Journal of Motor Behavior, Vol. 44, No. 6, 2012

RESEARCH ARTICLE

Interactions Between Tactile and Proprioceptive Representations in Haptics

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ABSTRACT. Neuroprosthetic limbs, regardless of their sophisticated motor control, require sensory feedback to viably interact with the environment. Toward that aim, the authors examined interrelationships between tactile and proprioceptive sensations. Through human psychophysics experiments, they evaluated error patterns of subjects estimating hand location in a horizontal 2-dimensional workspace under 3 tactile conditions. While tactile cues did not significantly affect the structure of the pattern of errors, touching the workspace reduced estimation errors. During neurophysiological experiments, a macaque grasped textured objects using 2 hand postures. Sensory coding showed dependence on both roughness of the manipulandum and posture. In summary, the authors suggest that tactile sensations underlying haptics are processed in a stable spatial reference frame provided by a proprioceptive system, and that tactile and proprioceptive inputs can be encoded simultaneously by individual cells. Such insights will be useful for providing stable, adaptive sensory feedback for neuroprosthetics.

Keywords: perception, stereognosis, neuroprosthetics, feedback

It is now possible to decode motor cortical activity, recorded using a variety of multichannel methods, into a signal that can be viably used to control computer cursors, robotic arms and hands, and neuroprosthetic limbs (Ganguly & Carmena, 2009; Hochberg et al., 2006; Shenoy et al., 2003; Taylor, Tillery, & Schwartz, 2002; Velliste, Perel, Spalding, Whitford, & Schwartz, 2008). Yet while the motor aspect of such prosthetics has progressed well in the past decade, the sensory side remains lacking. Somatosensory prostheses remain rudimentary when compared to auditory and visual prostheses. Neuroprosthetic hands, for example, regardless of the sophistication of their motor control algorithms, are far from providing the kind of sensations that are crucial for manipulating objects and physically interacting with the environment. When grasping an object, the central nervous system (CNS) extracts object features such as size, texture, and also spatial elements based on hand posture and touch receptors activated by the contact. Technology is just now getting to a point to provide those kinds of sensations (Dhillon & Horch, 2005; Fishel & Loeb, 2012; Kuiken, Marasco, Lock, Harden, & Dewald, 2007; Marasco, Kim, Colgate, Peshkin, & Kuiken, 2011; O'Doherty et al., 2011; Su, Fishel, Yamamoto, & Loeb, 2012; Wettels, Santos, Johansson, & Loeb, 2008). Moreover, the same sensory signals are used to monitor the status of ongoing manipulations and are thus crucial for normal motor control (Ghez, Gordon, Ghilardi, Christakos, & Cooper, 1990). It follows that to be able to provide natural feedback from an artificial hand to the user of a neuroprosthetic device, it is necessary to provide both tactile and proprioceptive information. However, there is still a lack of understanding of the interaction between internal representations of proprioception and touch. With an overall goal of recreating such sensations, we have been motivated to study this interaction.

Specifically, how do signals in these channels interact in order to form a unified perception of an object? Recent stimulation work has provided evidence that signals in both proprioceptive and cutaneous neural channels are required for stereognosis (Horch, Meek, Taylor, & Hutchinson, 2011). Proprioceptive and tactile signals provided through their respective channels allowed one amputee to discriminate grasped objects, while information about finger position and object compliance provided solely through tactile channels was not enough to allow object discrimination above chance levels for another amputee. This study highlights the significance of providing meaningful and relevant proprioceptive and tactile signals for stereognosis. Understanding how signals in these two channels are affected by stimuli will be crucial for allowing users of prosthetic devices to identify and manipulate objects.

Despite these clear interactions, proprioceptive and tactile signals are perceived as separate and likely work at different levels of consciousness. When manipulating an object, individuals are immediately conscious of contact through tactile receptors: they can distinguish roughness, temperatures, edges, and surface curvature. By contrast, perception of body posture is much less vivid and works at a more subconscious level (Berlucchi & Aglioti, 2009; Carruthers, 2008). Indeed, these signals are not only perceived differently but they might have different cortical representations. It is well known that tactile signals are represented in a somatotopic manner in the somatosensory cortex; however, such representation has not yet been found for proprioception. Nevertheless, several studies on body representations and individuals' sense of embodiment suggest that there is a stable internal representation that encodes the position of body parts in space and that somatotopic maps interact with such body representations (Berlucchi & Aglioti, 2009; Carruthers, 2008; Longo & Haggard, 2010; Serino & Haggard, 2010). If proprioception is a critical component of this stable representation and tactile signals interact with it, studying how the

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internal representations of touch and proprioception interact at both the perceptual and cortical levels would be critical for understanding how to provide sensation in a neuroprosthetic system.

With experiments probing the internal representation of arm location and the somatotopic representation of touch, we addressed how signals in proprioceptive and tactile channels are affected by stimuli that drive primarily the other channel. We have been examining the interrelationships between these two signals at the psychophysical and neurophysiological levels (Rincon-Gonzalez, Buneo, & Helms Tillery, 2011; Rincon-Gonzalez, Warren, Meller, & Helms Tillery, 2011; Warren & Helms Tillery, 2011; Warren, Santello, & Helms Tillery, 2010, 2011). Having previously reconstructed a map of proprioception based on subjects' perception of arm location in space, we first investigated the effect of tactile signals on the internal representation of arm location at the behavioral level. Second, we extended our previous work separating neural signals arising from tactile and proprioceptive stimulation by examining more directly the interaction of these signals in a single neural channel.

