Haptic Interaction of Touch and Proprioception: Implications for Neuroprosthetics

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***Abstract*—Somatosensation is divided into multiple discrete modalities that we think of separably: e.g. tactile, proprioceptive, and temperature sensation. However, in processes such as haptics, those modalities all interact. If one intended to artificially generate a sensation that could be used for stereognosis, for example, it would be crucial to understand these interactions. We are presently examining the relationship between tactile and proprioceptive modalities in this context. In this overview of some of our recent work, we show that signals that would normally be attributed to two of these systems separately, tactile contact and self-movement, interact both perceptually and physiologically in ways that complicate the understanding of haptic processing. In the first study described here, we show that a tactile illusion on the fingertips, the cutaneous rabbit effect, can be abolished by changing the posture of the fingers. We then discuss activity in primary somatosensory cortical neurons illustrating the interrelationship of tactile and postural signals. In this study, we used a robot-enhanced virtual environment to show that many neurons in primary somatosensory cortex with cutaneous receptive fields encode elements both of tactile contact and self-motion. We then show the results of studies examining the structure of the process which extracts the spatial location of the hand from proprioceptive signals. The structure of the spatial errors in these maps indicates that the proprioceptive-spatial map is constructed individually.**

These seemingly disparate studies lead us to suggest that tactile sensation is encoded in a two-dimensional map, but one which undergoes continual dynamic modification by an underlying proprioceptive map. Understanding how the disparate signals that comprise the somatosensory system are processed to produce sensation is an important step in realizing the kind of seamless integration aspired to in neuroprosthetics.

***Index Terms*—About four key words or phrases in alphabetical order, separated by commas. For a list of suggested keywords, send a blank e-mail to keywords@ieee.org or visit http://www.ieee.org/organizations/pubs/ani_prod/keywrd98.txt**

I. INTRODUCTION

Traditionally somatosensation is divided into multiple discrete modalities that we think of separably: e.g. tactile, proprioceptive, and temperature sensation. In fact, all those modalities participate together to create the final perception of the environmental elements that we are interacting with and how that interaction is structured. This is the process of *haptics*. Clearly this process cannot proceed from any of the single modalities on their own. To generate a sensation that can be used for haptics, it is crucial to understand how these processes interact. Our current hypothesis is that tactile sensation comprises a two-dimensional map, one which is captured by the cortical homunculus, and that rides upon a separate dynamic geometry reflecting the body schema. That schema, in turn, is derived from a combination of proprioception (likely both deep and cutaneous receptors), efference copy, and perhaps visual representation of the body's posture.

In this overview of some of our recent work, we show that signals that would normally be attributed separately to cutaneous and proprioceptive modalities, tactile contact and self-movement, interact both perceptually and physiologically in ways that complicate the understanding of signal processing for haptics. By making use of a striking tactile illusion, the cutaneous rabbit effect [1-12], we have shown that tactile perception can be strongly impacted by changes in body posture [13]. In agreement with earlier work [14-19], we have also shown that signals which would traditionally be considered tactile and proprioceptive are frequently simultaneously present in the activity of single neurons in the somatosensory system, but that with careful experimentation, those two components of somatic neural coding can be dissociated. Finally, we have begun to examine the detailed structure of the proprioceptive map which we believe underlies tactile processing. We have shown that these maps are stable and highly idiosyncratic, and exhibit a striking mirror-image symmetry across the arms.

Our overall goal is to improve neuroprosthetic systems by deepening our understanding of the neural processes which underlie haptics. Careful understanding of these systems will enhance our ability to drive information to and from neuroprosthetic systems..

II. IMPACT OF POSTURE ON TACTILE PERCEPTION

Haptics is the combination of somatic sensations to create a unified and coherent representation of objects in the world. In deference to Bregman [20], we emphasize this to underline that one key purpose of somatosensation is to interpret the world around us through our physical interactions. Thus, it is trivial to discriminate between a cardboard coffee cup and a ceramic mug using only haptics. Both objects have a curved surface and are 2 to 3 inches in diameter: these features can be discerned from the pattern of pressure on the fingertips and

the configuration of the hand. However, the cardboard cup has a slight roughness because it is composed of a fibrous material, and it transmits heat into the skin, whereas the mug is smoother and feels cooler since it is mostly transmitting heat away from the skin. In creating these mental images, our brain assumes that patterns of stimulation follow well-behaved rules that derive from prior experience interacting with physical objects. As in the case of visual perception, the associations built up by experience with the physical world are useful for filling in blanks, but can sometimes lead to illusions.

One such tactile illusion is the Cutaneous Rabbit Effect (CRE). This illusion uses carefully ordered sequences of taps on the skin to create the illusory perception that the skin was tapped at a location that was untouched. For example, if one stimulates the index, middle, ring, and little fingertips in succession you would expect to perceive those stimuli correctly on those fingertips. However, the illusion can create the identical perception that the middle finger was stimulated even though only the index, ring, and little fingertips were tapped [12].
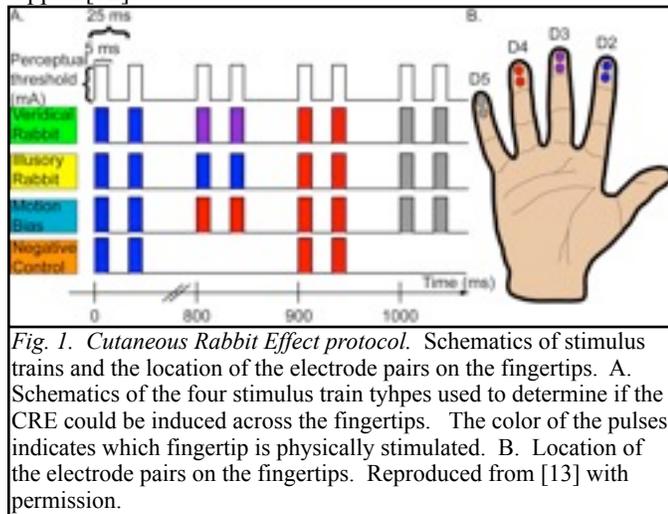

Fig. 1. *Cutaneous Rabbit Effect protocol.* Schematics of stimulus trains and the location of the electrode pairs on the fingertips. A. Schematics of the four stimulus train tyhpes used to determine if the CRE could be induced across the fingertips. The color of the pulses indicates which fingertip is physically stimulated. B. Location of the electrode pairs on the fingertips. Reproduced from [13] with permission.

