itself or to update memory for future use in planning and feedforward control (Johansson 1996).

The load force applied to lift the object must be tailored to the weight of the object. The reaction to the load force is a force on each digit that acts in a direction tangential to the skin surface. In principle, load force could be signaled by receptors in the muscles generating the forces or even by efference copy of the motor commands (Gandevia et al. 1992). Important for this review, low-threshold mechanoreceptors in the glabrous skin of the finger tips are highly sensitive to forces tangential to the skin (Birznieks et al. 2001).

Maintaining a stable grasp on the object requires a grip force of sufficient magnitude to prevent slip, but the grip force should not be excessive so that unnecessary energy expenditure and muscle fatigue do not occur and delicate objects are not damaged. Humans select a grip force with a “reasonable” safety margin that varies with the task and varies between subjects, but usually grip force is of the order of 1.2 to 2 times the minimum force required to prevent slip (Gysin et al. 2003, Westling & Johansson 1984). The reaction of the grip force acts on the skin of the digits in a direction normal to the skin surface and is equivalent to the indenting forces commonly used in somatosensory experiments. Like load force, grip force could be signaled by muscle receptors or efference copy. Indentation normal to the skin excites low-threshold cutaneous mechanoreceptors (Darian-Smith 1984,
Vallo 1995). There are two equivalent ways of treating contact force. Either it can be resolved into the two orthogonal component magnitudes, normal and tangential to the skin, or it can be treated as a single force vector with a magnitude and a direction.

The shape of the object has a substantial effect on grip and lift tasks (Jenmalm & Johansson 1997, Jenmalm et al. 1998), particularly if some tilt is involved (Goodwin et al. 1998). More precisely, this should be referred to as the local shape of the object because it is only the shape in the region of contact with the skin that is relevant. The distinction between local and global shape is critical when considering sources of feedback in a grip and lift task. It is natural to associate object shape with joint angles. However, Figure 1B shows that when gripping a block with flat parallel sides or a sphere of equivalent size, the joint angles are the same. The local shapes of the two objects contacting the skin are vastly different, and the only signals from the hand for local shape are those from the cutaneous afferents.

The position of contact on the digits effects the balance of forces between the thumb and the index finger and impacts on grasp stability (Montana 1988). Excluding vision, position on the skin can only be gauged from cutaneous responses, in particular those from mechanoreceptors.

Limits on the relationship between the grip and load forces are set by the effective coefficient of friction between the object and the digits. The nature of the coefficient of friction between skin and a flat surface is complex; it depends on factors like skin hydration, related to sweating, and does not obey Amonton’s law, which assumes a constant coefficient of friction, independent of the grip force magnitude (Koudine et al. 2000). The concept of an effective coefficient of friction between the skin and a curved surface that partially indents into the skin is even more challenging (Pawluk & Howe 1999). Humans adjust their grip and lift strategies appropriately when the frictional characteristics of flat grip surfaces are changed (Johansson & Westling 1984, Forssberg et al. 1995). How frictional information is calculated by the brain is not known, but it is possible to calculate it from the force ratios at instances of slip or microslip (Tremblay & Cutkowsky 1993). Cutaneous afferents are responsive to slips (Johansson & Westling 1987, Srinivasan et al. 1990).

Although the grip and lift tasks, and variants of them, are relatively simple manipulations, they have provided a wealth of information, largely because it is possible to control the tasks so well and to define and measure the component events of the manipulation with precision. Everyday manipulations like peeling a potato or eating a grape are far more complex and demanding, but the principles of sensory feedback are the same. An instructive example for our purposes is the task, familiar to all of us, of doing up a button in the absence of vision. It is clear that the motor control system requires information about the local shape of the button, its position on the digital skin, and the normal and tangential force components. Much of this information is provided by the cutaneous receptors, as is shown below.
Haptic Exploration

Tactile perception of an object requires manual exploration of the object. This may be relatively simple, like scanning the fingertips over a flat textured surface, or more complex, like exploring an intricate three-dimensional carving. This form of hand movement is often covered under the rubric of haptics—for reviews see Craig & Rollman (1999) and Klatzky & Lederman (2003). It is self-evident that signals from the cutaneous mechanoreceptive afferents are essential for tactile perception and cognition. Perception of surface texture, which encompasses roughness, is a quintessential tactile task. If you wish to determine the fine texture of a surface, it is invariably tactile perception that you resort to, not vision (Heller 1989). Because of space constraints, we deliberately exclude the large field of texture; it has been reviewed by Johnson & Hsiao (1992) and is covered in Craig & Rollman (1999).