EXPERIMENT 1: HUMAN PSYCHOPHYSICS

Many behavioral studies have provided clues as to the relationship between tactile and proprioceptive signals. Tactile cues have been shown to improve accuracy of pointing movements and estimations of hand location (Jeka & Lackner, 1995; Lackner & Dizio, 1994; Rabin & Gordon, 2004; Rao & Gordon, 2001; Rincon-Gonzalez, Buneo, et al., 2011; Rincon-Gonzalez, Warren, et al., 2011; Tillery, Flanders, & Soechting, 1994), suggesting that tactile signals can enhance proprioception. Conversely, proprioception has been shown to affect aspects of tactile processing in that posture affects the perception of tactile events (Aglioti, Smania, & Peru, 1999; Roberts & Humphreys, 2010; Warren et al., 2011; Yamamoto & Kitazawa, 2001). For example, we have shown that a tactile illusion elicited by electrotactile stimulation to the fingertips could be eliminated by having subjects assume certain hand postures (Warren et al., 2011). It remains unclear how the relationship between touch and proprioception contributes to internal representations such as this, which in turn support and enhance physical interactions with the environment.

One clue as to the structure of this representation comes from the pattern of estimation errors when subjects estimate the location of their unseen hands (Rincon-Gonzalez, Buneo, et al., 2011; Rincon-Gonzalez, Warren, et al., 2011). Strikingly, the patterns of errors on a horizontal surface were constant and systematic across hands, time, and touch conditions. These results suggest long-term stability in the structure of this pattern of errors, which we refer to as the proprioceptive map of the arm. Several other sensorimotor studies have also reported that errors in estimating hand location and end-point movements were constant and systematic (Brown, Rosenbaum, & Sainburg, 2003; Desmurget, Vindras, Grea, Viviani, & Grafton, 2000; Tillery et al., 1994; van Beers, Sittig, & Denier van der Gon, 1998; Wann & Ibrahim, 1992). In fact, research on visuomotor adaptation and motor learning has provided some insight into the stability and plasticity of this system: proprioception has been shown to adapt after visuomotor adaptations and motor learning (Cressman & Henriques, 2011; Mattar, Nasir, Darainy, & Ostry, 2011). Thus proprioception is stable to small everyday perturbations but flexible to long-term adaptations.

Here, we further examined the role of tactile signals on the proprioceptive map by incorporating electrotactile feedback as one of the experimental conditions. To examine this issue, we reconstructed and analyzed the pattern of errors that resulted when subjects estimated the location of their unseen hand on a two-dimensional horizontal workspace. Subjects made these estimates in three tactile conditions: (a) touching the surface of the workspace (touch [T] condition), (b) receiving electrotactile stimulation without touching the surface (electrical [E] condition), or (c) receiving no stimulation at all (no touch [NT] condition). We have previously reported that tactile signals (touching the surface of the workspace) did not affect the structure of the pattern of estimation errors (Rincon-Gonzalez, Buneo, et al., 2011). In the experiments described here, we asked whether the completely artificial sensation elicited with electrotactile stimulation could induce the effects we observed from the interaction between the proprioceptive and tactile sensing modalities, or whether the natural sensation arising from the contact of the fingertip with the surface was central to this interaction.

Method

In our psychophysical experiments, we reconstructed and analyzed the pattern of errors that resulted when subjects estimated their hand location across a two-dimensional horizontal workspace. The setup and analyses have been previously described (Rincon-Gonzalez, Buneo, et al., 2011) and are briefly summarized here.

According to a protocol approved and monitored by the Arizona State University Institutional Review Board, seven right-handed subjects participated in an experiment with three tactile conditions in which their right hand was passively moved by the experimenter to one of 100 targets on a horizontal grid while their eyes were closed (Figure 1A). At each target location, one of three tactile conditions was applied before passively returning the subject's hand to the resting position. Then, subjects were asked to open their eyes and verbally report the location where their hand had just been at by using the row letters, column numbers, and target colors (see Figure 1A). In the NT condition, the extended index finger was held by the experimenter 2 cm above the target for 5 s. In the T condition, the subject's index finger lightly touched the surface of the grid at the target location for 5 s. In the E condition, electrical stimulation was applied to the fingertip while the finger was held above the target as in the NT condition (see Figure 1B). For this experimental