The Cutaneous Rabbit is interpreted as an attractee stimulus that is moved in space depending on the pulse sequence. When originally discovered, physical taps at several locations along the forearm produced the perception that the taps were occurring at and between the sites of the physical stimuli at the frequency of the stimuli [1]. However, newer stimulation paradigms have revealed that only three taps at two locations are necessary to induce the illusion [2]. In this 'reduced rabbit' paradigm, the first stimulus is termed the 'locator' stimulus; it establishes the spatial (and perhaps temporal) origin for the illusion. This stimulus is followed by an 'attractee' stimulus delivered to the same physical site as the 'locator' stimulus but shortly after. The 'attractor' stimulus is presented at a different physical site than the 'locator' and 'attractee' stimuli, a short time after the 'attractee' stimulus. The location and timing of the 'attractor' shifts the perceived location of the 'attractee' to a site closer to the 'attractor's' location.

In our experiments, we used a stimulus train of four pulses to compare percepts that evoked the CRE and similar trains that served as controls. The paradigms used were designed to avoid attentional biases by having the subjects focus attention on the site of the illusory stimulus, namely the middle finger [21]. In each paradigm the subjects were asked whether they
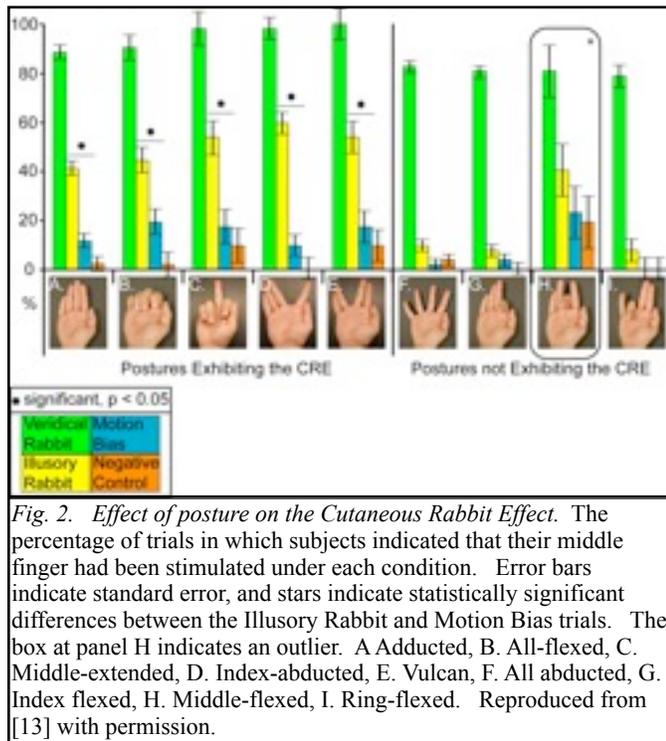
felt a stimulus on the middle finger. The Illusory Rabbit Train (Fig. 1, yellow) evoked the baseline illusion; it consisted of pairs of stimuli to the index, index, ring, and little fingertips while all the fingers were extended in the adducted posture (Fig. 2a). This resulted in the perception that a subject's middle fingertip was stimulated although the subject did not receive a stimulus on their middle fingertip.

Three other train types served as controls. In the Veridical Rabbit Train (Fig. 1, green), all four fingers were actually stimulated in sequence. This provided a positive control against which we could measure responses. The Negative Control Train (Fig. 1, orange) included only regularly spaced stimulus pairs applied to the index and ring fingers. This stimulation pattern was not expected to produce any illusion. The Motion Bias Train (Fig. 1, blue) provided one pair of stimuli to the index finger and two subsequent stimulus pairs on the ring finger; thus the attractee stimulus occurred at the same location as the attractor stimulus. The Cutaneous Rabbit was determined to be present if the middle finger was perceived as being stimulated more often in the Illusory Rabbit Train than in the Motion Bias Train [12,21]. One of our goals in using the CRE was specifically to examine the impact of posture on the overall perception of these stimulus patterns. Thus, it was important to use a stimulation that allowed us to repeat the stimulus pattern with high fidelity, but in varying hand postures. To achieve this goal, we opted to use electrotactile stimulation, as this involves only fine wires and small electrodes attached to the fingers, thus allowing a good range of movement. Briefly, pairs of electrodes were affixed to the volar aspect of the index, middle, ring, and little fingertips of the subjects (n=14) (Fig. 1). The stimulus trains consisted of pairs of anodic half-rectified square waves 5 ms in duration separated by 25 ms at each stimulation site (Fig. 1B). The attractee stimuli were delivered 800 ms after the onset of the locator stimuli. The first of the two sets of attractor stimuli were delivered 100 ms after the onset of the second (attractee) stimulus and the second 100 ms after the onset of the first. To ensure that each stimulus was perceived, each subject's perceptual threshold, i.e. the minimum current necessary to be detectable in 10 consecutive stimulations, was determined by the method of limits [9]. For details of the stimulation methods, see some of our earlier work [22, 23].

We used a two-factor design to determine whether the CRE could be induced in each posture. The factors were stimulus train type (Fig. 1) and posture (Fig. 2). Each subject performed the experiment in either 3 or 4 total postures. Each subject had Adducted posture trials and two or three other posture trials so that the Adducted posture had 14 data points and each other posture had 4 data points. A data point consisted of the percentage of responses where a subject indicated that their middle fingertip was stimulated for a particular posture and stimulus train. There were 13 replicates of each combination of posture and stimulus train. Posture order was randomized across all subjects, and in each posture stimulus trains were randomized. In the non-flexed postures the subject's fingers are extended at each finger joint. In postures requiring finger flexion, each of the flexed fingers was flexed at the metacarpophalangeal (MCP), proximal interphalangeal (PIP), and distal interphalangeal (DIP) joints.