CUTANEOUS MECHANORECEPTORS AND AFFERENTS

Glabrous skin covering the volar surface of the digits, with its characteristic fingerprint pattern, is highly specialized. Its structure and innervation have been reviewed previously (Darian-Smith 1984, Vallbo 1995) and is not dealt with extensively here. There are four classes of low-threshold mechanoreceptors in human glabrous skin innervated by four classes of peripheral afferent nerve fibers. The more superficial Merkel complexes and Meissner corpuscles are innervated by slowly adapting type I afferents (SAI afferents) and so-called fast-adapting type I afferents (FAI afferents), respectively. The deeper Ruffini organs and Pacinian corpuscles are innervated by slowly adapting type II (SAII) afferents and fast-adapting type II (FAII) afferents, respectively. This nomenclature, developed for human microneurography studies, is invariably used for classifying human afferents.

Glabrous skin in the monkey is similar to that in humans except that there are no reports of Ruffini organs or SAII afferents. It is not known what is the significance of this difference. Nor is it known whether glabrous skin in the apes, which fall between humans and monkeys on the evolutionary scale, is innervated by SAII afferents. The nomenclature used for the monkey is more variable than that used for humans; Merkel afferents are usually called SA (sometimes SAI) afferents, Meissner afferents are usually called RA (sometimes FAI, and in the older literature, QA) afferents, and Pacinian afferents are usually called PC or (sometimes FAII) afferents. In this review we use the human nomenclature for both human afferents and the three afferents present in the monkey.

The relationship between receptors and afferents is complex; single afferents innervate multiple receptors and single receptors are innervated by multiple afferents, but the details of the anatomical convergence and divergence are not known (Cauna 1956, Pare et al. 2002b). The distinction between afferents and receptors is important in this review because we concentrate on resolution and relating it to the afferent innervation density.
Skin Mechanics and Models of the Finger

In the simplest models of glabrous skin mechanics, which have provided valuable insights into afferent response characteristics, it was assumed that the skin was flat and/or uniform in structure, and no account was taken of its layered or ridged nature (Phillips & Johnson 1981b, Srinivasan 1989). However, the majority of experiments are performed on the distal segment of the finger, which is the region that has most contact during manipulation and haptic exploration (Christel 1993). The distal segment has the following mechanical complications: (a) Part of the volar surface is relatively flat (or gently curved), but the radial and ulnar sides are highly and nonuniformly curved, and the same is true for the distal tip; (b) the distal phalanx, an incompressible bone with a distinctive shape, is at the center of the segment; (c) at the proximal end of the segment, the skin on the volar surface is partially anchored by the interphalangeal crease; (d) on the dorsal surface, the nail is a stiff structure that is tightly anchored to the distal phalanx. Some models of skin mechanics have begun addressing these issues by modeling the finger in two dimensions and including bone at the center (Maeno & Kobayashi 1998, Srinivasan & Dandekar 1996). As yet, no model comes close to including all the factors that influence real fingertip skin mechanics. This is a significant gap in our knowledge because skin mechanics plays a major role in the transduction of tactile stimuli into afferent responses; without a realistic model it is not possible to predict the responses of an afferent from any location on the fingertip to an arbitrary stimulus.

SINGLE AFFERENT RESPONSES TO LOCAL SHAPE

A convenient way of defining the local shape of an object is in terms of its curvatures. In fact the shape of any three-dimensional object can be defined in terms of two orthogonal curvatures at each point on its surface (Koenderink & van Doorn 1992). In many studies of shape, simple objects such as spheres, cylinders, or torroids are used. These are particularly amenable to experimentation and analysis because of the ease of quantifying the shape.

Vierck (1979) observed that slowly adapting afferents in the cat’s hairy skin were sensitive to the edges of indenting stimuli. Phillips & Johnson (1981a) characterized the edge sensitivity of SAI afferents in the monkey’s finger (Figure 2A), and Johansson et al. (1982) showed that in human glabrous skin SAI afferents, and to a lesser extent FAI afferents, were edge sensitive. Although the authors did not discuss their findings explicitly in the context of shape, these were the first indications that cutaneous afferents may be signaling the local shape of objects contacting the skin.

To investigate tactile shape more directly, LaMotte & Srinivasan (LaMotte & Srinivasan 1987a,b; Srinivasan & LaMotte 1987) applied sinusoidally shaped steps to the monkey’s fingerpad. In some experiments the stimuli were indented into the skin (analogous to the situation when grasping and lifting a glass of water), and in
Figure 2  Responses of single SAI afferents in the monkey’s fingerpad. (A) Responses to a 3-mm bar stepped across the receptive field; the origin for position in the receptive field is arbitrary. Redrawn from Phillips & Johnson (1981a). (B) Responses to shaped steps. Each step is a half sine wave (from peak to trough) characterized by the step width (half the period). Redrawn from Srinivasan & LaMotte (1987).

others the stimuli were scanned across the skin (analogous to haptic exploration). Both the SAI and FAI afferent responses were modulated by the shapes of the stimuli, but the effect was more pronounced and more reliable for the SAI afferents (Figure 2B). Although the sinusoidal steps could be graded and specified precisely, the local shape over such a step is not constant, and this compromised quantifying the relationship between afferent responses and object shape.

