Decoding tactile afferent activity to obtain an estimate of instantaneous force and torque applied to the fingertip

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Khamis H, Birznieks I, Redmond SJ. Decoding tactile afferent activity to obtain an estimate of instantaneous force and torque applied to the fingertip. J Neurophysiol 114: 474–484, 2015. First published May 6, 2015; doi:10.1152/jn.00040.2015.—Dexterous manipulation is not possible without sensory knowledge about object properties and manipulative forces. Fundamental neuroscience has been unable to demonstrate how information about multiple stimulus parameters may be continuously extracted, concurrently, from a population of tactile afferents. This is the first study to demonstrate this, using spike trains recorded from tactile afferents innervating the monkey fingertip. A multiple-regression model, requiring no a priori knowledge of stimulus-onset times or stimulus combination, was developed to obtain continuous estimates of instantaneous force and torque. The stimuli consisted of a normal-force ramp (to a plateau of 1.8, 2.2, or 2.5 N), on top of which −3.5, −2.0, 0, +2.0, or +3.5 mNm torque was applied about the normal to the skin surface. The model inputs were sliding windows of binned spike counts recorded from each afferent. Models were trained and tested by 15-fold cross-validation to estimate instantaneous normal force and torque over the entire stimulation period. With the use of the spike trains from 58 slow-adapting type I and 25 fast-adapting type I afferents, the instantaneous normal force and torque could be estimated with small error. This study demonstrated that instantaneous force and torque parameters could be reliably extracted from a small number of tactile afferent responses in a real-time fashion with stimulus combinations that the model had not been exposed to during training. Analysis of the model weights may reveal how interactions between stimulus parameters could be disentangled for complex population responses and could be used to test neurophysiologically relevant hypotheses about encoding mechanisms.

A person’s ability to handle and manipulate objects is crucial for performing everyday activities and maintaining a high quality of life. Receptors in the fingers and hand provide tactile information to the motor-control system, enabling dexterous manipulation (Johansson and Flanagan 2009). The tactile afferents innervating these receptors encode manipulative parameters for maintaining grasp stability, including the grip or normal force, as well as torque (Crevecoeur et al. 2011; Goodwin et al. 1998; Johansson and Westling 1987; Kinoshita et al. 1997). Coordinated manipulation largely depends on predictive strategies, based on internal representations that are updated by sensory inputs (Birznieks et al. 1998; Crevecoeur et al. 2010; Flanagan et al. 2008; Johansson and Cole 1992; Johansson and Westling 1988b; Nowak et al. 2003; Witney et al. 2004). Corrective responses are triggered when an event occurs that conflicts with predictions (Johansson and Westling 1984, 1988a).

There is a wealth of data demonstrating single afferent responses to simple controlled mechanical stimulation (Goodwin and Wheat 2004; Johnson et al. 2000; Macefield and Birznieks 2009). Likewise, discrimination of single-stimulus parameters, such as shape, texture, and forces, has been demonstrated in constrained settings using classification of discrete stimulus features with a limited number of degrees of freedom (Jenmalm et al. 2003; Khalsa et al. 1998; LaMotte et al. 1994). Most of these approaches use response measures, whereby spike information has been integrated over relatively long time intervals, such as the number of spikes during the first second of stimulation [e.g., Wheat and Goodwin (2001)], and are not capable of continuous encoding of changing stimulus parameters.

Recently, classification of cumulative spike counts from populations of afferents was shown to discriminate normal force and torque (magnitude and direction as separate parameters) concurrently (Birznieks et al. 2010; Redmond et al. 2010b). A limited multiple-regression analysis has been performed to estimate normal-force and torque magnitude (Fu et al. 2012). Features, such as the first spike latency, from the stimulus-onset time also contain information about the stimuli (Johansson and Birznieks 2004; Saal et al. 2009), and similar classification accuracy was achieved with spike-latency features compared with spike-count features (Redmond et al. 2010a). These approaches rely on knowledge of stimulus-onset times, and validation was performed when normal force was constant, and torque was loaded. It has never been demonstrated how sensory information could be extracted from tactile afferent responses, continuously, without knowledge of stimulus-onset times or combinations of different concurrent stimulus parameters.