Subjects were prompted to initiate each stimulus train during the experiment via a computer screen. In response to

Fig. 2. Effect of posture on the Cutaneous Rabbit Effect. The percentage of trials in which subjects indicated that their middle finger had been stimulated under each condition. Error bars indicate standard error, and stars indicate statistically significant differences between the Illusory Rabbit and Motion Bias trials. The box at panel H indicates an outlier. A Adducted, B. All-flexed, C. Middle-extended, D. Index-abducted, E. Vulcan, F. All abducted, G. Index flexed, H. Middle-flexed, I. Ring-flexed. Reproduced from [13] with permission.

each stimulus train they were asked, "Did the preceding stimulus train contain a stimulus on your middle fingertip?" They were able to indicate 'Yes' or 'No'. Their response was recorded and later averaged with the rest of the like stimulus trains in each posture for analysis. Analysis of variance statistics were computed for the two-factor factorial design using Design-Expert® (Design-Expert v 7.0, Stat-Ease, Inc.). Fisher's Least Significant Difference (LSD) tests were performed to compare between the stimulus train types within a posture.

We found that the effect of hand posture was significant by ANOVA ($\alpha < .05$, $p < .0001$). In a number of postures, subjects reported stimulation of the middle fingertip (Fig. 2): Adducted, All-Flexed, Middle-Extended, Index-Abducted, and Vulcan postures exhibited significantly different responses between the *Illusory Rabbit* and *Motion Bias* trains (ANOVAs, $\alpha < .05$, $p < .0323$, $p < .0219$, $p < .0001$, and $p < .0055$ respectively). However, in the other postures subjects did not perceive that their middle fingertips were stimulated as often nor were there differences between how they perceived the Illusory Rabbit and Motion Bias Trains (Fig. 2, ANOVAs, $\alpha < .05$, $p = .1332$ Abducted, $p = .4537$ Index-Flexed, $p = .4332$ Middle-Flexed, and $p = .4222$ Ring-Flexed).

We had initially anticipated that the cutaneous rabbit effect would be abolished when the subjects adopted hand postures which violated the expected geometry of a saltation proceeding in a line. Thus, we expected the adducted and all-flexed to experience the illusion, whereas the middle-flexed and middle-extended would not. Instead, we found that the illusion was particularly sensitive to the stimulated fingers being arranged in a line, but was indifferent to the location of the finger which experienced the illusory perception. It appears to us that the proprioceptive changes were only effective when they were combined with a direct tactile input. This suggests to us that proprioception serves as a modulatory role upon which tactile sensation arises.

Having shown that hand posture significantly affects tactile processing from the fingers, we set out to examine how this interdependence is encoded in the activity of somatosensory neurons.

III. MIXING OF POSTURAL AND CONTACT ACTIVITY IN PRIMARY SOMATOSENSORY CORTEX

We recorded the activity of cortical neurons in primary somatosensory cortex (SI) in order to examine this relationship between neural activity coding posture/movement and neural activity encoding tactile contact. It is reasonably established that neurons with cutaneous receptive fields, both peripherally and centrally, encode elements of body movement in their firing patterns [14-19]. Thus, we set out to examine these two elements of neural coding separately, but in a naturalistic movement task. To this end, we designed a novel reach-to-grasp (RTG) behavioral task in which all visual cues were provided by a Virtual Reality Simulation (VRS). Only units with tactile receptive fields on the volar and dorsal surfaces of the palm and digits were analyzed. Grasp objects were presented in a random sequence of *physical* (object presented in both the physical and virtual workspaces) or *virtual* (object presented only in the VRS) trials in order to distinguish neural activity caused by haptic interaction (contact and grasp) from non-contact-driven neural activity.

All of the animal procedures described here were carried out with the approval of ASU's Institutional Animal Care and Use Committee and in accordance with the "Guide for the Care and Use of Laboratory Animals".
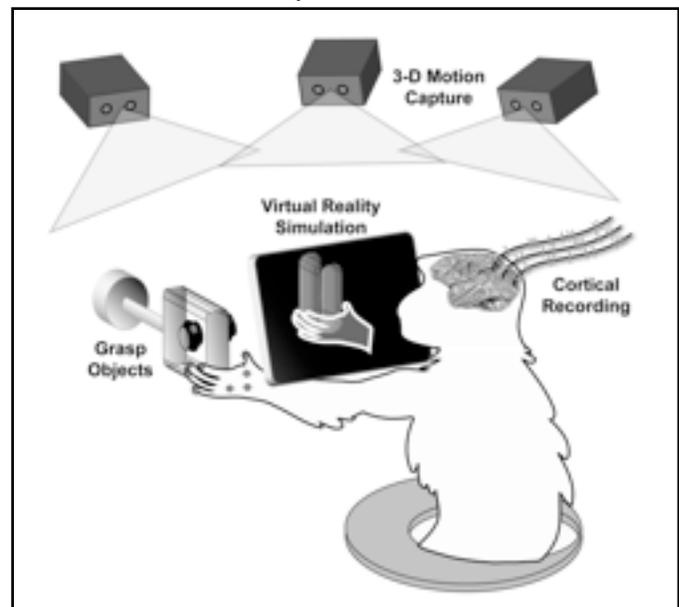

Fig. 3. Robot-enhanced virtual environment. Experimental setup for distinguishing neural responses driven by external (contact-driven) stimuli from those driven by self-generated (movement-driven) stimuli. Subjects observed the VRS from a mirror and grasped real and/or virtual objects as neurons were recorded from S1.

