Tactile Information Processing in Primate Hand
Somatosensory Cortex (S1) during Passive Arm Movement

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Abstract

Motor output mostly depends on sensory input, which also can be affected by action. In order to further our understanding of how tactile information is processed in the primary somatosensory cortex (S1) in dynamic environments, we recorded neural responses to tactile stimulation of the hand in three awake monkeys under arm/hand passive movement and rest. We found that neurons generally responded to tactile stimulation under both conditions and were modulated by movement: with a higher baseline firing rate, a suppressed peak rate, and a smaller dynamic range during passive movement than during rest, while the area under the response curve was stable across these two states. By using an information-theory based method, the mutual information between tactile stimulation and neural responses was quantified with rate and spatial coding models under the two conditions. The two potential encoding models showed different contributions depending on behavioral contexts. Tactile information encoded with rate coding from individual units was lower than spatial coding of unit pairs, especially during movement; however, spatial coding had redundant information between unit pairs. Passive movement regulated the mutual information, and such regulation might play different roles depending on the encoding strategies used. Thus, the underlying mechanisms of our observation most likely come from a bottom up strategy, where neurons in S1 were regulated through the activation of the peripheral tactile/proprioceptive receptors and the interactions between these different types of information.

Key Words: neural encoding and decoding, tactile information, sensory gating
INTRODUCTION

In order to live and thrive, animals need to transmit sensory information across many levels (from peripheral receptors to the spinal cord, dorsal column nuclei, thalamus on to the cortex) and perceive it efficiently and act promptly. But how sensory information is encoded and processed in the brain in a dynamic environment is still unclear. It is commonly observed that neural activities across the sensory pathway show behaviorally dependent modulation (Dubner 1988). Neurons in S1 can be activated through the stimulation of the peripheral tactile receptors by movements themselves (Cohen et al. 1994; Fetz et al. 1980; Lin and Sessle 1994; Soso and Fetz 1980) or by centrally generated movement-related signals in S1 (Bernier et al. 2009; Chapman and Ageranioti-Belanger 1991; Christensen et al. 2007; Gardner et al. 2007; Jiang et al. 1991; Prud'homme and Kalaska 1994), and even by simple observation of movement (Voisin et al. 2011). On the other hand, this vast variable sensory information needs to be regulated or filtered in order to extract the relevant information from the brain to make a proper action, thus it is often suppressed or gated by movement (Chapin and Woodward 1982; Cromwell et al. 2007). This sensory gating can be through lateral inhibition, top down or bottom-up strategies at the spinal (Ghez and Pisa 1972; Seki and Fetz 2012), brainstem (Furuta et al. 2008), thalamus (Aguilar and Castro-Alamancos 2005; Lavallee et al. 2005; Urbain and Deschenes 2007) and cortical levels (Jiang et al. 1991; Urbain and Deschenes 2007). The gating also demonstrates dependence on either behavior or on the modality of the stimuli (Chapman et al. 2002; Cohen et al. 1994; Meftah et al. 2009; Meftah et al. 2002). Sensory information is more strongly gated during active movement than passive movement (London and Miller 2012; Seki and Fetz 2012), while gating is also observed during the preparatory or initiation period before movement onset (Nelson et al. 1991b; Ogata et al. 2009; Seki and Fetz 2012).

Traditionally it is assumed that sensory information is represented by the firing rate of individual neurons (Adrian 1926) or of populations of neural ensembles (Fernandez et al. 2000). However,
the interactions between neurons might also carry important information for neural coding (Salinas and Sejnowski 2001). Correlation/synchronization has been observed during demanding or sensory selective processing tasks (Alloway et al. 2002; Panzeri et al. 2001; Roy et al. 2007; Steinmetz et al. 2000), which may relate with cognition or attention, but it has also been found in S1 under both anesthetized (Reed et al. 2008) and quiet awake conditions (Song et al. 2013), thus correlated spiking might play a role in information processing in the cortex (Nicolelis et al. 1998; Niebur et al. 2002; Panzeri et al. 2001; Reed et al. 2008; Roy et al. 2007; Salinas and Sejnowski 2001; Steinmetz et al. 2000). However, which encoding strategy is utilized by the brain is still an open question, how the correlation arising from different sources contributes to tactile encoding is not well understood, and how this correlated firing is regulated/gated by movement has not been extensively studied.

To better understand how tactile information is processed in S1 and how it is modulated with behavior, we studied the neural responses to tactile stimulation of the hand during passive movement and rest. By using an information theory based analysis, we directly quantified the information encoded in individual units as well as in unit pairs, and two putative coding strategies/models (rate coding and spatial coding) were tested. The contribution of correlated firing to the tactile information encoding and movement related sensory gating/modulation was studied.