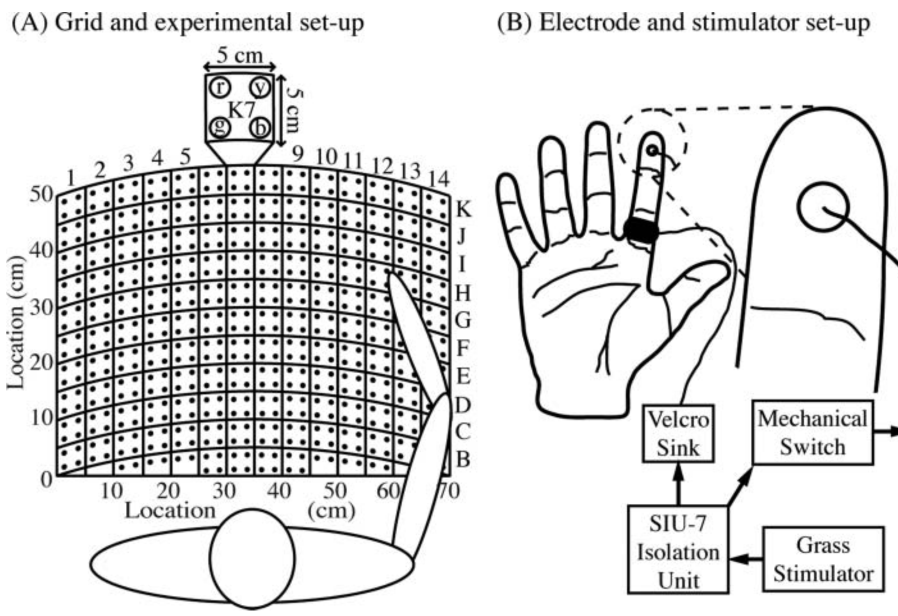

FIGURE 1. Psychophysics experiment setup. (**A**) Horizontal surface grid used for the three experimental conditions: No touch, touch, and electrical. Each square in the grid was labeled with a row letter (A–K), a column number (1–14), and four colored circles (red, green, yellow, and blue). A total of 616 targets were equally spaced from each other by 1.25 cm. (**B**) Diagram of stimulator connections and electrode setup for the electrical stimulation condition. A single round (3.2 mm diameter) electrode was centered on the volar aspect of the index finger on the distal phalanx and a reference electrode centered on the volar aspect of the same finger on the proximal phalanx.

condition, subjects were outfitted with a 3.2 mm diameter electrode centered on the volar aspect of the index finger on the distal phalanx and a reference electrode centered on the volar aspect of the same finger on the proximal phalanx. The waveform parameters were chosen (75 Hz, 0.5 ms duration) to maximize detectability. Prior to beginning the electrical condition, subjects' thresholds were determined to be the minimum current level at which the stimulus felt electrical in nature. Subjects were instructed to report if they stopped feeling the electrical stimulation during the experiment, at which point the current amplitude was adjusted accordingly. This E condition was included to control for the fact that the proprioceptive information associated with NT and T were not completely equivalent. That is, the E condition provided tactile feedback while providing the same proprioceptive information as in NT. In each condition, no feedback was provided as to the actual location of the target. Each subject performed three experiments with the same set of 100 targets.

To analyze the structure of the pattern of errors, we measured the direction and magnitude between the actual and estimated target locations, and then reconstructed the resulting pattern of errors as vector fields (see Figure 2). We measured the effect of the tactile conditions on the estimation errors by comparing two vector fields at a time. To this end, we first quantified the similarity of the resulting vector fields between two tactile conditions using a vector correlation (VC) method (Buneo, 2011; Rincon-Gonzalez, Buneo, et al., 2011). This method performs a pairwise correlation of two vector fields (e.g., NT vs. T or Figure 2A vs. Figure 2B) in which each pair of vectors at one target location is correlated. This VC method also accounts for any scaling, rotational, or reflectional relationship between the two vector fields. As a control, we randomized the spatial location of each of the vectors on one vector field before performing the correlation analysis between the two vector fields. In other words, we shuffled the vectors in Figure 2A before performing the correlation between this vector field and that in Figure 2B. In this analysis, a negative correlation coefficient indicates that the relationship between the two vector fields being compared is better explained by a reflection of one of the vector fields, while a positive correlation indicates that the relationship between the two vector fields is better explained by a rotation of one of the vector fields. To further examine the similarities between fields, we also analyzed the direction of the errors using a Kolmogorov-Smirnov (KS) test, which measures whether two cumulative distributions are different from each other. In this analysis, we superimposed the pattern of errors from two tactile conditions for one subject, in the same way as explained previously, and measured the resulting absolute angle between each pair of superimposed vector errors. As a control, we used the same data-shuffling technique explained previously. Then, we compared the nonrandomized to the randomized (control) cumulative distribution of angles, in which a statistical difference indicated that the two nonrandomized patterns of errors were more similar than

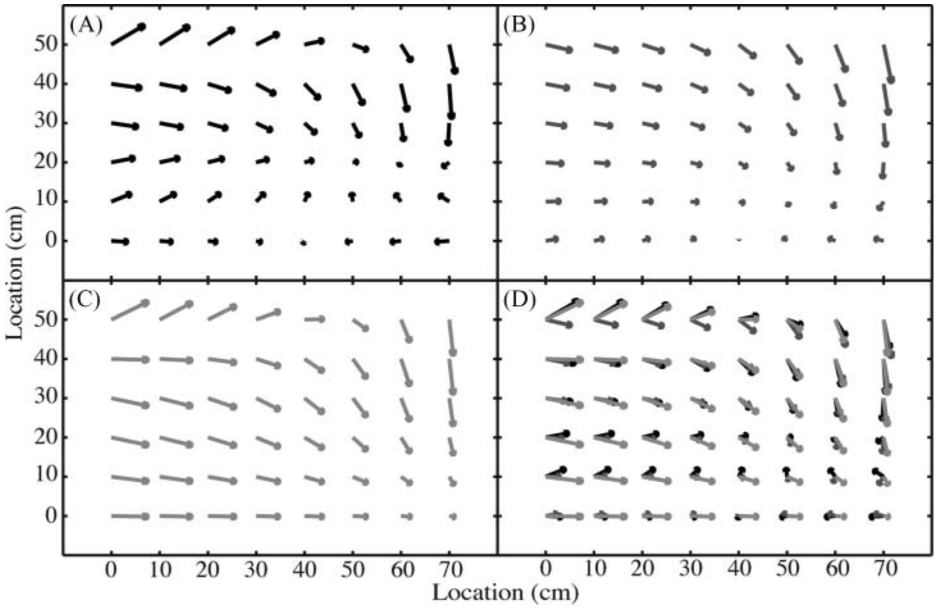

FIGURE 2. Similarity of pattern of errors across tactile conditions. Distribution of errors from one exemplary subject for the three experimental conditions. (**A**) Vector field of estimation errors for the no touch condition, (**B**) for the touch condition, and (**C**) for the electrical condition. (**D**) The three vector fields from A, B, and C superimposed.

would be expected by chance. Finally, we used repeated measures analysis of variance (ANOVA) with three levels (NT × T × E; $df = 2099$) where we pooled the 100 estimation errors for each of the seven subjects ($n = 700$ trials per tactile condition), to analyze the effect of tactile condition on the magnitude of the estimation errors. We performed pairwise comparisons with the Bonferroni correction as a post hoc test.