This limitation was not present in the experiments of Goodwin and colleagues (Goodwin et al. 1995), who chose spherical stimuli; the shape of a sphere is completely specified by a single number, its curvature, which is constant over the whole sphere. For this simple shape the curvature is the reciprocal of the radius of the sphere. When spheres were indented into a monkey’s fingerpad, a clear monotonic relationship existed between the curvature of the stimulus and the responses of SAI afferents. Moreover, all the SAI afferents had the same curvature-response function except for a multiplicative factor. This factor was a reflection of the variation of sensitivity among SAI afferents, which had been described previously for indenting probes (Knibestol 1975). The curvature of the spheres had only a minor effect on FAI responses.

An important feature in both of the above series of experiments is that the shapes were applied at constant force. In the majority of experiments on cutaneous mechanoreceptive afferents, the stimulus has been applied with a controlled depth of indentation, which was entirely appropriate to the aims of those experiments. However, when relating sensory neural events to manipulation or haptic
exploration, force (which has both a tangential and a normal component) is a more appropriate parameter than skin displacement. Normal force and depth of indentation are, of course, related but in a complex nonlinear manner with considerable depth saturation (Pawluk & Howe 1999).

For any shape more complex than a sphere, more than one parameter is needed to define it, and most objects have an orientation. Two relatively simple objects with an orientation that are used to study tactile shape are cylinders and torroids. A cylinder has a curvature of zero in the direction of the cylinder’s long axis and a constant curvature (the reciprocal of the radius) in the orthogonal direction, and it is defined by the orientation of the major axis and the curvature along the minor axis. SAI afferent responses are monotonically related to the curvature of an indenting cylinder in much the same way as for spheres, but they are also modulated by the orientation of the cylinder (Dodson et al. 1998). The shapes of “wavy surfaces” (a succession of convex and concave cylinders with decrementing radii) scanned over the monkey’s fingerpad affect responses in SAI and FAI afferents (LaMotte & Srinivasan 1996). A torroid is defined by three parameters, two orthogonal curvatures and an orientation. Both SAI and FAI afferent responses are modulated by torroids scanned over the monkey’s finger with more information evident in the SAI afferent responses (LaMotte et al. 1998).

Only two studies have addressed the responses of human cutaneous afferents to shape. For spheres and cylinders, the results are comparable to those described above for the monkey (Goodwin et al. 1997). In a more recent study, Jenmalm et al. (2003) employed forces similar to those used by humans in everyday manipulations. Compared to the monkey experiments, the forces were larger in magnitude (4 N), more rapid (125-ms duration for the rising phase), and applied in 5 different directions. They used a flat surface and two spheres and found that curvature significantly modulated responses in SAI, SAII, and FAI afferents.

The experiments described in this section show that responses of mechanoreceptive afferent fibers are affected by the local shape of a stimulus contacting the receptive field. The effect is most pronounced for SAI afferents but is also present in FAI afferents and in SAII afferents in humans.

**POPULATION RESPONSES**

**Rudimentary Population Responses**

Demonstrating that the curvature or shape of a stimulus modulates single afferent responses is the crucial first step, but in itself it does not allow us to appreciate how the brain might extract details about the local shape of an object. Such information can only be obtained by combining responses from a number of afferents or, in general, by examining the entire population of active afferents.

Ideally the responses from each afferent in the entire active population (many hundreds of fibers) should be recorded simultaneously, but currently this is not remotely possible. Virtually all isolated-unit peripheral nerve recording is from single
fibers; occasionally, with microneurography, two or three fibers are recorded from together (Wessberg et al. 2003). Thus, the only way to analyze whole-population responses is to model them in some way. There are many examples of population models in a diverse range of neural systems; a small sample includes sound localization (Fitzpatrick et al. 1997), visual motion perception (Shadlen et al. 1996), determination of visual shape (Pasupathy & Connor 2002), motor control of upper limb trajectories (Lukashin & Georgopoulos 1993), and cockroach escape turns (Levi & Camhi 2000).

In the somatosensory system, a simple method of approximating rudimentary population responses has been used extensively. By plotting the receptive field profile of a single cell (the response of the cell as a function of the position of the stimulus in the receptive field), that profile can be viewed as a population response, described by Mountcastle & Powell (1959) as “reciprocal interpretation.” Despite the limitations of this approach (see later sections) it does provide a visual appreciation of the basic pattern of responses across the population. For example, the profiles in Figure 3A, derived essentially by the above method, clearly depict how the orientation and shape of a cylinder is represented in the SAI afferent population.