**MATERIALS AND METHODS**

**Surgical procedure**

Three macaques (JK: male rhesus; AC: female bonnet; AX: female bonnet), weighing approximately 4-5 kg, were used in these experiments. Care and treatment of the animals during all stages of the experiments conformed to the procedures approved by the Division of Laboratory Animal Resources and Institutional Animal Care and Use Committee of SUNY Downstate Medical Center, and with established United States Department of Agriculture
standards. Monkeys were implanted with a titanium head-post and electrode arrays (Blackrock Microsystems) utilizing our nesting platform, as previously described (Chhatbar et al. 2010). Briefly, monkeys were initially anesthetized by using Ketamine (20 mg/kg), followed by intubation and respiration with isoflurane gas (1 - 3%) and oxygen. A midline, or oval incision was made and the skin was retracted to expose the skull. Two approximately 20mm by 20mm bone flaps were removed on each side of the midline over the S1/M1 hand region. After dura flaps were cut and opened, we mapped the receptive fields in S1 with sharp electrodes (Microprobes Com.) by lightly touching and manipulating the finger pads, palms, arm to shoulder; then two 96-Platinum-Iridum microelectrode arrays (10 by 10; electrode pitch 400 um and electrode length 1.0mm; Blackrock Microsystems) were pneumatically inserted in the 'hot spot' of the hand area that demonstrated clear receptive fields during the mapping process, and two arrays in the arm regions of M1 bilaterally. The S1 implant was placed as close as possible to the central sulcus on the postcentral gyrus to enable recording as many neurons in the area 1 as possible(Fig1 D). Thus our recording neurons were mostly from area 1 and some possibly from area 2. As the monkeys are still under research, there is no histological confirmation at this moment. Following the surgery, analgesics (Buprenex, 0.02mg/Kg; Rimadyl, 2mg/Kg) and antibiotics (Baytril, 6mg/Kg) were administered to the recovering animals for 3 and 5 days, respectively. Bicillin (1ml/20lbs) was administered every other day for 14 days. Experiments began three weeks after cortical implantation. We present only the recordings from the left S1, which is contralateral to the stimulated right hand, in this report.

Neural recording and offline sorting

Neural data was recorded with a multi-channel acquisition processor (MAP, Plexon Inc.) commencing at least 3 weeks after surgery. In each recording session monkeys were seated comfortably in a customized restraining chair within a soundproof chamber. Unity gain preamplifier head-stages (Plexon Inc.) were connected to the ICS-96 array connectors
(Blackrock Microsystems) via flexible wire cables, and head-stage outputs were fed to the MAP system. Neural signals were band-pass filtered (154 Hz to 8.8 KHz) and digitized at a sampling rate of 40 KHz. Spikes were detected online when above a threshold (3 S.D ) baseline noise level. The detected spiking times and spike waveforms were saved for off-line analysis. Single units (SUs) and/or multi-units (MUs) were isolated offline using Offline Sorter (Plexon Inc.). SUs were defined subjectively by the presence of clear waveform shapes, good separation in principal components feature space, and inter-spike intervals greater than 1.6 ms. Activities that did not show clear isolation were taken as MUs. Up to 50 channels of neural activity at a time on the array presented good neural signals, and 1 or 2 individual units (SUs or MUs) from most single electrodes could be isolated.

**Tactile stimulator and training protocols**

Tactile stimulation was achieved by using a push type solenoid actuator (STA-195201, Ladex Inc.), which was mounted under a finger cast. The finger cast and hand cast were attached to an exoskeletal robotic system KINARM (BKIN Technologies) (Fig. 1A). This allowed the arm to be moved freely while the system delivered reliable tactile stimuli. The solenoid was controlled by a PC via a digital card (PCI-6229, National Instruments Inc.) through a customized program written in Matlab (Mathworks, Inc.). A return spring was used to pull the plunger back after each tactile indentation. The diameter of the solenoid plunger, which indents the skin, was 1mm. The tactile stimuli were applied to the finger pad that showed a receptive field when lightly touching. Each tactile stimulation control pulse could produce skin displacement around 1 mm deep for 0.3s. The tactile stimuli were applied randomly at a mean frequency of 0.5 Hz during periods in which the animal’s arm was passively moved or rested without moving.

Before recording began monkeys were well trained to be seated quietly in a non-human primate chair with their right arms and hands restrained to the KINARM. The finger to be
stimulated was fixed in the finger cast (customized based on the individual finger of each monkey) just above the solenoid plunger (see figure 1A). The right arm was either passively moved or resting on the KINARM during tactile stimulation without movement. Passive arm movement was achieved by manually moving the robot KINARM forearm in the horizontal plane slowly and smoothly, where the endpoint of the KINARM was across a workspace of 30 cm by 40 cm. Figure 1B shows the endpoint position and speed distribution in an example session during passive movement. There was no obvious active movement observed during either rest or arm passive movement, and we did not use those sessions if animals showed active movement, which could be felt by the experimenter and confirmed with electromyography activities recorded from several major forearm muscles (Fig.1C). The experimenter held the KINARM during the resting sessions to keep the environment similar to the passive movement sessions. Each daily training session consisted of several 5-min tactile stimulation trials of either resting or passively moving. 10 sessions from three monkeys (JK: 6; AC: 2; AX: 2) were used in our analysis.