Results

We report that tactile cues did not significantly affect the structure of the proprioceptive map but touching the grid reduced the magnitude of the estimation errors. Figure 2 shows the resulting pattern of errors for one representative subject on the three experimental conditions. Panel A corresponds to the NT condition, panel B to the T condition, panel C to the E condition, and panel D shows the three superimposed vector fields. This exemplary figure shows that the resulting pattern of errors from the three tactile conditions have a similar spatial structure. The figure also shows that the magnitude of the errors under the T condition is slightly smaller than that of the other two conditions. The statistical analyses support this observation. Table 1 shows the results from the KS test and VC analysis for the comparisons between tactile conditions for each subject. The values under the KS column represent the p values and the values under the VC columns represent the correlation coefficient for the nonrandomized and

TABLE 1. Test of Similarity Between Tactile Conditions (No Touch [NT], Touch [T], Electrical [E])

	NT-T			NT-E			T-E		
Subject	KS: p	VC: ρ	VC_c: ρ	KS: p	VC: ρ	VC_c: ρ	KS: p	VC: ρ	VC_c: ρ
1	.001	0.46	−0.07	.010	−0.37	−0.07	<.001	0.40	0.03
2	.007	0.39	−0.07	.017	0.15	0.03	.202	0.31	−0.03
3	<.001	0.63	−0.03	<.001	0.54	0.04	.002	0.50	0.03
4	.001	0.42	−0.03	.002	0.37	−0.06	.001	0.40	−0.05
5	.001	0.39	0.06	.010	0.39	−0.05	.013	0.38	0.05
6	.001	0.43	0.05	.006	0.35	−0.05	.005	0.34	0.05
7	<.001	0.54	0.04	<.001	0.63	0.10	<.001	0.56	0.03

Note. Resulting p-values from the Kolmogorov-Smirnov (KS) test and resulting correlation coefficients (ρ) from the Vector Correlation analysis for the non-randomized ("VC") and control ("VC_c") comparisons.

randomized (control) comparisons. Under the VC analysis, all vector fields were highly correlated with one another as compared with the control condition, suggesting that touch and electrical stimulation had no effect on the overall structure of the pattern of errors. The KS test also supported this conclusion. All comparisons but one were significantly more similar than would be expected by chance ($\alpha = .05$). Finally, the repeated measures ANOVA test determined that the mean estimation error differed significantly across tactile conditions, $F(2, 1398) = 12.61, p < .0001$. The post hoc tests using the Bonferroni correction revealed that solely touching the grid resulted in significantly smaller estimation errors than in either E or NT conditions, while the E condition was not significantly different from the NT condition (NT vs. T: 5.76 ± 0.14 vs. $5.06 \pm 0.12, p = .0001$; NT vs. E: 5.76 ± 0.14 vs. $5.80 \pm 0.13, p = 1$; T vs. E: 5.06 ± 0.12 vs. $5.80 \pm 0.13, p = .00002$). Despite this change in accuracy, the overall structure of the map was independent of these tactile conditions.

EXPERIMENT 2: NEUROPHYSIOLOGY

Neurophysiological studies can help us further understand and complement the relationship between proprioceptive and tactile signals that we report at the behavioral level. Neural activity in response to tactile and proprioceptive stimulation has been extensively examined in somatosensory cortical areas (Bensmaia, Denchev, Dammann, Craig, & Hsiao, 2008; Pei, Denchev, Hsiao, Craig, & Bensmaia, 2009; Pei, Hsiao, Craig, & Bensmaia, 2010, 2011; Rincon-Gonzalez, Warren, et al., 2011; Simons, Chiu, Favorov, Whitsel, & Tommerdahl, 2007; Tommerdahl, Favorov, & Whitsel, 2010). These systematic and controlled studies have shown remarkable details in the responsiveness of primary somatosensory cortex (S1) neurons during passive stimulation. However, studying the interaction between proprioception and tactile sensing requires both movement of the fingers and cutaneous contact such as occurs in stereognosis. Evidence for interaction of these signals has been seen in naturalistic grasp tasks (Gardner, Ro, Debowy, & Ghosh, 1999). A key difficulty with this approach though is that it is difficult to either control the pattern of skin deformation induced by the grasp, or to have detailed knowledge of that mechanical interaction. Thus, it remains unclear how well the responses of somatosensory neurons during natural grasp can be predicted by knowing the structure of their receptive fields. For example, during naturalistic movements, the firing patterns of neurons appear to contain information about hand movement, object identity, and even the planned manipulation of an object, in addition to information about contact (Gardner et al., 1999; Rincon-Gonzalez, Warren, et al., 2011; Ro, Debowy, Ghosh, & Gardner, 2000). This is certainly to be expected from the coupling between, for example, tactile systems and movement, as well as the convergence observed in ascending systems (Johansson & Flanagan, 2009). However, tactile and proprioceptive modalities are often treated as separate signals, which are competing for or polluting specialized channels. It is our contention that the intermixing of signals related to contact and those related to hand proprioception is crucial to creating perceptual representations of objects. Indeed, many studies have reported neurons in somatosensory cortex having both cutaneous and proprioceptive receptive fields (Cohen, Prud'homme, & Kalaska, 1994; Rincon-Gonzalez, Warren, et al., 2011; Ro et al., 2000; Weber et al., 2011). The approach that we have taken is to generate tasks that manipulate posture and contact in controlled and separable ways, expecting to see an effect of posture on the neural responses to tactile stimulation.