Figure 3 illustrates the experimental setup used in this study. Two male rhesus macaques (*Macaca mulatta*) were trained to perform a behavioral task while seated in a

restraining chair with head fixed. The left arm was restrained throughout the task. A mirror was located 4 inches in front of the monkey at a 45-degree angle to reflect the screen image from a 3-dimensional (3D) monitor (SeeReal Technologies) mounted horizontally and directly above the seating area. The monitor displayed the VRS and provided all visual cues during the task, including a virtual hold pad, hand and grasp objects. Hand position and kinematics were captured using an active marker motion capture system (Phasespace, Inc.). At no time could a subject see its hand or the objects being presented in the workspace immediately behind the mirror. Grasp objects were presented to a single location near the body midline and at shoulder height by a 6-axis robotic arm (VS-6556-G, Denso

sensed contact events with the grasp objects. Single-unit neurophysiological recordings of task-related units were captured during the task using a multi-channel recording system (Plexon, Inc.).

The behavioral task was designed to distinguish cortical sensory feedback from the hand originating from two distinct sensory stimuli: haptic contact and hand movement. Subjects were required to perform the RTG task in which they briefly grasped an object presented in the workspace directly ahead. All visual task cues came from the VRS. *Physical trials* (actual object was presented) were pseudorandomly interspersed with *virtual trials*, in which a virtual object was depicted in the VRS, but was not actually presented in the
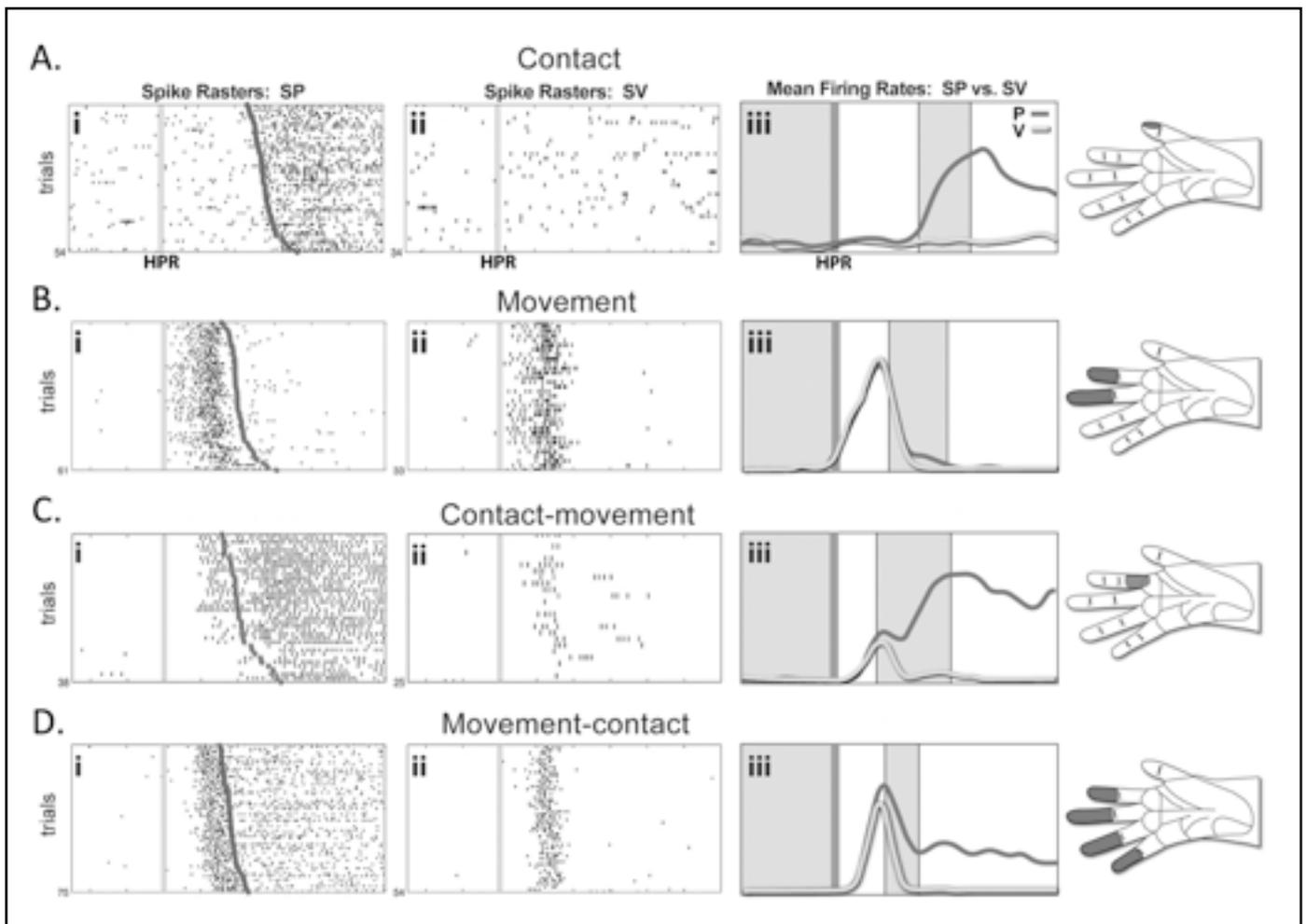

Fig. 4 *Firing rate analysis of neural response types*. Simple responses (A, B) had a single dominant response trait, whereas mixed responses (C, D) had primary and secondary response traits. Spike time rasters (columns ii and ii) aligned on hold-pad release (t=0) show singule-trial unit responses to (i) physical (SP, left column) and (ii) virtual (SV, middle column) object presentations. Panel rows end in comparison plots of mean firing rates for both task conditions. Object contact events are marked with filled circuls in the physical task. The approximate cutaneous receptive field of each unit is shown at right. A. Simple contact-driven unit has a strong response during haptic interaction with the object, but is silent during virtual tasks. B. A simple movement-driven response is complementary to the Simple contact driven response. C and D show mixed responses, driven both by contact and movement.

Robotics) fitted with a pneumatic tool changer (QC-11, *ATI Industrial Automation*) on the end effector. A 6 degree-of-freedom (DOF) force and torque sensor (Mini85, ATI Industrial Automation) also mounted on the end effector

workspace.

Each trial was divided into four distinct phases: Hold, Reach, Contact and Grasp. Trials were aligned on the *hold pad release* (HPR) event, defined as the first departure of the

monkey's hand from the hold pad after the *go* cue. The Hold phase was defined as the interval [-500, -50] ms with respect to HPR. The short offset from HPR (50 ms) excluded neural activity caused by slight pre-reach anticipatory movements or from tactile responses caused by contact with the hold pad itself.