Data analysis

**Neural activity modulation.** In order to test how units (SUs/MUs) were modulated by tactile stimulation, peri-stimulus time histograms (PSTHs) were constructed for both the ensemble of units as well as individual units. The PSTHs were smoothed with a Gaussian density kernel (20 ms window length) to obtain the firing rate, as shown in figure 2A. Then firing rates were examined in the following two testing windows: a) the window encompassing 50ms before touch onset (baseline window in Fig. 2A) and b) the window encompassing 50ms from touch onset (response window in Fig. 2A). The 50ms length was based on the optimized window length in the following information analysis (see figure 5C). Neuronal modulation was analyzed by the following metrics: a) firing peak (f_{pk}), which is the peak firing rate in the response window, b)
baseline rate ($f_{bl}$), which is the mean rate during baseline window, c) activation duration ($T_a$ in Fig. 2 A), which is calculated as width of the response curve at the half of the response range ($h/2$ in Fig. 2A), d) the peak latency, which is the time from touch onset to firing peak within the response window, e) modulation strength, which is defined as the ratio of response range ($h$) to the baseline rate ($f_{bl}$), f) the area under the response curve (shaded area in Fig. 2 A), which relates with the synaptic transmission of the neural circuit (Abeles 1991), and g) Fano factor (FF), which represents a trial-to-trial spike-count variability in the response to the stimuli and is defined as

$$F = \frac{\sigma^2}{\mu}$$

where $\sigma^2$ and $\mu$ are the variance and the mean of spike counts in the response window, respectively. FF can be viewed as a statistical measure of the reliability or dynamics of a unit’s firing. If the firing peak of a unit was above 3 standard deviations of the baseline rate, we called the unit “touch-responsive”, otherwise it was classified as “non-touch responsive”.

**Mutual information between tactile stimulus and neural activity.** Mutual information is a measure of how much information one random variable shares with another random variable. Compared with the simple statistical test or other traditional correlational methods, mutual information provides a quantitative measurement of tactile information encoded in the neural activity. We tested two putative coding strategies (rate coding and spatial coding) in individual unit as well as in unit pairs (see figure 5 A and B for more detail). The mutual information between response and stimulus is defined as

$$I(R, s) = \sum_R \sum_s p(R, s) \log_2 \left( \frac{p(R, s)}{p(R) \cdot p(s)} \right)$$

where $s$ is the stimulus, a binary state (touch or no-touch) in our experiment; $R$ represents neural response after each stimulus, which is a spike count matrix within a response window from either individual units or unit pairs in our cases. $p(R), p(s)$ and $p(R, s)$ are the marginal and
joint probability distribution functions of $R$, $s$, respectively. The window parameters (length and center) were optimized by setting different window length centered at different lags after stimulus onset (see figure 5C and D). Based on the optimized parameters, we calculated the tactile stimuli encoded in the activities of individual unit or unit pairs during rest and during movement. For the spatial coding of unit pairs, mutual information was further decomposed into different components (Magri et al. 2009) as follows:

$$I(R, s) = I_{	ext{lin}} + I_{	ext{syn}} = I_{	ext{lin}} + I_{S-\text{cor}} + I_{N-\text{cor}}$$ (3)

$$I_{\text{lin}} = -\sum_j \sum_{r_j} P(r_j) \log_2 P(r_j) + \sum_{r,s} P_{\text{ind}}(r|s) \log_2 P_{\text{ind}}(r|s)$$ (4)

$$I_{S-\text{cor}} = -\sum_r P_{\text{ind}}(r) \log_2 P_{\text{ind}}(r) + \sum_j \sum_{r_j} P(r_j) \log_2 P(r_j)$$ (5)

$$I_{N-\text{cor}} = I(R, s) - \sum_{r,s} P_{\text{ind}}(r|s) \log_2 P_{\text{ind}}(r|s) + \sum_r P_{\text{ind}}(r) \log_2 P_{\text{ind}}(r)$$ (6)

where $I(R, s)$ is the total mutual information carried by unit pairs about the stimulus. $P_{\text{ind}}(r)$ and $P_{\text{ind}}(r|s)$ indicate the independent response probability and the conditionally independent response probability respectively. $I_{\text{lin}}$ is the sum of information carried by each unit as if it was independently firing, and $I_{\text{syn}}$ represents the synergy (>0) or redundancy (<0) arising from the correlation of unit pairs. Then $I_{\text{syn}}$ is further decomposed into 'signal correlation' ($I_{S-\text{cor}}$) and 'noise correlation' ($I_{N-\text{cor}}$). Signal correlation represents the reduction in information due to similar responses of individual units to a given stimulus, while noise correlation is the correlation between units seen in the fluctuations of their responses around their respective mean response to a given stimulus (see (Averbeck et al. 2006) Fig. 1 and 2). In order to test the effect of movement on the encoded tactile information, we defined the gated mutual information ($I_g$) as the difference between information at rest and information during movement for each component. $I_g$>0 indicates movement gating tactile information; $I_g$<0 indicates movement facilitating tactile information.

Information calculated with the empirical probability distribution can have a strong bias when the number of trials is limited; however it can be alleviated by using advanced techniques.
When the number of trials is large enough compared to the number of responses so that every possible response occurs many times (Ns/R > 32), analytical approximations to the bias can be estimated (Panzeri et al. 2007). In the absence of knowledge about some specific feature of the neural response statistics, a resampling strategy can be applied. Combined strategies showed better performance for bias correction even when Ns/R was small (Magri et al. 2009). Thus we combined a quadratic extrapolation and bootstrap procedure to correct for the bias for our calculation (Ns / R >30), which was implemented as part of an information breakdown toolkit (Magri et al. 2009).