Method

We further probed the relationship between tactile and proprioceptive perceptions with neurophysiology (the data reported here were first reported in Naufel, 2011). We did so by evaluating single-unit neural activity in somatosensory cortex during haptic and naturalistic tasks. The setup and analyses have been previously described (Naufel, 2011) and are briefly summarized here. According to a protocol approved and monitored by the Arizona State University Institutional Animal Care and Use Committee, a male rhesus macaque (Macaca mulatta; monkey K, 7.2 kg) was trained to perform a single-handed reach-to-grasp task while the nonworking arm remained restrained. Two target objects outfitted with textured grip plates (100% cotton cloth or 60-grit sandpaper) were presented by a robotic arm (VS-6556-G, Denso Robotics, Long Beach, CA). The subject was required to use a precision grip to grasp the object, which was instrumented with two load cells (Nano17 force/torque sensor, ATI Industrial Automation, Apex, NC). Forces and torques in the *x*, *y*, and *z* directions were recorded for the thumb and finger separately. The basic experimental setup is shown in Figure 3.

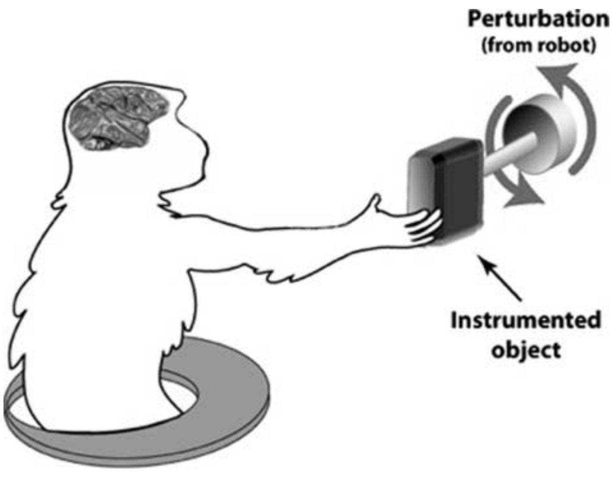

FIGURE 3. Neurophysiology experiment setup. During each experimental session, the monkey executed a reach-to-grasp task in which a target manipulandum was grasped during a static and perturbation phase.

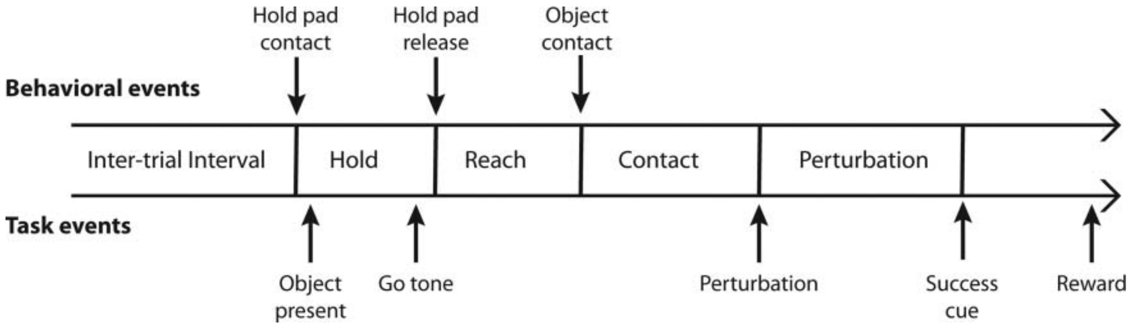

FIGURE 4. Task and behavioral events timeline. Each task trial was divided into four epochs for analysis. The Hold Interval, during which the subject placed its hand on a hold pad, provided baseline neural data. The Reach Interval specified the transition period between hold pad and grasping the manipulandum. The Contact Interval was when the subject's hand was in contact with the manipulandum, but did not include the perturbation, which was reserved for the Perturbation Interval.

A timeline with each of the tasks and behavioral events performed by the subject is presented in Figure 4. The subject initiated each trial by putting its right hand on a hold pad located at mid-abdominal height. This signaled robotic presentation of the target object in the monkey's workspace. The object was presented with either a presentation angle of zero, meaning that the object was oriented vertically, or rotated negative 30° to encourage pronation. The hold interval was defined as the half-second prior to hold pad release, and was used to record baseline data. The subject was free to reach for the object after an audible go cue, and had 2 s after leaving the hold pad to make contact with the object. The interval from when the animal departed the hold pad until object contact was detected constituted the reach interval. First contact with the object was registered when a minimum torque threshold of 0.2 N m was recorded by a sensor on the end effector of the robot (Mini85, ATI Industrial Automation, Apex, NC). After a randomized interval between 0 and 1 s following object contact, the perturbation phase of the task began. This interval, from object contact until onset of a brief rotational perturbation, constituted the contact interval.

The perturbation phase consisted of three perturbation conditions, which were randomly presented: (a) counterclockwise rotation (as viewed by the subject) of the object by 15° and then back, (b) clockwise rotation, and (c) no rotation. In some sessions, translational perturbations were used instead of rotational ones, in which the manipulandum was displaced either 5 mm to the left or right and then returned to the starting position. From the onset of the first perturbation to the end of the trial was the perturbation interval. A successful trial required the monkey to maintain contact with the object throughout the perturbation phase, and was signaled by an audible success cue and juice reward. No audible cue or juice reward was delivered for failed trials. Full data for a cell included 2–5 blocks for each of the two textures, which were alternated during the object presentations. Each block consisted of six trials for a certain texture that included a different combination of object presentation angles and type of perturbation (2 object presentation angles × 3 types of perturbations).