Once the animals were trained, chambers were implanted over the left primary sensory cortex in order to capture task-related neural activity arising from the contralateral working hand. The time occurrence of action potentials from isolated units was recorded and the instantaneous firing rate was calculated using binned time intervals of 20 ms, smoothed with a triangular convolution kernel [24]. Recording location (stereotaxic coordinates, recording depth), cutaneous receptive field location and real-time neural response attributes were used to guide the selection of recording sites to the hand representation of SI, similar to the procedure described by Mountcastle et al. [25]. Post-mortem verification of recording sites was obtained for one experimental subject in order to verify the empirical method of identifying the hand representation of SI (areas 3b and 1). In addition, MR imaging data were combined using *Monkey Cicerone* [26] to reconstruct the chamber location and track electrode penetrations. Finally, intracortical microstimulation (ICMS) experiments carried out in both subjects verified that the overwhelming majority of units were recorded in SI.

All of the units retained and analyzed for this study had clearly identifiable cutaneous receptive fields on the volar or dorsal surface of the palm or digits. Cutaneous receptive fields were identified using mechanical stimuli and passive joint manipulation. A unit response was considered *task-related* if the mean firing rate during any single task phase was significantly different from the mean rate during any other task phase. Statistical significance ($\alpha = .05$) was assessed using an unbalanced ANOVA test of mean firing rate bins grouped by task phase. We recorded a total of 371 single units with tactile receptivity in SI in two male rhesus monkeys (monkey *F*: 63%, monkey *I*: 37%). Of these, 285 units (77%) exhibited statistically significant task related activity and were included in the analysis (monkey *F*: 59%, monkey *I*: 41%). The remaining 86 unused units appeared to exhibit significant task-related activity at the time of recording but, upon further analysis, were not significantly modulated by the experimental task.

In Fig. 4 we show example activity from four separate somatosensory cortical neurons recorded in this task. The receptive fields for the neurons are shown in the figurines to the right. Those with a response in the Contact/Grasp phase to the physical target (P) were labeled as *Contact-Driven* (see e.g. the third column of Fig. 4 A, C, and D). Neurons with a response in the Reach phase were labeled as *Movement-Driven* (see e.g. 4 B, C, and D). Note that since the animal does not know whether there is a physical object, there should be no difference between physical and virtual trials during the reach phase. Cells with *Simple* response types had neural activity that was statistically significant only for one element of the task; contact (Fig. 4A) or movement (Fig 4B). Neurons

which modulated during the reach phase (*Movement-driven)* and again during the Contact/Grasp phase for physical trials only (*Contact-driven*) were classified as *Mixed* response types. Altogether, only 42% of the neurons recorded in our sample neural population had *Simple* response types. Despite carefully and specifically selecting for neurons with cutaneous receptive fields on the hands, only 31% of neurons in our sample population were modulated by the RTG task in the manner shown in Fig. 4A, in which only information about object contact was encoded (C).

In fact, a slight *majority* (52%) of neural responses were *Mixed*, encoding both contact and movement-driven sensory information. Examples of these unit responses are shown in Fig. 4C and D. These cells typically had a primary response to either contact (4C) or movement (4D), but were also modulated during all phases of the task, as indicated in the histograms in column iii. Including *Simple movement-driven* (M) responses, fully 63% of the sampled neural population consisted of neurons whose firing rate modulation was driven to one extent or another by hand movement.

The majority of cortical units (55%, 158/285) were primarily *contact-driven* (Cx), however, nearly half of this population (44%, 69/158) simultaneously exhibited significant, but secondary, pre-contact activity (Cm) during the Reach phase of the task. Primarily *movement-driven* (Mx) units were a significant portion of the overall sampled population (39%, 112/285), yet 71% (80/112) of this population also exhibited significant, but secondary, responses (Mc) during haptic task phases. These results demonstrate that single units in SI appear to encode multiple sensory phenomena. Furthermore, the manner in which each of the contact and movement-driven components were manifest in the mean overall firing rate demonstrated that contributions from each modality are linearly superimposed in a simple rate code.

A. *Single Units in SI Encode Multiple Sensory Phenomena*

The major finding of this study is that single units in the hand representation of SI simultaneously encode multiple distinct sensory phenomena in components of their overall firing rate. *Contact-driven* and *movement-driven* responses to a stereotyped behavioral task were distinguished and quantified with the aid of a virtual reality simulation by removing the correspondence between the expected and actual task outcome. The results show that a *majority* of single units in the hand representation of SI with clear cutaneous receptive fields encoded both *contact-driven* and *movement-driven* sensory modalities, which might correspond to tactile and kinesthetic sensibility, respectively. The great variety of individual unit responses observed in our sample of the neural population suggest a broad distribution of response types in SI with varying combinations of *contact-driven* and *movement-driven* response traits. We made some effort to determine whether there were differences in receptive field structure, depth, or chamber coordinates amongst the cell types, but

found only subtle statistical differences rather than any clear distinguishing characteristics.

There are several possible non-exclusive explanations for the presence of movement-related signals in neurons with cutaneous receptive fields. First, as stated above, it is well established that certain peripheral receptors can be modulated by movement, particularly SAII receptors on the dorsum of the hand [17, 27, 28]. In addition, it is known that efference copy has access to somatosensory cortex, at least as measured by fMRI [29]. Thus, it is possible that the modulation we are seeing is arising from corollary discharge from motor cortical areas. It is also known that somatosensory cortical activity can be modulated by attention [30]. Irrespective of the source of the modulation, it remains the case that functionally it is present, and thus carries information relevant to haptics.

As stated at the start of this paper, creating a haptic image requires the integration of signals from multiple sensory modalities, even within somatosensation. There is no *a priori* reason to assign that integration to some remote location in cortex, particularly when the signals are evidently already intermingled. Instead, our view is that this mixed signal is part and parcel of the processing. For example, the mixed signals here may be similar to the area 7a neurons, which have been shown to combine eye position signals and retinotopic signals into "gain fields" [31, 32].