**Statistical analysis.** For individual unit analysis, no significant difference was found between animals, thus we pooled the data from the three monkeys together. The following statistics were tested: (1) A non-parametric test (ranksum or signrank, MATLAB) was used to test whether the change was significant between different behavioral states. (2) Two-sample Kolmogorov-Smirnov test (kstest2, MATLAB) was performed to compare whether two variables were likely to have come from the same distribution or not. All the significance levels of the above tests were set at 0.05, unless stated otherwise. All data analyses were performed using MATLAB (MathWorks Inc.).

**RESULTS**

We recorded neural responses to tactile stimulation under two conditions (passive movement vs. rest) in three monkeys (JK: 6 sessions; AC: 2 sessions and AX: 2 sessions). Among all the units recorded, 256 units were classified as single units (SUs), and 189 units were classified as multi-units (MUs). As SU and MU showed similar results, and MU appears to follow a pattern predictable from a set of SU data, we combined them together without differentiation and will call them **individual units** (SUs and MUs) in the following results.
Neural modulation and the effect of movement

Tactile stimulation caused broad neuronal responses in S1. The general peak response patterns were similar between rest and passive movement (Fig. 1E). The correlation coefficient of the two peak response maps was over 0.9 for each of the sessions (Matlab, xcorr2). We first analyzed these responses at the population level by pooling individual units (SUs/MUs). Figure 2A shows the firing rate of an example population response. When looking across sessions, the baseline firing rate (Fig. 2 B) was significantly higher (signrank, p< 0.05) during movement than during rest, while the peak firing rate was not significantly decreased during movement (Fig. 2 C). The strength of neural responses to tactile stimulation was higher during rest than during passive movement (Fig. 2 D). Contrary to our expectations, the peak latency was significantly shorter during movement (Fig. 2 E). Interestingly, the area under the response curve (Fig. 2 F), which represents the efficacy of synaptic transmission of the stimulus (Abeles 1991), was not significantly different during movement and during rest.

The ensemble analysis, where all units were pooled in each session, demonstrated the network level modulation, but as non-tactile responsive units were also included, thus the results might have had a bias toward non-tactile related units. We thus further looked at the neural responses by classifying units into four types based on the neural responsiveness to tactile stimulation: move only cells were only responsive to touch during arm movement (Fig. 3 A); rest only cells were only responsive under rest condition (Fig. 3B); both cells were responsive under both conditions (Fig. 3 C); none cells did not respond to tactile stimulation under either condition. From all units recorded, half (50%) of the units were activated by tactile stimulation under both the rest and moving conditions, and more units (16%) were suppressed than were activated (4%) by movement (Fig. 3 D). In the following analysis we only looked at the both type subpopulation under rest and movement conditions, but the whole population showed the same statistics as the subpopulation of 'both' units.
Similar to the ensemble analysis, we found that the subpopulation of ‘both’ units also showed elevated baseline firing rates during movement (Fig. 4 A). The non-significant suppressed peak firing rate during movement in the ensemble was significantly suppressed in the tactile responsive subpopulation (Fig. 4 B). Similar to the ensemble analysis the modulation strength was stronger during rest than during movement (Fig. 4 C). Also there was a short peak latency (Fig. 4 D) during passive movement than during rest. The areas under the response curve were stable and there was no significant difference between the two states (Fig. 4 E).

Parallel to modulation of individual units, the correlation coefficient between unit pairs was also calculated after binning (50ms window) the two spike trains into two time series, and we found that there was a significant decrease during movement (Fig. 4 F).

**Tactile information encoding strategies and the gating effect of movement**

The above analysis only showed that the neurons significantly responded to tactile stimuli in a movement dependent manner. By using an information based method, the tactile information encoded in the neural activity can be quantitatively calculated (see figure 5 for method). In order to optimize the calculation of mutual information between tactile stimulus and neural activity, we first optimized the window's length (since touch onset), and found that the mutual information showed an increase as the window length increased until maximized at around 50 ms (Fig. 5C). Then we optimized the window center by taking the above optimal window length and found that the information peaked when the window centered at 20 ms after tactile stimulus onset (Fig. 5D), which agrees with the above population peak response (as seen in figure 2A). In line with the above short peak latency results (Fig. 2A), the mutual information also peaked earlier during movement than during rest (Fig. 5C). By using the optimized window parameters (50ms length centered at 20ms after touch onset), the mutual information was calculated for all the subsequent analysis.
At first we tested the tactile stimulus encoded in the neural activity with rate coding. Tactile information encoded in either individual units or unit pairs was significantly higher during rest than during passive movement, which indicates that tactile information might be gated by movement (Fig 6. A). As the sensory gating by movement was also observed in the above firing rate modulation, we tested the correlation between the gated information ($I_g$), which is the difference of mutual information at rest ($I_{rest}$) and at movement ($I_{move}$), and gated firing rate or gated neural dynamics, which is represented as the Fano factor (FF). Although neural dynamics has been commonly regarded as noise (Faisal et al. 2008), it may also mean high information (Scaglione et al., 2011). We found that the gated information ($I_g$) was positively correlated with the gated firing rate (rest-move) (robustfit, MATLAB; $R^2 =0.33; p<0.001$)(Fig.6 B), while negatively correlated with the gated FF (rest-move) (robustfit, MATLAB; $R^2 =0.17; p<0.001$) (Fig.6C). Thus this further confirmed that the information analysis correlated with and is consistent with the traditional firing rate modulation analysis. However the following analysis shows it can also provide additional power for separating different contributions.