For stimuli scanned across the skin, the equivalent approach is termed a spatial event plot (Johnson & Lamb 1981). As the stimulus is scanned over the two-dimensional receptive field, a dot marks the occurrence of each action potential and, by reciprocal interpretation, depicts the pattern of impulses in a population of afferents. For example, in Figure 3B spatial event plots are shown for a torroid scanned over the receptive field of an SAI afferent, and it is evident how the shape and orientation of the torroid could be represented.

Multiple-Parameter Population Reconstruction

An obvious deficiency of the rudimentary population responses described above is that, in general, all stimulus parameters except one are held constant. However, the primary afferent responses modulated by the shape of the stimulus are also affected by other parameters of the stimulus, such as force magnitude and direction (Birznieks et al. 2001), the position of the stimulus in the receptive field (Wheat et al. 1995), the orientation of nonspherical surfaces (Dodson et al. 1998), and the speed and direction of the scanning motion (LaMotte & Srinivasan 1987b). During real manipulation and haptic exploration, many of the stimulus parameters change concurrently, and a useful population reconstruction should reveal how each of these parameters might be signaled to the brain independently of the others. It is obvious that a change in a single afferent’s response cannot convey which parameter or parameters have changed; this can only be determined unambiguously from the population response.

Approaches to Reconstruction

For stimuli contacting the finger, two approaches have been used for acquiring the single fiber responses that form the basis of the reconstruction. In the more
A Cylinders

B Toroids

Figure 3  Rudimentary population reconstructions from responses of SAI afferents in the monkey’s fingerpad. (A) Two-dimensional receptive field profiles, interpreted as population responses, depict the representation of the orientation of a cylinder indented into the fingerpad. The cylinder, with a curvature of 172 m\(^{-1}\), was oriented at 0° or 15°. Modified from Dodson et al. (1998). (B) Spatial event plots of a toroid scanned over the fingerpad show the representation of its orientation. The 1 × 5-mm toroid was oriented at 90° or 0°. Redrawn from LaMotte et al. (1998).

common approach, the stimulus is positioned relative to the receptive field center, regardless of the location of that receptive field on the digits (Johnson 1974, Srinivasan & LaMotte 1987). The advantage of this method is that it allows a precise characterization of the receptive field properties of the fibers, and it is usually simple to factor out the effects of differing fiber sensitivities. The disadvantage is that it can only be used for populations (or subpopulations) in which the skin mechanics can be expected to be uniform for all fibers, for example, the relatively flat portion of the fingerpad. In the alternative approach, the stimulus is always located at the same nominal position on the digit (Birznieks et al. 2001, Khalsa et al. 1998). The advantage of this method is that it allows responses to be characterized for afferents innervating parts of the digits with vastly different skin mechanics, including the highly curved sides and distal tip of the digit as well as the relatively
flat pad. The disadvantage of this approach is that there is more experimental error because of the variation in geometry from finger to finger, the difficulty of accurately locating a common contact point on different fingers, and the uncertainty in characterizing the position of receptive fields relative to the contact point; it is also more difficult to factor out the differences in fiber sensitivities.

Using the receptive field approach (first approach described above) for spheres indented into the relatively flat portion of the monkey’s fingerpad, Goodwin and colleagues (Goodwin et al. 1995, Wheat et al. 1995) performed a detailed parametric analysis of the three key parameters, namely the curvature of the stimulus, the position of contact on the finger, and the contact force normal to the skin. All SAI afferents could be characterized by a single multiparametric stimulus-response function. The only difference between fibers was a difference in sensitivity, which could be accounted for by a multiplicative factor; the statistical distribution of sensitivities was measured.

The mathematical description of single afferent responses enabled a population reconstruction for any arbitrary combination of curvature, position, and force. Figure 4A shows a reconstruction for a sphere of curvature $694 \text{ m}^{-1}$ (radius of sphere 1.44 mm) contacting the center of the fingerpad. The effect of changing either the curvature, position, or contact force is depicted in Figure 4B, C, and D, respectively. At a qualitative level it is evident that changing the curvature changes the shape of the population response profile, changing the position of contact on the skin shifts the population response correspondingly, and changing the contact force scales the whole profile. This depiction also suggests that the brain could extract each of the three parameters independently even when they are changing concurrently. In this series of studies only SAI afferent responses were reconstructed because, for these stimuli, the FAI afferents did not contain shape information, although they did contain some information about position (Goodwin et al. 1995, Wheat et al. 1995).