We think the analogy here may be fair. A typical somatotopic map, as described by a homunculus, is a two-dimensional representation of a stimulus location on the skin, much as a retinotopic map is a two-dimensional representation of a stimulus location projected on the retina. However, assigning either of those stimuli, somatic or visual, to spatial coordinates, requires transforming that map by a dynamically changing underlying map. In the case of vision, it would be the orientation of the eyes in the head (or of the head on the shoulders, etc.). In the case of somatosensation, that would be the posture of the arm and fingers.

Thus, the question now arises, what would be the structure of the proprioceptive map that underlies haptic analysis? Understanding the cognitive structure of this map for the hand may be difficult because of the high dimensionality of hand movements. However, a series of studies have allowed us to examine the structure of this map for the arm.

IV. THE STRUCTURE OF THE UNDERLYING PROPRIOCEPTIVE MAP

Although multiple investigators have examined the ability of subjects to identify the spatial location of their hand based on visual and proprioceptive signals [33-54], still relatively little is known about what the spatial map looks like and how it is constructed. As a starting point, we took the observation made by several groups that the patterns of errors observed when subjects were asked to estimate hand location in space appeared to be subject specific [37, 39, 40, 49, 54-56]. While a few studies have reported that errors on estimation of hand location are not uniform across the workspace [50, 52, 57, 58], it occurred to us that a detailed analysis of the patterns of

those errors may reveal something fundamental about the structure of the proprioceptive map that could provide insight into how body sense contributes to haptics.

Constructing and analyzing the spatial patterns of errors as subjects estimate the location of their hand has proven difficult. One could argue that the spatial errors for individual subjects are large and vary substantially from trial-to-trial, making it difficult to capture patterns within and between subjects. Conversely, one might conclude that the complex patterns observed in previous reports were the result of overfitting noisy data sets. Thereby, some researchers discarded this noise as unexplained drift and variability during data analysis [50, 59]. There is another temptation, which is to treat this transformation from a proprioceptive representation of arm posture to a visual representation of hand location as an experimental trick. However, the elegant work by Vindras and colleagues [48] showed that the pattern of errors observed in this transformation could also be seen in movement when subjects were making movements from unseen starting postures. Thus, we thought it worth examining these error patterns in detail.

In order to investigate the spatial structure of the proprioceptive map, we reconstructed and analyzed the patterns of errors that resulted when subjects estimated hand location across a 2D horizontal workspace (Rincon-Gonzalez and Helms Tillery 2011, in review). We extended existing studies by building these error maps for both arms and also separately for when the subjects received tactile feedback. This latter probe was based on the observation that proprioceptive estimation improves when subjects have tactile contact with a surface [42, 44, 52, 60-67].
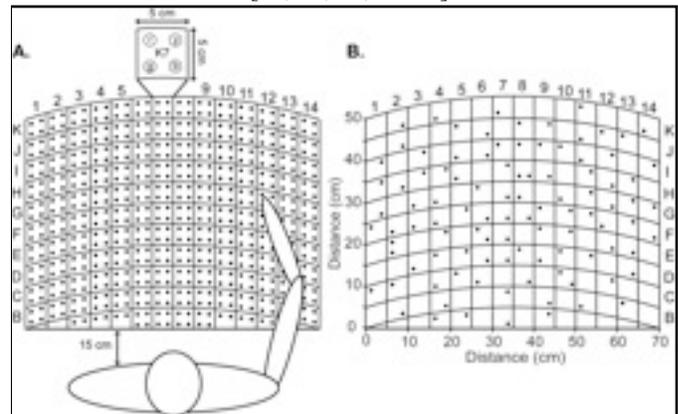

Fig. 5. Proprioceptive mapping setup. A. A grid was marked with rows A-K and columns 1-14. Each square had four colored targets (red, yellow, green, blue). A total of 616 potential targets were located on a 1.25 cm grid. Subjects sad in front of and centered on the grid.. B. An example target set included 100 targets chosen to be evenly distributed on the grid. The target distribution was varied slightly among subjects to account for differences in arm lengths. The same sete of targets was used in the same order for the same subject and was mirrored across the midline for the left hand.

We investigated how proprioception varied across the workspace by testing subjects at 100 different target locations that were evenly distributed throughout the workspace (Fig. 5B). In the task, the experimenter passively moved the

subject's hand to a spatial location on the grid while the subject's eyes were closed. The experimenter either a) applied tactile stimulation by allowing the index fingertip to touch the surface of the workspace for 5 sec or b) as a control, hovered the fingertip 2 cm over the target. After returning the hand to the initial position, we asked the subjects to open their eyes and verbally report the location of their fingertip. The subjects used the column letters, row numbers, and target colors to identify the estimated location (Fig. 5A). Finally, we had 6 right-handed and 3 left-handed subjects complete the test with both hands to investigate whether there was a limb or handedness effect on the structure of the proprioceptive map. To summarize, each subject performed 4 experiments in a blocked design with 100 targets each: one experiment for each hand with tactile feedback, and another experiment for each hand with no feedback.
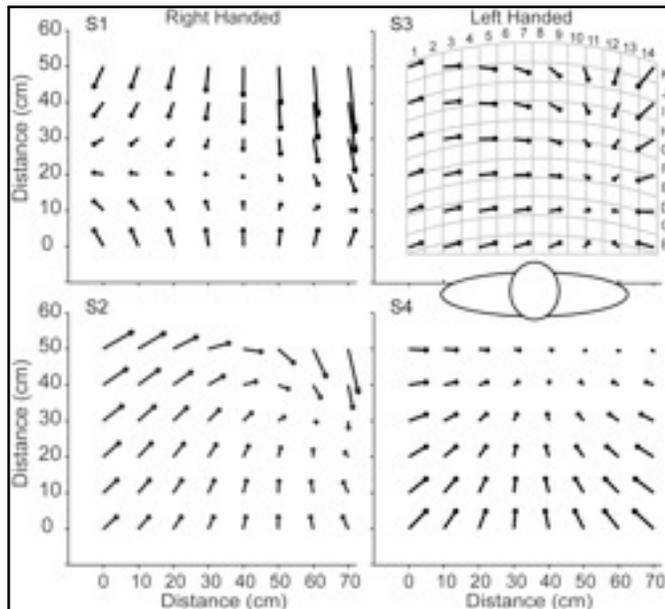