As correlated firing has been observed during demanding or sensory selective processing tasks (Alloway et al. 2002; Panzeri et al. 2001; Roy et al. 2007; Steinmetz et al. 2000), we tested for this possibility in the tactile information encoded in firing patterns of unit pairs with a spatial coding model. Similar to rate coding, mutual information of spatial coding was also suppressed by movement (Fig. 6D). For unit pairs, the mutual information of spatial coding ($I_{spatial}$) was significantly higher than that of rate coding ($I_{rate}$) (Fig. 6A and Fig. 6D), and the information gain ($I_g = I_{spatial} - I_{rate}$) showed a significant increase during movement compared with rest(Fig. 6 E). Although the absolute value of the information gain is small, the gain as a percentage change to rate coding was clearer and larger during movement than during rest (signrank, $p<0.001$) (Fig.6F).
Going further, by using a newly developed “information breakdown” toolbox (Panzeri et al. 2007), the mutual information of spatial coding was decomposed into components arising from uncorrelated (Fig 7.A) and correlated (Fig 7.B) firing of unit pairs. As reported earlier that correlation often encodes very little information (Petersen et al. 2001), we found that most of the unit pairs contained redundant information ($I_{syn} < 0$) under both moving and rest conditions (Fig. 7 B). Interestingly, movement had different effects on these two information components. The information component from uncorrelated activities ($I_{lin}$) was significantly suppressed/gated by movement (Fig. 7 C); on the contrary, movement significantly (kstest, p<1e-10)reduced redundancy and increased the synergistic information, which was seen as a reduced gating effect during movement (Fig. 7D). In general for $I_{lin}$, around 80% of the unit pairs showed sensory gating by movement, while for $I_{syn}$ only around 30% of the unit pairs showed gating (Fig. 7E). After further decomposition of the synergistic information ($I_{syn}$) into the contributions from 'signal correlation' ($I_{S-cor}$) and the contribution from 'noise correlation' ($I_{N-cor}$), we found that for most of the unit pairs both $I_{S-cor}$ and $I_{N-cor}$ were enhanced instead of gated by movement (Fig. 7F). All these suggest that different tactile encoding strategies might play different roles to regulate the sensory information transmission depending on behavior. Although the amount of information encoded in the correlation of unit pairs was small, this information was gated less than those encoded in independent firing.

DISCUSSION

Tactile Information modulation by movement

We observed that the passive movement caused an elevated baseline firing rate for neurons in S1. Our electrode array (1mm length) was implanted next to the central sulcus and covered an area of 3.6 mm by 3.6 mm, thus the recorded neurons were mostly from layer IV/V in area 1 and possibly some from area 2. Although area 1 neurons have predominantly cutaneous receptive
fields, they also frequently show deep receptive fields as well as kinesthetic/motor maps (Moore et al. 2000; Nelson et al. 1991b; Prud'homme and Kalaska 1994). Movement itself can activate peripheral sensory receptors and neurons throughout the sensory pathway (Abbruzzese et al. 1981; Cohen et al. 1994). Thus, our observation of an increased baseline firing rate could be explained by the activation of the peripheral tactile receptors by the movements themselves as well as the inputs of proprioceptive receptors.

It has been reported that the firing of area 1 neurons is modulated by movement in a layer specific manner (Prud'homme et al. 1994), where layer IV/V is the convergent point of ascending and descending information (see discussion in (Prud'homme et al. 1994)), thus different modalities of information could interact in S1. Tactile signals have been found to interact with proprioceptive signals and encoding of hand location, posture and self-motion in S1 (Rincon-Gonzalez et al. 2011a; Rincon-Gonzalez et al. 2011b; Wolpaw 1980). In agreement with sensory gating, which has been observed at the spinal cord (Seki and Fetz 2012), brainstem (Furuta et al. 2008), thalamus (Aguilar and Castro-Alamancos 2005; McCormick and Bal 1994), and at cortical level (Jiang et al. 1991; Seki and Fetz 2012) in a task-dependent manner (Ogata et al. 2009; Seki and Fetz 2012; Urbain and Deschenes 2007), we found both a suppressed firing peak and an elevated baseline firing rate in the tactile responsive units. An earlier report showed that area 1 neurons with cutaneous receptive fields were less responsive to tactile stimuli during movement (Nelson et al. 1991a), this might explain the suppressed peak rate we found here as well as the observation of more ‘rest only’ than ‘move only’ units. Active movement generally shows stronger somatosensory suppression than passive movement (London and Miller 2012; Rushton et al. 1981; Seki and Fetz 2012). Compared with the previous tasks used (London and Miller 2012; Seki and Fetz 2012), our testing had neither an explicitly motivated motor planning phase or active sensing phase nor any reward or cognition involvement, thus the dominant tactile sensory gating in S1 was presumably from the
competition / inhibition from 'proprioceptive' inputs by passive movement, as well as cutaneous stimulation stemming from the movements. Similar to what has been found with movement gating of proprioception in humans (Abbruzzese et al. 1981), the gating of tactile information would most likely come from a bottom-up strategy by the activation of neurons from the ascending pathway and in S1. The 'gating' of cutaneous information might be through S1 neurons that have long-range horizontal connections with other more proprioceptive influences. We cannot exclude the possibility that a centrally generated movement related signal in S1 could also have regulated the sensory information in our work, while the regulation through an efferent copy should be small (London and Miller 2012; Urbain and Deschenes 2007).