Single-unit neural recordings were made during the execution of this task using a Plexon Multi-Acquisition Processor (Plexon Inc., Dallas, TX). The head was restrained throughout each experimental session. Placement of a vertically oriented recording chamber and subsequent electrode penetrations were based on coregistered magnetic resonance imaging and computed tomography data as per the methods described in McAndrew, Lingo VanGilder, Naufel, and Helms Tillery (2012). The target cortical regions were in primary somatosensory cortex, specifically the hand representations in areas 1 and 3b. Recording depths, relative to the depth seen for the first recorded neuron, ranged from the surface to 5 mm along the electrode track. Cutaneous receptive fields were found by stimulating the monkey's hand with a paintbrush or gloved fingers. Cells with receptive fields found to be on other parts of the body were omitted from this analysis, while cells with no clear receptive fields were kept if they were in close proximity to other cells with receptive fields on the hand.

Results

Timestamps for the firing of each isolated cell were recorded and binned into time intervals of 20 ms. These data were subsequently smoothed with a triangular convolution kernel to get a final instantaneous firing rate (Nawrot, Aertsen, & Rotter, 1999). The convolution was applied prior to dividing the dataset into the intervals of interest: hold, reach, contact, and perturbation. The mean firing rates for these phases of the task were isolated for successful trials, which were grouped according to category: all categories, cotton, 60-grit sandpaper, zero presentation angle, negative 30 presentation angle. 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 comparisons of data for each

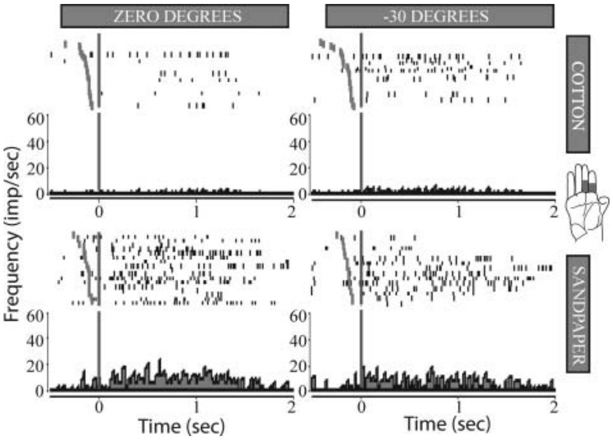

FIGURE 5. Rasters for an exemplary cell tuned to texture. In this case, the firing rate of the cell is statistically significant when the finger is in contact with the sandpaper surface (Figure 5 borrowed with permission from Naufel, 2011).

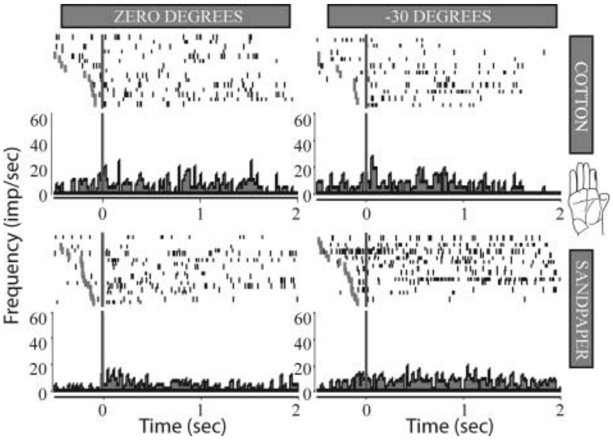

FIGURE 6. Rasters for an exemplary cell tuned to posture. In this case, the firing rate of the cell was statistically significant when the target object was rotated, and the hand was pronated. (Figure 6 borrowed with permission from Naufel, 2011).

cell were evaluated using a one-way ANOVA at the 95% confidence level ($\alpha = .05$). The ANOVA had three levels and examined main effects of task phase, texture, and posture. Cells were classified as having texture-tuned responses if there was a statistical difference in the firing rates between trials for different textures. Cells were classified as having posture-tuned responses if there was a statistical difference in the firing rates between trials for different object presentation angles. Cells with mixed responses had statistical differences in the firing rates for both texture-variable and posture-variable trials. Of the 167 cells that were isolated in monkey K for this experiment, 42 were used in this study's statistical analysis. Of these, 37 units (88%) exhibited statistically significant task-related activity ($p < .05$).

Figure 5 shows rasters for an exemplary cell that had task-related activity and was tuned to texture ($p = .0134$). A receptive field was not identified for this specific cell. However, another cell recorded about 300 μm deeper in the same experimental session had a receptive field on the proximal segments of the volar aspect of the index and middle finger (see inset to right in Figure 5). Firing rates for contact with the sandpaper texture were distinctly greater than those for cotton for this particular cell. Twenty-two of the 42 units described here had significant modulation with texture. Figure 6 shows exemplary rasters for a cell that had task-related activity and was tuned to orientation ($p = .0040$). This cell's receptive field was on the radial side of the distal segment of the index finger (see hand figure on right). Sixteen of the 42 neurons reported here had statistically significant tuning to object orientation. Ten of the cells (24%) exhibited statistically significant tuning to both texture and orientation ($p < .05$). Figure 7 shows exemplary rasters for such a cell ($p = .0011$ for texture, $p = .0062$ for orientation). This cell did not have an identifiable receptive field, although a cell that was found about 700 μm deeper along the electrode track in the same session had a receptive field on the volar aspect of the index and middle fingers.