This investigation significantly extends prior work by implementing two regression models—one for estimating the instantaneous normal force and one for estimating torque—of a stimulus from real afferent spike data recorded from monkeys. The models are not required to have encountered a given stimulus combination during training or to “know” the onset times. Furthermore, the trained models do not require any retraining and therefore, can estimate the stimulus parameters continuously with a delay comparable with the processing time of the nervous system and relevant to the sensorimotor control loops. To acknowledge these physiologically relevant processing time constraints, we therefore refer to our model as oper-
MATeRIALS AND METHODS

Neural recordings. Neural recordings of single afferents were made from three anesthetized *Macaca nemestrina* monkeys, as described in Birznieks et al. (2010). The procedure was performed with approval from the University of Melbourne Ethics Committee and conforms to the National Health and Medical Research Council of Australia’s Code of Practice for nonhuman primate research.

After inducing surgical anesthesia, single, cutaneous mechanoreceptor afferents in the median nerve were isolated and recorded, using standard procedures (Goodwin et al. 1995). Each single fiber was classified by mapping the region of sensitivity and response to static or dynamic stimulation (Vallbo and Johansson 1984). There are four types of tactile afferents innervating the glabrous skin of the human hand. Those that persistently respond to static stimuli are denoted as slowly adapting (SA), and those that only respond transiently to changing stimuli are denoted as fast adapting (FA) (Vallbo and Johansson 1984). Tactile afferents with small receptive fields with distinct borders are known as type I afferents, and those with large receptive fields with diffuse borders are known as type II afferents. The glabrous skin of the human hand contains SA type I (SA-I), SA type II (SA-II), FA type I (FA-I), and FA type II (FA-II) afferents. The glabrous skin of a monkey contains SA-I, FA-I, and FA-II, but SA-II afferents have not been distinguished (Darian-Smith and Kenins 1980).

To combine data from different digits and different animals, receptive field centers (RFCs) and stimulus directions were referenced to a standardized fingertip on the right hand. For afferents innervating the left hand, an anatomical match was obtained by mirror imaging the location of the RFC and the stimulus (Birznieks et al. 2010). For the analysis presented here, recordings from 83 afferents (58 SA-I and 25 FA-I) were used, for which all combinations of the stimuli were applied. The RFCs of these 83 afferents are shown in Fig. 1A.

Stimulation procedure. A custom-built stimulator was used to apply normal forces and torques to the fingertip, as described in Birznieks et al. (2010). During stimulation, the fingers were maintained by a validated technique (Birznieks et al. 2001) that allows the fingertip to deform as it might if it were actively pressed against a surface (Birznieks et al. 2010). The stimulus applicator was a flat, circular surface (diameter 24 mm), covered with fine-grain sandpaper (500 grade) that was renewed for each afferent recording. The three-dimensional forces and torques applied to the fingertip were measured using a six-axis, force-torque transducer (Nano F/T; ATI Industrial Automation, Apex, NC) with a force resolution of 0.0125 N and a torque resolution of 0.0625 mNm, sampled at 200 Hz. The force-torque transducer was mounted directly between the stimulus applicator and the custom-built stimulator. The stimulation protocol included three contact normal forces: 1.8, 2.2, and 2.5 N, in combination with five torques, −3.5, −2.0, 0, +2.0, and +3.5 mNm. Torque, a vector quantity comprising both a magnitude and direction, was defined here as rotation about the axis normal to the surface of the finger and relative to the principle anatomical directions, regardless of which hand to which the torque was applied (Birznieks et al. 2010), as indicated in Fig. 1B. Each combination of normal force and torque was applied six times ($N_{rep} = 6$). The number of combinations of normal force and torque was 15 ($N_{stim} = 15$; three normal forces × five torques).