Tactile information processing in S1 during passive movement was not simply limited to sensory gating. With the absence of an actively generated movement, or motor plan, the dominant contribution to the modulation of neural responses to tactile stimulation was most likely from submodality interactions in S1, such as between light cutaneous and proprioceptive. It has been found that a majority S1 cells response to cutaneous stimulus, while some cells preferentially response to 'proprioceptive' stimuli (McKenna et al. 1982). The cutaneous cells show response to tactile stimulation during rest, but could be gated totally or partially by passive movement, which was in agreement with our 'rest only' and 'both' units. The proprioceptive cells may elevate the background activity through activation by movement and also suppress the tactile information during passive movement possibly through lateral inhibition. There are still other S1 neurons that get inputs from both skin and deep afferents through direct or indirect routes(McKenna et al. 1982). They could respond to co-activation of both cutaneous and proprioceptive receptors in selective spatio-temporal patterns. These cells might constitute our "both" and 'move only' units, and could provide a higher-order feature-extracting capability dependent on behavioral context (Iwamura 1998; Prud'homme and Kalaska 1994).
Contrary to our expectations, a shorter peak latency in the neural response to tactile stimulation was observed during movement (Fig. 2 E and Fig. 4 C), but we are unclear whether and how sensory gating was related with conduction speed or on neuron type (Bellavance et al. 2010; Nelson et al. 1991a). Interestingly, the area under the response curve, which represents synaptic transmission from stimuli to the neural circuit (Abeles 1991), was not significantly changed during movement and during rest (Fig. 2 F and Fig. 4 E), thus this might indicate that the gating/modulation could be the result of a redistribution of the synaptic transmission between different signals sources, but the exact underlying redistribution or interaction mechanism needs further research (Rincon-Gonzalez et al. 2011b). It should be noted that all the individual or pair-wise based analysis (also for the information analysis) was only from the subpopulation of ‘both’ type units. When considering the larger number of ‘rest only’ vs. that of ‘move only’, the gating influence was even clearer and stronger.

**Information encoding strategy and the effect of movement**

The neural modulation analysis tested if neurons were responsive to tactile stimulus and their responses were regulated by movement (Fig. 2 and 4). Beside firing rate based analysis, correlated spiking has also been observed during demanding tasks (Alloway et al. 2002; Panzeri et al. 2001; Roy et al. 2007; Steinmetz et al. 2000), under quiet wakefulness (Song et al. 2013), and even in the anesthetized state (Reed et al. 2008). Information based methods provide the convenience to quantitatively calculate how much information is present, and hence available to the nervous system. The sensory information modulation by movement can also be calculated directly as we have presented in this work. The information can be further decomposed into components to distinguish the sources of correlation, which may help to better understand the underlying mechanism, which was the motivation for our use of information measures.
Our information based analysis agrees with the rate modulation based method in that
the mutual information between tactile stimulus and neural activity was also gated by movement
under either rate coding or spatial coding models. Similar to what has been reported in
somatosensory cortex in the rat (Petersen et al. 2001), the information encoded in the
correlation of unit pairs was small, and most unit pairs (75% from all the unit pairs) showed
information redundancy. In line with the decreased unit pair correlation coefficient (see Fig. 3 F),
the mutual information was also decreased by movement. Interestingly, movement showed
different gating influences based on the information coming from either uncorrelated firing ($I_{\text{uncor}}$)
or from correlated firing of unit pairs ($I_{\text{cor}}$): the $I_{\text{uncor}}$ was mostly gated by movement, on the other
hand, the $I_{\text{cor}}$ was mostly enhanced by the movement as compared to rest. After decomposition
of the $I_{\text{cor}}$, we found that both the information arising from 'noise correlation' ($I_{\text{N-cor}}$) and that
information from 'signal correlation' ($I_{\text{S-cor}}$) were mostly enhanced rather than gated by the
movement (see figure 6 F). As 'noise correlation' is derived from the activity fluctuations that are
observed from trial to trial for the same constant stimulus (Tomko and Crapper 1974), it is not
necessarily useless and may encode information about the brain's state (Averbeck and Lee
2004). The 'signal' here represents the mean neural response to a tactile stimulus, and 'signal
correlation' is a measure of the similarity of this mean neural response between a pair of units.
On the other hand, the total correlation of the 'noise' and 'signal' is related with the synchrony
(Averbeck and Lee 2004), which might also be involved in the gating of information flow in the
cortex (Steinmetz et al. 2000). As the dominant contribution to synchrony is from 'signal
correlation', this indicates either correlation or synchrony was another potential strategy to
transmit sensory information with less information lost. However it must be said that the
'synchrony' we present here was from a longer timescale (not 'synchrony' in a strict sense). We
did find that the synchrony on a fine timescale (1ms bin) of ensemble units was gated by
movement (data not shown). Although the absolute value of the information gain ($I_g > 0$) by using
spatial coding instead of rate coding for each unit pair is small, the gain as a percentage change was clear especially during movement. Taken together, although our data does not show whether or not the information encoded in correlation is utilized by the brain, or which encoding strategy (rate coding vs spatial coding) is utilized by the brain, which requires more sophisticated experimental approaches to test, it provides what information is present and hence available to the nervous system. Our result also indicates that different encoding strategies might potentially play different roles depending on behavioral contexts. The regulation of sensory information transmission by movement is very clear. Another interesting topic would be the study of whether the movement related kinematic information is encoded, and how it complements / interacts with the gated tactile information (Rincon-Gonzalez et al. 2011b). If there is a compensation, it might suggest that the nervous system not only stabilizes the circuit synaptic transmission as seen from the constant area under the response curve, but also regulates and optimizes the information content from different stimulus modes depending on behavior.