GENERAL DISCUSSION

The results presented here capture what we believe are two key elements in this process of interpreting tactile and postural sensations to create a representation of the physical world. First, spatial problems come with a frame of reference. In the proprioceptive task, we observed that when the natural

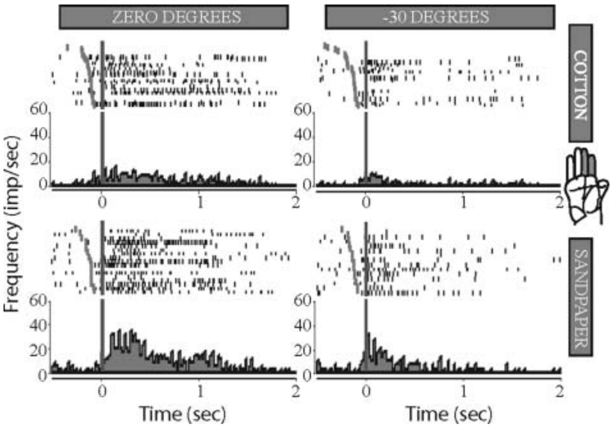

FIGURE 7. Rasters for an exemplary cell that is tuned to both texture and posture. In this case, the firing rates are statistically significant for each combination of texture and object orientation. (Figure 7 borrowed with permission from Naufel, 2011).

tactile apparatus is engaged, the accuracy of spatial estimates is improved even though the overall structure of the estimates is not changed. This suggests that proprioception provides a stable frame of reference for somatic sensation. While proprioception is a three-dimensional spatial process existing in an intrinsic reference frame, tactile perception has only the two-dimensional somatotopic map provided by the skin to serve as a coordinate system. These intrinsic reference frames can be transformed into external reference frames when the tactile problem is essentially spatial. Second, the coding of surface characteristics of objects is modulated by spatial parameters and both tactile and proprioceptive information can be encoded in individual S1 cells. Here we observed that the coding of roughness is dependent not only on the intrinsic roughness of the grasped object, but also on the orientation of the hand during the grasp. Postural changes elicited changes in the firing of primary somatosensory cortical neurons with cutaneous receptive fields. This is in direct analogy to our previously reported results that the coding of object contact is not fully specified by just the contact, but that the movement of the hand and arm also contributed to the firing of these neurons (Rincon-Gonzalez, Warren, et al., 2011). Thus, our view is that the interaction between deep and cutaneous senses takes place in a reference frame that is determined by the proprioceptive system.

Tactile Input Impacts, But Does Not Disrupt, Proprioceptive Representations

In previous studies, we reported that touch did not affect the pattern of errors for either hand but it did decrease the magnitude of the errors when using the right hand only (Rincon-Gonzalez, Buneo, et al., 2011; Rincon-Gonzalez, Warren, et al., 2011). We concluded that the spatial structure of proprioception was subject-specific, stable across hands, tactile conditions, and time. Here we report that electrotactile stimulation did not affect the direction or magnitude of the estimation errors. Therefore, all these results taken together suggest that subjects estimate the location of their hands using a stable proprioceptive representation of their arms, one that is not spatially affected by touch. This conclusion is in agreement with the idea that one of the features of the internal body representation is to be conservative and stable (Carruthers, 2008; Ivanenko et al., 2011).

Although the direction of the errors did not change in any of the three conditions, the T condition resulted in a decrease of the error magnitude. There were two main differences between the T and E conditions that could account for this observed effect. First, in the NT and E conditions the experimenter held the subject's hand 1–2 cm above the target while in the T condition the experimenter lowered the hand until it made contact with the workspace. It is possible that the muscular activity between these two manipulations was different. However, we do not believe it was a major difference as the experimenter held on to the subject's hand throughout each trial for the three conditions. It is also possible that the proprioceptive information was different between these two positions. Although we did not control the arm posture at each target, it is unlikely that the 1 ± 1 cm difference made a significant difference in arm posture. Second, the tactile feedback provided by touching the table in the T condition and the one provided by the electrotactile stimulation were perceived differently. Touching the finger to the workspace activated mechanoreceptors on the skin while electrotactile stimulation to the surface of the skin probably activated the mechanoreceptors' afferents. Previous results had suggested that the direction of shear on the fingertip was an important component of the effect of tactile input in reducing error in estimating hand location (Lackner & DiZio, 2000). This seemed implausible because in many of the tasks, the shear was either nominal, or always directed along the long axis of the finger, thus providing no clear spatial information that varied with hand location. Here we reasoned that if shear on the fingertip were the key element, removing the shear while providing tactile stimulation should result in a return to the magnitude of error observed with no tactile input since electrotactile stimulation would provide tactile stimulation with no deformation of the skin.

What Is Being Processed in the Hand Area of S1?

The single-unit data suggest that primary somatosensory cortex is engaged in the process of extracting and synthesizing a variety of object features. While cells were identified that responded significantly differently to only one experimental variable, either texture or object orientation, it is notable that a quarter of the neurons analyzed to date in this study show tuning to both object orientation and texture.

That these cells contain a combination of coding properties is a physiological feature that could be useful to the development of neuroprosthetics. If single cells can encode multiple sensory modalities, it may ultimately be possible to deliver a wider range of sensory information by focusing on object features rather than receptive field structure, potentially reducing the number of stimulation channels required to provide a tactile representation.