For their torroidal stimuli, Khalsa et al. (1998) adopted the alternative approach to population reconstruction. They indented the torroids into the monkey’s fingers at a constant nominal position and harvested a population of single afferents at a variety of two-dimensional positions on the fingertip. Their measured population response included the variation in sensitivity among afferents. For their SAI afferent population, the results were analogous to those in Figure 4. For the torroids, the radially symmetric Gaussian-like profiles in Figure 4 became Gaussian-like profiles with different major and minor axes reflecting the major and minor axes of the torroids. Thus, both the shape and orientation of the torroids are evident in the population responses. They also reconstructed FAI afferent population responses and found no reliable representation of the shape or orientation of the torroid in that population.

The power of this second approach to population analysis is evident in experiments from which afferents innervating all regions of glabrous skin on the distal segment of the digit are recorded. Indenting spheres at a constant nominal point on the monkey’s fingerpad, Bisley et al. (2000) showed that SAI afferents
Figure 4  Representation of multiple parameters in the population response of SAI afferents in the monkey’s fingerpad. (A) A sphere of curvature 694 m$^{-1}$ indenting the fingerpad. (B) Changing the curvature (shape) of the sphere to 256 m$^{-1}$ changes the shape of the population response. (C) Changing the position of the sphere on the skin by 1 mm shifts the profile a corresponding amount. (D) Changing the contact force scales the population response. Modified from Goodwin et al. (1995).

on the highly curved sides and end of the distal segment respond significantly. In a study of human primary afferents, a major goal of Birznieks et al. (2001) and Jennalm et al. (2003) was to obtain data applicable to real-life human manipulation. Thus they applied spherical stimuli to a constant nominal point on the fingertip and recorded from afferents terminating all over the glabrous skin of the distal segment of the digit using relatively larger and faster contact forces than used previously (rising to 4 N in 125 ms). They also varied the direction of the contact force. Under these conditions, significant information about the force direction and the stimulus curvature was present in the SAI, SAI, and FAI afferent populations. Although a specific population reconstruction was not performed, their data for the effect of curvature on SAI afferent responses is consistent with the data from monkeys. The marked effect of curvature on their FAI afferent responses is different from that in the monkey, presumably because of the larger and faster contact forces.
This second approach to population reconstruction can also be used for stimuli scanned over the skin. Friedman et al. (2002) scanned torroids over the monkey’s fingerpad along one of eight nominally standard trajectories and recorded from SAI and FAI afferents over the volar surface of the distal segment. Analysis of these population responses showed that the location and direction of the object moving over the skin was represented in both the SAI and FAI afferent populations, but with greater fidelity in the SAI afferent population.

The reconstructions illustrated in this section indicate how multiple stimulus parameters can be represented, simultaneously, in a single population of afferents, allowing each of the parameters to be determined independently.

**PSYCHOPHYSICS**

The primacy of sensorimotor integration in hand function poses a number of difficulties for psychophysical studies. We have argued above that sensory input about stimulus parameters is critical for both manipulation and tactile perception. The initial pathway for processing the sensory signals is the same in both cases, but the final processing is different (Figure 5). Nor is it clear where the branch point is, and it may vary from task to task. The advantage of this parallel pathway is that information about sensory input can be obtained in two ways: either from behavioral experiments in manipulation or from psychophysical experiments in sensory perception. The disadvantage is that caution is required in using data from

![Figure 5](image-url)
manipulation experiments to draw inferences about sensory perception and in using data from perceptual psychophysics to draw conclusions about manipulation.

Behavioral experiments embracing a number of grip and lift tasks, and variants thereof, have clearly demonstrated the critical role of tactile sensory input (Johansson 1996). However, the design of most studies is such that definitive separation of cutaneous input from proprioceptive input is not possible, and in many cases visual input is also a potential confounding factor.

Similarly, in most experiments in the large field of haptic perception, multisensory information is present (Klatzky & Lederman 2003). Even in those experiments where vision is occluded, it is usually not possible to determine whether the sensory information arises from cutaneous sources, proprioceptive sources, or a combination of both. For example, Davidson (1972) and Kappers et al. (1994) measured the subject’s ability to determine curvature using touch, but because haptic exploration involves movement of the fingers over the curved surface it was not possible to isolate cutaneous from proprioceptive contributions. In a subset of haptics experiments, the subject contacts the stimulus without scanning the skin over the surface. In such experiments proprioceptive information may play a role in enabling the subject to execute the task, but the stimulus attributes being tested can only be conveyed by cutaneous cues. For example, in the experiments of Loomis (1979) a finger guide prevented lateral motion of the subject’s finger; the digit could only be flexed to contact a tack, and subjects could judge its position with a resolution of about 0.2 mm.