Fig. 6. Proprioceptive map across subjects.   Distribution of errors from two right-handed and two left-handed subjects when using the right hand with tactile feedback. A 4th order multivariate regression model was used to plot the spatial organization of the error vectors by using 48 locations even distributed over the target space. This method allows us to capture spatial regularities without repeated measures.   Each arrow represents the constant error predicted by the regression, with the tail of the arrows at the targets, and the arrowheads at the indicated location

To analyze the structure of the proprioceptive map, we measured the direction and magnitude of the errors. The direction of the errors was analyzed to give us a measure of the similarity of the patterns of errors between arms, conditions, and subjects. In specific, we superimposed the pattern of errors from one experiment onto another (i.e. in Fig. 6 top right panel onto bottom left panel) and measured the resulting absolute angle between each pair of superimposed vector errors. As a control, we performed the same comparison but one set of pattern of errors was randomized. Then, we used the Kolmogorov-Smirnov test to compare the randomized and non-randomized distributions of angles.   A statistical difference between those two distributions indicates that the two patterns of errors are significantly more similar than

would be expected by chance. Similarly, we analyzed the magnitude of the errors to give us a measure of the performance across conditions, subjects and within the workspace using a 4-factor ANOVA: stimulation (Touch, No Touch), hand dominance (right-handed, left-handed), hand used (right hand, left hand), subjects (1-9). We also examined two interactions in particular: stimulation X hand, stimulation X hand dominance.   We used Tukey's HSD posthoc test to identify which factors were responsible for significant effects.

We report three separate findings with respect to the spatial pattern of errors, which indicate that each individual generates a unique but systematic proprioceptive map that depends on where our hand is in space relative to our bodies. The structure of the map is not affected by tactile sensation but subserves tactile perception.

First, the pattern of errors is idiosyncratic; it is statistically no more similar across subjects than one would expect by chance. Fig. 6 shows the errors made by two right-handed and two left-handed subjects at each target location for the right hand in the Touch condition. Each of the four panels represents a complete grid with the midline set at 35 cm. The top right panel shows the alignment of the subjects with respect to the target grid. Each error is represented with an arrow indicating magnitude and direction. The beginning of the arrow indicates the target where the finger was positioned by the experimenter, and the arrowhead indicates subject's estimation of hand location. We compared these maps between all pairs of subjects for each of the four conditions (9 subjects gives 36 pairs X 4 tasks gives 144 total comparisons). Out of those 144 comparisons, only 4 showed a greater than chance degree of similarity at α=.05. These results are in agreement with previous reports in the literature about a subject specific pattern of errors [37, 39, 40, 48, 49, 52, 55, 68]. Although none of these other groups reconstructed and analyzed the resulting pattern of errors, they still commented that each subject made a different set of systematic errors.

Second, the pattern of errors is systematic and stable; subjects exhibited a significantly higher than chance similarity between the pattern of errors across hands and feedback conditions. Figure 7 shows the errors made by one left-handed subject at each target location for both hands and conditions. Note the similarities between the four panels. Although idiosyncratic, all subjects had a resulting pattern that seemed symmetric across hands and tasks. That is, the errors made with the right hand looked like an approximate mirror image of the errors made with the left hand and the errors made with each hand did not seem to vary much. Based on the Kolmogorov-Smirnov test, individuals exhibited a significantly higher than chance similarity between the pattern of errors across hands and tasks. This result was true for all subjects but one. The mirror-image characteristic of the errors between right and left arms indicates that the calculation is performed in the same way for the inputs from the two arms. This mirror-image phenomenon has been previously reported by Haggard et al. 2000, who suggested that hand position is represented in a frame of reference that is shifted toward the reachable workspace of the arm and centered around the

shoulder [69]. Furthermore, the pattern was not affected when subjects were re-recruited 4 months after the initial set of experiments. The right hand was completed first for all subjects in one block of experiments, and then subjects were re-recruited 4 months later to repeat the experiment with their left arms. Since the pattern of errors was conserved across hands, tasks, and time, we suggest that there is one proprioceptive map that is used by both hands over and over.
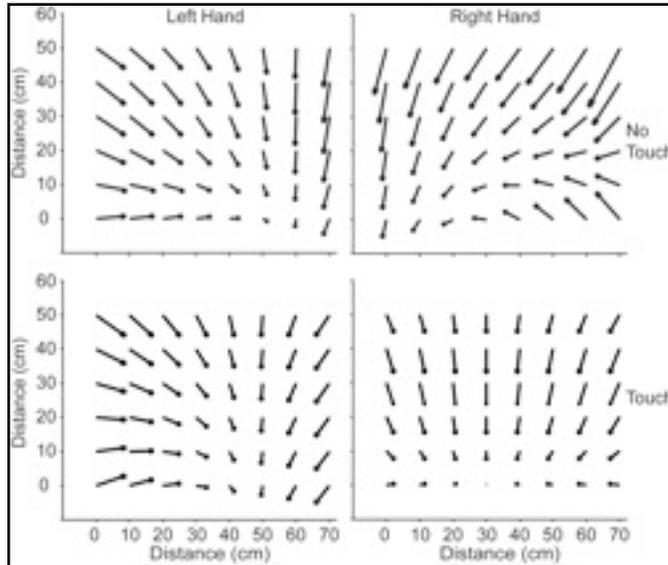

Fig 7. Proprioceptive map with subject but across tasks and arms. The pattern of errors is systematically constant and stable. Distribution of errors from one left-handed subject for both hands with and without tactile feedback.   The resulting pattern looks symmetric across hands and similar across tasks.   Format as Fig. 6

Third, tactile input had an effect on the magnitude of the errors but not on the direction. The post-hoc test revealed that when subjects used their right hand along with tactile feedback, the magnitude of the errors was significantly smaller than with no feedback (Post-hoc Stats: $p<.05$, LSmean (Touch,Right)=4.92, LSmean (NoTouch,Right)=6.05, std error=0.18); this effect is limited to the right hand and not dependent on handedness. On the other hand, adding tactile feedback did not affect the direction of the errors as the pattern of errors between feedback conditions for each hand and subject exhibited a significantly higher than chance similarity. These results suggest that this proprioceptive map is not affected by touch.