This is also suggested by the difference between the sensations elicited by isolated, passive afferent stimulation, which have been vividly described (Ochoa & Torebjörk, 1983), and those sensations elicited when moving or interacting with the environment during everyday tasks. When single afferents are passively stimulated, subjects describe such sensations as punctate pressure, or localized flutter. Despite the fact that subjects can imagine natural stimuli, which would evoke such sensations, these types of sensations are not typically experienced when we are interacting naturally with the environment. In this case, it is the felt characteristics of the object that are vivid (e.g., the smoothness and coolness of a glass, the texture of a desktop, the keys amidst the coins in a pocket), even though the stimulus is being delivered to the nervous system by the same afferents. For other afferents, notably those associated with proprioception, direct stimulation does not appear to generate any clear sensation. Likewise, the perceptions elicited simply by the movements of the hand in isolation may be less vivid. Nonetheless, those sensations are likely critical for decoding the accompanying tactile signals. Percepts of objects arise from a synthesis of all the information provided by the sensory apparatus.

Our preliminary conclusions from this study are necessarily tentative. Most obvious to note is that the reach-to-grasp task is relatively unconstrained. While the animal was trained to grasp the target object with the index and thumb, there was no other restriction on hand motion, largely so that we could encourage naturalistic grasps. While we consider this a strength, the possibility for high variability in grasp parameters makes interpretation of the results more tentative. Still, even in a relatively unconstrained task, it is encouraging that we are able to detect changes in firing that were dependent both on contact and hand posture. Other somatosensory experiments (Pei et al., 2010, 2011) are elegantly designed for control and consistency, and do well to categorically quantify what is going on in S1 during sensation. In such experiments the subject's hand is held in place while stimuli are passively presented on the fingertip. However, in individuals' interactions with the world, they do not wait for sensations to come to them, but rather are actively reaching out to haptically explore their environment. Individuals reach out to manipulate cloth between fingers to gauge texture and thickness, and swipe a finger along a table to identify its subtle topography. Individuals' somatosensory understanding of the world is not passive but quite contingent on such active interrogations of their environment.

What Does the Psychophysics Suggest About the Combination of Kinesthetic and Tactile Signals?

It is a standing observation that contact of the fingertip with a surface improves performance on a variety of spatial and dynamic tasks, provided that surface is assumed to be stable (Jeka & Lackner, 1995; Lackner & Dizio, 1994; Rabin & Gordon, 2004). This is perhaps not surprising, as the external environment has more spatial stability than individuals' bodies. It is puzzling, though, that touching a finger to a surface (even if contact is achieved through passive movement of the hand by an experimenter) should reduce the error in knowing where that finger is in space (Rincon-Gonzalez, Buneo, et al., 2011; Rincon-Gonzalez, Warren, et al., 2011; Tillery et al., 1994). The location in space of the index finger, for example, depends on the state of a serial chain of joints. Touching the finger to a surface does not have any clear ramifications for joint angle sensors when posture remains constant. Instead, it appears that touching the skin invokes additional somatosensory processing.

One possibility is that touching the surface changes the estimation task itself. When the hand is held over some location, estimating the location of the fingertip is a truly proprioceptive problem: information about the states of the joints must be derived from a variety of sensors, and that information integrated to estimate the location of the fingertip relative to the rest of the body. Once the finger is touched to a surface, individuals are no longer estimating the location of the fingertip but are rather estimating an external location in space and the properties of the surface being touched by the finger. While the sources of information are largely the same, the processing appears to be different: the nervous system is now explicitly processing the signals to determine the spatial location of the hand, all the while assuming a stable set of cues in the environment. That is, with contact between the fingertip and the environment, the estimation task transitions from one of posture in an intrinsic reference frame to one of spatial location of the hand in an extrinsic reference frame.

This is all relevant to stereognosis, which is necessarily an integrative process: determining both the surface characteristics of a grasped object and the spatial relationships between those characteristics requires input from receptor systems which convey contact as well as hand configuration. The recordings described here of S1 responses to textures at different orientations, along with our previous report of S1 responses to elements of grasp as well as contact (Rincon-Gonzalez, Warren, et al., 2011), contribute insight to this process. This interaction between signals for proprioception and touch is to be expected from both the requirement of integration for stereognosis and from the observed convergence and divergence in the ascending lemniscal pathways (Johansson & Flanagan, 2009). Determining how those signals are processed to produce coherent tactile images of grasped objects, however, remains a nontrivial challenge.

Thus, we show here important insights into the interaction between proprioception and touch. First, the observation that proprioceptive estimates of hand position are spatially robust to tactile conditions indicates that somatospatial problems utilize a stable frame of reference, which is provided by the proprioceptive system. Second, our work with monkeys grasping textured surfaces in different orientations shows that the neural coding of surface characteristics of objects can be modulated by spatial parameters including the orientation of the grasped object. We propose that the tactile sensations that underlie haptics are processed in a reference frame that is provided by the proprioceptive system. While the spatial structure of the proprioceptive map is essentially stable, the representations underlying object perception depend on posture, and are thus likely dynamic. Elucidating the interactions between tactile and proprioceptive representations will be useful for understanding the consequences of dysfunction in each of the two systems, and will be necessary for providing both stable and adaptive sensory feedback in neuroprosthetic applications.

ACKNOWLEDGMENTS

The authors thank Rachele Valente for help with the primate experiments. This work supported partly under NSF Grant No. 0932389 (Santos), and NIH R01-NS050267 and R01-NS063372-02S1 (Helms Tillery).

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Received February 29, 2012
Revised September 18, 2012
Accepted October 30, 2012