The protocol for applying normal force consisted of the following: a normal-force loading phase, during which the contact force was increased from zero to the desired value (1.8, 2.2, or 2.5 N): a normal-force plateau, for which the normal force was held approximately constant; and a normal-force unloading phase, during which the normal force was removed. The protocol for applying torque consisted of the following: a torque-loading phase, during which the torque was applied, ramping from zero to the desired value (−3.5, −2.0, 0, +2.0, or +3.5 mNm); a torque-plateau phase, for which the torque was held approximately constant; and a torque-unloading phase, during which the torque is removed. The torque is superimposed on the normal force during the normal-force plateau. The duration of the interstimulus interval was 3.5 s.

To build an ensemble from the spike trains of the 83 afferents recorded, the force and torque waveforms that are applied must be reproducible, whereas the waveforms may have any arbitrary shape. To determine the shape of the normal-force stimulus waveform for

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**Fig. 1.** A: the position of receptive field centers (RFCs) of afferents on a standardized monkey fingertip on the right hand: 58 slowly adapting type I (SA-I) afferents and 25 fast-adapting type I (FA-I) afferents; the 1st contact point of the stimulator applicator is indicated by an “X.” B: the direction of normal force and torque relative to the surface of the fingertip and the 4 principal anatomical directions (distal, ulnar, proximal, radial).
each plateau level of normal force, the normal force at each time sample was averaged across multiple presentations of that normal-force plateau level (i.e., across afferents, torques, and repetitions). Similarly, to obtain the shape of the torque-stimulus waveform for each torque-plateau level, the torque at each time sample was averaged across multiple presentations of stimuli with the same torque-plateau level (i.e., across afferents, normal forces, and repetitions). The temporal sequence of the averaged stimulation normal forces and torques is shown in Fig. 2.

A torque reversal is observed during unloading from 4.15 to 4.6 s (Fig. 2), where the torque is observed to be in the opposite direction to that applied during the plateau, rather than unloading directly to zero torque. During each trial, the possibility of overt slips was meticulously, visually monitored, and no overt slips were present in the analyzed data. However, the observed direction change in torque during unloading was possibly due to localized slip-and-stick events in the peripheral part of the skin-contact area during torque loading, resulting in an inversion in the torque during unloading when the peripheral skin area is stuck again, and the applicator rotated back to its starting position. Such deviations from an ideal stimulus waveform shape, whereby forces and torques are loaded/unloaded with linear ramps, were regarded as advantageous, providing a richer data set for training and validating the model. Furthermore, the stimulus was reasonably reproducible (see Fig. 2), which is essential for building a population ensemble from individually recorded afferents.

The stimulus contains regions with various combinations of force and torque: regions when no stimulus is applied (interstimulus period); a normal force is changing, and no torque is applied (normal-force loading); a static normal force, and no torque is applied (normal-force plateau before the start of torque loading); a static normal force is applied, and the torque is changing (torque loading and torque unloading); both normal force and torque are static (torque plateau); and both normal force and torque are changing at the same time at the end of stimulation and stimulus retraction (4.3–4.6 s).

Features. The procedure for extracting features from the afferent spike trains is described below and illustrated in Fig. 3.

Fig. 2. Temporal sequence of the force and torque stimuli. Black lines represent the mean, and edges of gray boxes are 25th and 75th percentiles at each time point of (A) normal force for plateau levels of 1.8, 2.2, and 2.5 N: loading 0.6–1.1 s, plateau 1.1–4.3 s, and unloading 4.3–5 s; and (B) torque for plateau levels of −3.5, −2.0, +2.0, and +3.5 mNm: loading 1.9–2.3 s, plateau 2.3–3.8 s, unloading 3.8–4.2 s, and torque reversal 4.2–4.6 s.