**CONCLUSION**

By simultaneously recording unit activities to tactile stimulation in three behaving monkeys during rest and passive movement, we found that neurons in S1 were responsive to tactile stimulation, and that movement gated this response. Information-based analysis further showed that the sensory modulation by movement was clear and consistent with more standard rate based neural modulation analysis often used by neurophysiologists. Although spatial coding seems superior to rate coding as shown by higher mutual information between tactile stimulus and neural activity, the absolute value of information gain was small. Tactile information could be mostly encoded in the firing rate of individual units, and the correlated firing of spatial coding might serve as a filter to regulate information transmission during movement. The underlying mechanisms of sensory modulation during passive movement could be mainly through a
bottom-up strategy via activation of neurons along the ascending pathway and the interaction of different modalities of sensory inputs.

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**FIGURE CAPTIONS**

**Figure 1.** Experimental protocol. 

A), Monkeys are seated comfortably in a non-human primate chair with their right arm and hand restrained on a KINARM (BKIN Technologies), which allows free 2-D movement of the arm in the horizontal plane. The fingers are held in place by a customized cast that allows tactile stimuli to be delivered reliably from a solenoid plunger under both the resting condition and the passive movement of the arm, which is moved randomly and smoothly within the workspace (WS) as shown from the end-point trajectory and speed distribution(B). Each tactile stimulus (one stroke of solenoid) is applied for 0.3 s on the skin, which indents the finger pad of either index, middle, or ring finger (whichever showed clear response to light touch) by 1 mm at a mean frequency of 0.5 Hz at random intervals. The relative position of the KINARM and WS is shown as the frame. There are no obvious active movements observed during either rest or passive movement as shown from the activities of several major muscles (C). Black(during rest) and red (during movement) traces show the raw electromyography from surface electrodes in biceps (BI) and flexor carpi muscles (FC); small triangles indicate the time of tactile stimuli. Neuronal activities are recorded from multichannel electrode arrays (Blackrock Inc.) in S1 (D). E), Activation maps show peak firing rate (color scale as in spikes/s) as a function of electrode position; each square corresponds to one electrode(either single unit or multi-unit) in the 10x10 array. A similar but weak response map is also consistently observed during passive arm movement (correlation coefficient (Matlab xcorr2) between the two peak rate maps is over 0.9 across each of the recording sessions).

**Figure 2.** Ensemble level neural modulation. 

A), Example ensemble firing rate of a typical session and the analysis method. Several parameters (B-F) are extracted from the response curve for testing the modulation. Ensemble baseline firing rate (B), which is the mean rate within the baseline window (baseline in A), is significantly higher during passive movement than during...
rest, while there is a decrease in peak firing rate (peak in the response window as in A) but non-significant (C). Thus the modulation strength, which is defined as the ratio of response range (h) to the baseline rate (f_{bl}), is significantly higher during movement than during rest (D). The peak latency (E) is significantly shorter during movement, while the area under the curve (gray area in A, arbitrary units) within the response window is not significantly different between rest and movement (F). T_a in A represents activation duration, which is the width at half range (h/2) of the response curve. Error bar in each panel indicates S.E. (*p<0.05 for signrank).

**Figure 3.** Modulation of individual units (SUs or MUs). A-C), Example Individual units show different responses to tactile stimulation at rest and movement. Raster plots (upper in each panel) and the corresponding PSTHs (lower in each panel) show the neural responses to touch during movement (red) and rest (black). Time zero indicates the touch onset. There are four types of cells classified: the **move only** cells are only responsive to touch during arm movement (A); the **rest only** cells are only responsive under rest condition (B); the **both** cells show response under both conditions (C); the **none** cells do not show response to tactile stimulation under both conditions. D), From all units recorded, half of the units show response to tactile stimulation during both rest and passive movement, and 16% of touch responsive units during rest are lost touch response during movement, while only 4% of non-touch responsive units are activated to be touch responsive by movement.