In some psychophysical experiments, the subject’s finger is restrained or immobilized in some way, and the stimulus is applied to the finger by a stimulator. With this design, the only information available to the subjects is that arising from cutaneous receptors in the contacted digit. Applying spheres at different positions on the skin, Wheat et al. (1995) found a difference limen of 0.38 mm and 0.55 mm for spheres of curvature 521 and 172 m⁻¹, respectively. It is significant that the resolution for position is markedly superior to figures obtained from simplistic application of the sampling theorem using the estimated receptor spacing of a millimeter or more. When Srinivasan & LaMotte (1987) indented sinusoidally shaped steps into the fingerpad, the subjects could discriminate different steps; however, because of their complex shape, it is not easy to interpret the data quantitatively. Using spheres, Goodwin et al. (1991) showed that humans could scale curvature over a large range and could discriminate differences in curvature of about 10%. For cylinders, humans can discriminate orientation differences of about 5° (Dodson et al. 1998, Lechelt 1992). It has been shown that humans can scale the depth of indentation of a contacting probe (Mountcastle 1967), but there have been few studies of perception of contact force (Cohen & Vierck 1993b). When spheres are indented into the finger, humans can scale the contact force, and they can perceive both the curvature and the contact force of the spheres when both are changed concurrently (Goodwin et al. 1991, Goodwin & Wheat 1992).

These psychophysical data, with stimuli applied to an immobilized finger, demonstrate that precise information about the local shape of handled objects,
their position on the skin, and the contact force is relayed by the mechanoreceptive afferents from the digital glabrous skin. Although there may be differences in the use of sensory information by the motor control system and by the processes leading to perception and cognition (Figure 5), the results of the manipulation experiments described at the beginning of this section make it likely that most, if not all, of this sensory information is accessed by the motor control system.

MODELING POPULATION RESPONSES

One reason for reconstructing population responses is to reveal how multiple stimulus parameters can be represented unambiguously even though the responses of individual single units are completely ambiguous (Figure 4). There are two additional compelling reasons (Figure 5). First, neural responses and neural computations are variable or noisy. Second, there are critical parameters intrinsic to the populations themselves, such as the pattern and density of innervation. These factors have a major impact on signal processing in the population, and unless they are addressed, it is not possible to fully appreciate the nature of the neural mechanisms and not possible to make meaningful comparisons with human behavior.

Realistic analysis of population responses requires a step beyond the rudimentary reconstructions described in a previous section and is dependent on mathematical models or computer simulations.

Neural Codes

In order to assess the accuracy with which individual stimulus parameters are represented in the population response, and to relate this to psychophysical measures of perception, it is necessary to extract a measure for that parameter from the population response. This metric is often called the neural code for the parameter. The metric quantifies the representation and indicates the potential for the brain to extract information about the parameter, but it is usually not meant to imply that the brain uses that particular computational process. As an example, the pattern of the spatial event plot in Figure 6A resembles the pattern of dots in the stimulus scanned over the monkey’s finger, but to relate the response to human perception of the roughness of the dots requires that some measure of roughness be extracted from the spatial event plot. Blake et al. (1997) extracted the spatial variation in the SAI afferent impulse pattern and showed a close correlation with perceived roughness (Figure 6B) over a wide range of dot heights and spacing.

As a metric for the position of the stimulus on the skin, Goodwin & Wheat (1999) used the centroid of the population response profile. The centroid was closely correlated with the position of the stimulus, and it was insensitive to changes in the curvature or contact force of the stimulus. In the presence of considerable noise, and even at innervation densities lower than that estimated for the human (Johansson & Vallbo 1979), the reliability of the centroid was sufficient to explain the human difference limen of about 0.5 mm. Their analysis also explained why
Figure 6  Roughness of a textured surface. (A) Spatial event plot (below) for an SAI afferent when the dot pattern (above) is scanned over the monkey’s finger. (B) Correlation between spatial variation within the SAI afferent responses and human perception of roughness. Redrawn from Blake et al. (1997).

the difference limen is less than that predicted from simplistic application of the sampling theorem, a phenomenon termed hyperacuity by Westheimer (1975). It is the shift of the whole population profile, determined by many afferents, that provides the positional information. Resolution in populations comprising neurons with overlapping broadly tuned response profiles, which is equivalent to the case here, has been analyzed in a number of systems including electro-reception in fish (Heiligenberg 1987) and has been addressed theoretically (Pouget et al. 1999, Snippe 1996). Center-of-gravity codes have been proposed in a range of sensory and motor systems (Georgopoulos et al. 1988, Lee et al. 1988, Zohary 1992).