Fig. 3. Example of feature extraction procedure for the number of 10 ms-wide time bins contained within a window (L\text{win}) = 5. A: spike events (80 ms), c^1_{a,r} from afferent 1 (a = 1) and afferent 2 (a = 2), for stimulus s = 1, and repetition r = 1. B: binned spike events. C: 1st 3 windows of binned spike events. D: concatenation of windows to form feature vectors, x^1_{s,r}, with time (and w) increasing from top to bottom.
analyzing a temporal pattern. Furthermore, the literature suggests that the spike trains from tactile afferents provide context information, which can trigger corrective actions, commencing \( \sim 100 \text{ ms} \) after contact (Johansson and Flanagan 2009). For these reasons, three values of \( L_{\text{win}} \) (two, five, and 10 bins) were investigated, giving window lengths of 20, 50, and 100 ms, respectively. Larger values of \( L_{\text{win}} \) would result in estimation delays too large to be relevant in the context of continuous sensory feedback to facilitate manipulation. The windowed data, \( \mathbf{v}_{a,s}^{w} \), for window \( w \in \{1,...,N_{\text{win}}\} \) of stimulus set \( s \), repeat \( r \), afferent \( a \), is an array of binned spike counts, where \( N_{\text{aff}} = N_{\text{win}} = L_{\text{win}} + 1 \); i.e., for \( L_{\text{win}} = 2, N_{\text{win}} = 499 \), and when \( L_{\text{win}} = 5, N_{\text{win}} = 496 \), and for \( L_{\text{win}} = 10, N_{\text{win}} = 491 \).

\[
\mathbf{y}^{w} = \mathbf{w}^{T} \mathbf{v}_{a,s}^{w} = \left[ \mathbf{w}^{T} \mathbf{v}_{a,s}^{1}, ..., \mathbf{w}^{T} \mathbf{v}_{a,s}^{L_{\text{win}} - 1} \right]
\]

The feature vector \( \mathbf{x}_{a,s}^{w} \), for stimulus set \( s \), repeat \( r \), window \( w \), is the concatenation of \( \mathbf{v}_{a,s}^{w} \) for all afferents \( \in \{1,...,N_{\text{aff}}\} \) (Fig. 3D).

\[
\mathbf{x}_{a,s}^{w} = \left[ \mathbf{x}_{1,s}^{w}, ..., \mathbf{x}_{N_{\text{aff}},s}^{w} \right]
\]

There is a delay between a stimulus causing deformation in a mechanoreceptor and the recording of a spike in the associated afferent in the median nerve at wrist level (Darian-Smith and Kenins 1980); therefore, information about a stimulus at a particular time will be conveyed in the afferent spiking after that time. For this reason, the scalar target values, i.e., each row of \( \mathbf{y} \), were the value of the normal force (in the case of the normal-force model) or torque (in the case of the torque model) at the first bin in the window, corresponding to the feature vector in the same row of \( \mathbf{X} \). Hence, the models operate by waiting for spikes to occur during the analysis window following the time of interest and then retrospectively comparing against the sensor-measured force or torque at the start of the analysis window.

Cross-validation. A cross-validation procedure was used to obtain an estimate of generalized regression-model performance (Duda et al. 2001). For each stimulus type (normal force and torque), a 15-fold (i.e., leave-six-out) cross-validation \( (N_{\text{stim}} = 15, N_{\text{rep}} = 6) \) was performed, where all six repetitions of a normal-force/torque combination were left out for training, and this combination was tested using the trained model. That is, \( 84 \times N_{\text{win}} \); i.e., \( (N_{\text{stim}} - 1) \times N_{\text{rep}} \times N_{\text{win}} \), feature vectors were used for training, i.e., to learn the regression weights, and the remaining \( 6 \times N_{\text{win}} \) feature vectors were used for testing. This was performed 15 times, and each feature vector was used as the test case exactly once. For example, the feature vectors used for training for fold one were \( \mathbf{x}_{a,s}^{w} \) for \( s \in \{2,...,N_{\text{stim}}\} \), repeat \( r \in \{1,...,N_{\text{rep}}\} \), and \( w \in \{1,...,N_{\text{win}}\} \). The testing set for each fold contains all repetitions of a stimulus combination of normal force and torque. The stimulus combination in the testing set was not seen during the model training.