This does not necessarily contradict our results that tactile perception is affected by proprioception nor that both modalities are coded in the same neuron.   In fact, all these data taken together suggests that this proprioceptive map plays a modulatory role for tactile maps.   In a certain respect, it's not entirely clear the nature of the underlying process that we are examining here.   It seems counterintuitive to think that the brain would normally extract a representation of hand location in spatial coordinates.   In fact, prior work has argued the opposite, that visually presented targets need to be transformed into kinesthetic coordinates prior to planning a movement (see e.g. [51, 70]).   However, Vindras et al. showed elegantly that if one examines the relationship

between these endpoint error maps and errors in movement, one can clearly see the endpoint errors propagated into point-to-point movement errors [48]. Likewise, Tagliabue and McIntyre have shown that the transformation from kinesthetic to visual is normal part of the sensory processing underlying sensorimotor integration [71]. This argues that whatever the nature of the process that we are probing, it reflects a basic processing of proprioceptive information for various purposes, including planning movement and representing somatosensory inputs.

Examples of this modulatory role can be seen in both electrophysiological and behavioral studies on the role of hand posture on the spatial interaction between vision and touch. Single-cell recordings have shown that the visual responses of visual-tactile neurons move along with the body part being touched as it changes posture, suggesting that these bimodal cells use a body-centered not a retinotopic reference frame [72-76]. Behavioral studies have also investigated the representation of visuotactile space and how these modalities are kept in spatial register with respect to the external world. Studies using the crossmodal congruency task and crossmodal precueing tests (for a review see [77]) have shown that spatial remapping between vision and touch is modulated by the posture of the hands [78-83]. Since the hands were kept out of view, the authors concluded that proprioceptive signals indicated the current position of the hand and thus remapped the visuo-tactile links.

Finally, our results suggest that each individual has his own unique solution to generating a proprioceptive map. The significantly different pattern of errors between subjects suggests that this transformation problem is solved through a learning mechanism. However, these errors were not random. The symmetry of the errors across hands, tasks and time indicates that there is a proprioceptive map that is systematically constructed and used over and over. The mirror-image characteristic of the errors between right and left arms indicates that the calculation is performed in the same way for the inputs from the two arms. Similarly, we found that the non-uniformity of this map is common across subjects. Therefore, we suggest that building and maintaining this map has an element of calibration about it, so that the area where we get the greatest amount of exposure (close to the body, near the midline) is where the calibration will be best, and that the calibration will fall off as you go away from that location. Finally, previous studies and our results suggest that proprioception constructs a stable framework that subserves visual and tactile maps.

These observations pose an interesting puzzle for the use of cortical stimulation to provide haptic feedback.   It is clear that both proprioceptive and tactile information will be required for full haptic perception, but based on our results it's not clear how to use this knowledge in prosthetics.   First, it appears that in large part the two signals are intermingled. How would one combine tactile and movement-related signals in a prosthetic signal. Would the relationship be additive or multiplicative? Since the maps are idiosyncratic, how would one go about establishing that map for a prosthetic arm or

hand? The answer to this question could depend on the neural mechanisms underlying the ongoing calibration. If the calibration takes place normally at the site of the representation (i.e. somatosensory cortex) then it might be okay to just simply assign a mapping and have the system figure it out, whereas if the neural calibration is elsewhere (e.g. cerebellum) and the task is to maintain congruency between two maps, then the system could be stymied by a map with unexpected structure. On the other hand, if, as seems plausible, the self-movement part of the signal comes from efference copy, then the prosthetic device may not need to provide that for haptics. Finally, there is no guarantee that processes which hold for the arm will hold for the hand. Answering these questions for the hand may require a new set of experimental and analytical tools. We hope that grappling with these issues for the arm will transport in some form or other into understanding the interaction of proprioceptive and tactile signals in haptics.

V.   CONCLUSIONS

There are clearly many issues to be resolved in providing somatosensory feedback from prosthetic devices. Examples range from methods and locations to stimulate (peripheral vs. central, microelectrodes vs. optogenetic, etc.). Here we limit our attention to what information should be input to have a viable sensory prosthetic, and in particular, to ask what kinds of information is most important for movement.

Part of this argument will center on whether it is more important to input tactile or proprioceptive information. Elegant work reviewed elsewhere in this issue has shown the value of each of those for having a functional neuroprosthetically controlled hand. Our argument is in fact that, at least for the case of using the hand as a haptic device, it will be crucial to be able to provide both proprioceptive and tactile input about the hand.

One of the overall goals of neuroprosthetics is often stated as creating a "seamless" interface, meaning that the device is structured in a way that allows the brain to incorporate that device into the body image. One might think that having proprioceptive input alone is good enough for that, but in fact even beginning with the earliest deafferentation studies [84, 85], it has been clear that removing sensation from the volar surface of the hand is enough to induce the disuse atrophy that is often attributed to proprioceptive deafferentation. Thus, it is certainly our contention that restoring tactile sensation from the glabrous surfaces ought to be a primary goal in delivering sensation from prosthetic systems. However, our recent work recording in S1 has convinced us that, in addition to tactile, it will be important to also provide proprioceptive information. The form that these two pieces of information will need to take remains unclear. The notion that input to areas 1/3b ought to be cutaneous whereas the input to areas 2/3a should be proprioceptive may be overly simplified. We know that many tactile receptors can be driven by self-motion, and so it strikes us as illogical to think that the two sensations should be kept separate. Our proposal is that the two signals could readily be multiplexed onto the same stimulation sites and thus used to drive tactile image analysis for haptics, although it remains unclear how to combine the signals.

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