Modeling the population response for a stimulus contacting the skin also highlights the dangers of using overly simplistic indicators of neural signals or overly simplistic codes. The variation in sensitivity from afferent to afferent is considerable. This, plus the presence of noise, distorts the response profiles and the position of the stimulus on the skin does not correspond to the point of maximum response in the population, but the centroid is insensitive to these variations (Goodwin & Wheat 1999). This is nontrivial because, within a single human finger, the variations in afferent sensitivity are large so that a robust signal is needed for the position of an object contacting different points on the finger.

If contact force is entirely normal to the skin, then the total response of the population (simply the summed response) is a viable code for this parameter. In several studies, the total population response has been used as a metric for the intensity of a probe indenting the skin (Cohen & Vierck 1993a, Johnson 1974, Ray & Doetsch 1990). Total responses have also been used as population codes for other
intensive sensory stimuli such as skin temperature (Johnson et al. 1979) and sound intensity (Relkin & Doucet 1997). In most manipulations or haptic explorations there are also components of force tangential to the skin, or, equivalently, the direction of the contact force varies and is not always normal to the skin. This complicates the extraction of force from the population response. It has been shown that humans can perceive tangential force components (Pare et al. 2002a, Wheat et al. 2004) and Birznieks et al. (2001) showed that the peripheral afferent responses are modulated by force direction; however, how force direction is represented in the population independently of force magnitude and other parameters of the stimulus is still not clear.

The local shape of the stimulus in contact with the skin is perhaps the most challenging stimulus parameter for which to formulate population codes. Most analyses of shape have been in relation to visual perception, but the principles are the same (Hegde & Van Essen 2000). The metric for curvature used by Goodwin & Wheat (Goodwin & Wheat 1999) demonstrates how curvature representation in the population can explain the human psychophysical performance and how humans can perceive curvature independently of the other stimulus parameters.

Noise

All neurons have some variability or noise associated with their responses. Noise is apparent in single-unit studies, but there is also covariance of variability between neurons, which is only manifest when analyzing groups or whole populations of neurons.

In populations responding to a single stimulus parameter, with all the constitutive neurons having the same characteristics, the fundamental question is, how does the size of the population influence the signal-to-noise ratio or the resolution? In such cases the metric used is usually the total or mean population response, and a statistical analysis can be used to show that resolution increases as the number of units in the population increases. Covariance between neurons decreases resolution and limits the benefit of increasing pool size (Johnson et al. 1979, Zohary et al. 1994).

For more complex population responses or more complex noise, analytical solutions are difficult and a computer simulation of some sort is usually used (Shadlen et al. 1996, Vogels 1990). Different types of noise have been observed in different structures in the central nervous system. Noise independent of the mean discharge rate of the neuron has been observed in the retina (Croner et al. 1993), but more commonly, variance proportional to the mean response has been reported (for review see Lestienne 2001). It is not known what types and levels of variance and covariance occur along the entire pathway for tactile perception and manipulation.

The noise in tactile peripheral afferents themselves is not significant (Jenmalm et al. 2003, Phillips & Johnson 1981a, Wheat et al. 1995). However, as the information from the peripheral afferent population is processed further in the CNS, leading
to perception and/or manipulation, substantial variability will be introduced, and this variability will interact with the peripherally determined population parameters (like the pattern and density of innervation). Goodwin & Wheat (Goodwin & Wheat 1999; Wheat & Goodwin 2000, 2001) used a single-hybrid population simulation in which the primary afferents were assigned noise attributes reflecting further processing along the CNS pathway. Their population metrics were superior to human performance even in the presence of considerable variance, whether dependent on or independent of the neurons’ mean responses. What is striking in their models is that while covariance has a deleterious effect on resolution for contact force (a total response code), it markedly improves resolution for position (a pattern code). This difference has been discussed in a theoretical context (Abbott & Dayan 1999, Johnson 1980), and it has been shown experimentally that resolution improves with increasing covariance for a measure based on differences in neural responses (a form of pattern code) (Romo et al. 2003).

A paradoxical property of noise is its capacity to enhance weak signals in nonlinear systems, known as stochastic resonance. In the tactile system, noise can enhance the detection of subthreshold indentation (Collins et al. 1997), and this enhancement is reflected in neural responses (Collins et al. 1997), and this enhancement is reflected in neural responses (Collins et al. 1997).