**Figure 4.** Response characteristics of the subpopulation of units (type **both** in Fig. 3 C) that are responsive to touch under both passive movement and rest. There are significantly elevated baseline firing rate (A), suppressed peak firing rate (B) and bigger modulation strength (C) during the passive movement. Also there is a short peak latency during the passive movement than rest (D), but the area under the response curve (arbitrary units) is not significantly different
Besides the firing rate modulation of individual unit, the correlation coefficient between unit pairs is also decreased during the movement. Each dot in panel A through E represents one unit, and the each dot in panel F represents the correlation coefficient of one unit pair. In each panel diagonal line indicates unit line; X-axis is for rest and Y-axis is for movement. (* p<0.01, for signrank).

**Figure 5.** Coding strategies and the window parameters optimization. Two coding strategies, rate coding (A) and spatial coding (B), are tested based on either individual unit or unit pairs. Rate coding will refer to the coding strategy that takes the total spike counts in a bin/window, whose parameters, window length (C) and window center (D), will be optimized. For unit pairs, there is another ‘spatial coding’, which will be referred when looking at binned spike counts from unit pairs while maintaining the ‘spatial’ identity of each unit (see cartoon in B). The information encoded in firing rate is first optimized by window length (C), and then by window center, using the optimal window length (50 ms as in C(D), (C and D)). X-axis represents post tactile stimulus time. The window parameters (50 ms window lengths centered at 20 ms from touch) will be used for the mutual information calculation and bias is corrected by combining quadratic extrapolation and bootstrap subtraction procedures. Error bars in C and D indicate S.E.

**Figure 6.** Mutual information in rate coding and spatial coding. Movement significantly suppressed the mutual information between tactile stimulus and neural activity with rate coding for either individual units or unit pairs (* p<0.01, for signrank) (A). The movement gating of mutual information (rest - move) is positively correlated with the movement gating of firing rate (rest - move) (B), while negatively correlated with the gating of Fano factor (rest - move) (C). In (B) and (C), each dot represents one unit, and gray line indicates trend line (robustfit, Matlab). Similar to rate coding, movement also significantly suppressed the mutual information calculated with spatial coding (* p<0.01, for signrank) (D). There is a positive information gain(mutual information
in spatial coding - mutual information in rate coding) during either movement or rest (*p<0.01, for signrank) (E). The cumulative probability is from all the unit pairs of the subpopulation (type both in Fig.3 C). Although the absolute information gain value is small, the gain as a percentage of information gain to rate coding is much clearer and significantly bigger during movement than during rest (*p<0.01, for signrank) (F). Error bars in A, D and F indicate S.E.

**Figure 7.** Mutual information calculated with spatial coding breakdown. The mutual information is decomposed into two components: $I_{lin}$, which is the total information carried by two units as firing independently, and $I_{syn}$, which represents the information arising from the correlation between the unit pair (synergy: $I_{syn} > 0$ or redundancy: $I_{syn} < 0$). (A) and (B) are the cumulative probability of $I_{lin}$ and $I_{syn}$ from the each pair, respectively. Movement shows different effects based on information from either independent firing or correlated firing: Movement mostly gates $I_{lin}$ (C), while it facilitates $I_{syn}$ (D). Shaded areas in (C) and (D) indicate movement gating. Around 80% of unit pairs show movement gating for $I_{lin}$, while this is only around 30% for $I_{syn}$ (E). After $I_{syn}$ is further decomposed into the information arising from 'signal correlation' ($I_{s-corr}$) and the information arising from 'noise correlation' ($I_{n-corr}$), only small percentage of unit pairs shows movement gating for both components (F). The units are from the subpopulation both type in Fig.3 C. (*p<0.01, for signrank and kstest2).
Figure 1

(A) KINARM FRAME (top view)
- Finger cast (solenoid underneath)
- Restrain casts

(B) Endpoint trajectory
- WS
- X-Direction (10 cm)
- Y-Direction

(Front view)
- Solenoid plunger (1 mm range)
- Finger cast

(C) Speed distribution
- Probability
- Speed (cm/s)

(D) Electrode #
- WS
- S1 array
- CS

(E) Electrode #
- Rest (R=0.92)
- Move
- Color scale 0-120
Figure 2

A. Graph showing time since touch (ms) vs. activity rate (spikes/s) with black line for 'rest' and red dotted line for 'move'.

B. Bar graph showing baseline rate with 'rest' and 'move' conditions.

C. Bar graph showing peak rate with 'rest' and 'move' conditions.

D. Bar graph showing modulation strength with 'rest' and 'move' conditions.

E. Bar graph showing peak latency with 'rest' and 'move' conditions.

F. Bar graph showing area under curve with 'rest' and 'move' conditions.

* denotes significant difference.
Figure 3

A

B

C

D

distribution of touch response cell

(n: 445)

Rest only  Move only  Both  None

16%  30%  50%  4%
Figure 4

A. baseline rate

B. peak rate

C. modulation strength

D. peak latency

E. area under curve

F. correlation coef.
Figure 5
Figure 6

A. Rate coding

B. Information in (rest - move) (bits)

C. Fano factor (rest - move)

D. Spatial coding

E. Information gain

F. % change of gain
Figure 7