**Intrinsic Population Characteristics**

Establishing the geometry of cutaneous mechanoreceptive afferent innervation of the finger is not straightforward. Unlike the elegant studies of rods and cones in the retina where the whole receptor mosaic can be visualized (Curico et al. 1987), it is not currently possible to visualize the mosaic of afferent innervation. Thus, indirect approaches combining single-unit recording with histological fiber counts are necessary. Only one study exists in the human, which is that of Johannson & Vallbo (1979). Their data show that, even in the distal segment of the finger, density is not uniform and reaches a maximum toward the tip of the segment of 0.7 and 1.4 mm$^{-2}$ for the SAI and FAI afferents, respectively. In the monkey there is also only one study, which is that of Darian-Smith & Kenins (1980). They did not subdivide the distal segment of the digit, and they obtained an overall estimate for this segment of 1.34 and 1.78 mm$^{-2}$ for the SAI and FAI afferents, respectively. These estimates are invaluable, but they are based on a number of uncertainties and simplifying assumptions as readily acknowledged by the authors.

When comparing human behavior with neural responses it is prudent to allow for this uncertainty in innervation density. Nor do the existing data give any indication of whether these numbers vary between individual humans or change with age. As our baseline we, and most others, use the peak figures from Johannson & Vallbo (1979), which, on the basis of uniform innervation, correspond to a separation between adjacent receptive field centers of 1.2 and 0.85 mm for the SAI and FAI afferents, respectively. But innervation is not uniform; at the very least there is a proximo-distal gradient within the distal segment of the digit, but the exact pattern of innervation is not known. Aging (Cauna 1965, Swallow 1966) and a number
of neurological diseases (Dyck & Winkelmann 1966) result in a decrease in the number of peripheral nerve fibers and/or mechanoreceptors. Moreover, it has been shown that in diabetic neuropathy the cutaneous afferents are affected before the onset of symptoms (Mackel 1989). Thus in many humans (perhaps most adults) there is some fiber or receptor dropout leading to a patchy pattern of innervation.

Rudimentary population reconstructions, such as those in Figure 4, should be viewed with caution. Those patterns are not what the brain "sees"; the patterns are sampled, probably nonuniformly, and they are distorted by noise and variation in sensitivity among fibers. Only through population simulations that allow arbitrary variations in the innervation pattern is it possible to appreciate the large impact on representation and resolution (Goodwin & Wheat 1999; Wheat & Goodwin 2000, 2001). These simulations also expose the high degree of interaction between the intrinsic population parameters and noise in limiting resolution.

FUTURE DIRECTIONS

When the fingertip contacts an object, the visco-elastic skin surrounding the entire distal phalanx is distorted. Thus an afferent innervating skin on any part of the segment may be activated even though its classical receptive field (delineated by von Frey hairs) is remote from the region of contact. Thus, to obtain a complete picture of sensory signals when objects are handled or explored, existing population models need to be extended to cover afferents over the entire distal segment. Moreover, these models should include all four cutaneous mechanoreceptive afferent types in a comprehensive interactive manner. In some current models the stimulus has been deliberately chosen to preferentially activate one subtype of afferent (Wheat & Goodwin 2001). In others, more than one subtype is reconstructed, but the populations are handled separately and no interactions between subtypes are considered (Khalsa et al. 1998). Even for relatively simple stimuli, it has been shown that the responses of SAI, FAI, and SAIII afferents are modulated by the direction of contact force and the curvature of the stimulus (Jenmalm et al. 2003), and in most realistic tasks all four afferent types would respond.

The stimuli used to date have been relatively simple, partly to facilitate tractable analysis and partly because of the limitation of the stimulators. Hand movements generating everyday manipulations and haptic explorations are rich and varied; ultimately, stimulators will need to simulate more of the essential components of these elaborate movements, and population models will need to cope with the more complex information.

There is an obvious need to incorporate somatosensory signals other than tactile in models of manipulation and haptic perception. When we handle objects, a potential wealth of information could be signaled by joint afferents from the hand as well as from muscle spindles and Golgi tendon organs in the extrinsic and intrinsic hand muscles. There is a great deal of information about muscle and joint receptors, but most of it was gathered in experiments on structures such as the
GOODWIN ■ WHEAT
cat’s hind limb (Banks 1994). There is only scant information about responses of these receptors in situations equivalent to normal hand function and not nearly enough to form the basis of a quantitative population reconstruction (Wessberg & Vallbo 1995). Movements of the hand are invariably accompanied by movements of the rest of the upper limb to varying degrees, and eventually sensory signals from the whole limb will need to be included. Some experimental paradigms used in somatosensory cortex research include many of these features, but as of yet we do not have a sound theoretical framework to drive the analysis of the neural responses (Gardner et al. 1999).

A major challenge for the future is to develop a global model of manipulation and haptic exploration encompassing all the senses. Under normal circumstances, vision plays a significant role in hand movements (Desmurget et al. 1998), and this is starting to be addressed at a number of levels including hand-eye coordination (Johansson et al. 2001). In related research, experiments in the posterior parietal cortex are beginning to unravel the complex interactions between visual sensory input, somatosensory input, and other sensory input in planning movements (Andersen et al. 1997).

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