The output of the cross-validation is an array of weights \( \mathbf{d}_{f,i} \) for each fold \( f \in \{1,...,N_{\text{stim}}\} \), afferent \( a \in \{1,...,N_{\text{aff}}\} \), and each bin within a window \( i \in \{1,...,L_{\text{win}}\} \)

**Regression performance analysis.** For the normal-force and torque models, the mean squared error (MSE) was calculated for each fold of cross-validation

\[
\text{MSE}_{f} = \sum_{j=1}^{n} \left( \mathbf{y}_{j} - \mathbf{y}_{j}^{*} \right)^{2}/n,
\]

where \( \mathbf{y}_{j} \) is the target value, and \( \mathbf{y}_{j}^{*} \) is the estimate value; where \( j \) sums over all time bins, for which an estimate was made in the test cases of fold \( f \in \{1,...,N_{\text{stim}}\} \); and \( n \) is the number of time bins in the test cases in each fold; i.e., \( n = N_{\text{rep}} \times N_{\text{win}} \).

To determine the baseline of performance for statistical comparison, permutation models for normal force and for torque were developed by performing cross-validation, where the target values were permuted randomly, and the feature vectors remain unchanged (Nichols and Holmes 2002); i.e., the time order of the target forces and torques was shuffled. The mean of the MSE for the 15 folds (mean MSE) was calculated. This was repeated 50 times, and the mean and SD of the MSE for 50 repetitions were calculated, providing a performance baseline with which other models could be compared.

**RESULTS**

**Combined SA-I/FA-I models.** In this section, the performance of the normal-force and torque-combined SA-I/FA-I models are evaluated, and the effects of varying window lengths are presented.

The MSE from the 15-fold cross-validation for the normal force and torque is shown in Table 1 for the three values of \( L_{\text{win}} \). The mean and SD from 50 repetitions of model evaluation are also presented in Table 1, randomly permuting the temporal order of the normal-force and torque values for each repeat. The metric used to evaluate any one of these 50 repeats is the mean MSE across all 15 cross-validation folds. The \( P \) value of a one-sample \( t \) test between the mean MSE for the 15 folds of the normal-force and torque-combined SA-I/FA-I models and that of the 50 permutations of the permutation model with the same \( L_{\text{win}} \) is also reported in Table 1.

At all three \( L_{\text{win}} \) values, a one-sample \( t \) test indicated a significant difference between the mean MSE for the 15 folds of the combined SA-I/FA-I model (Table 1) and that of the 50 permutations of the permutation model (Table 1) for both normal force and torque \( (P \leq 0.001; \text{Table 1}) \). The smallest MSE in the normal force and torque is observed when \( L_{\text{win}} \) is equal to 10 bins (a window length of 100 ms).

| \( L_{\text{win}} \) | Window length, ms | Normal-force MSE, \( N^{2} \) | | Torque MSE, mNm\^2 | |
|---|---|---|---|---|
| | Mean for 15 folds (SD) | Mean of 50 means for 15 folds (SD) | \( t \)-Test, \( P \) value | Mean for 15 folds (SD) | Mean of 50 means for 15 folds (SD) | \( t \)-Test, \( P \) value |
| 2 | 20 | 0.216 (0.041) | 1.388 (0.006) | 5.50E-22* | 0.640 (0.208) | 1.660 (0.006) | 3.30E-12* |
| 5 | 50 | 0.083 (0.017) | 1.255 (0.005) | 2.70E-27* | 0.356 (0.094) | 1.681 (0.001) | 6.50E-18* |
| 10 | 100 | 0.045 (0.013) | 1.190 (0.005) | 6.70E-29* | 0.242 (0.056) | 1.716 (0.002) | 4.00E-20* |

MSE, mean squared error; SA-I, slow-adapting type I; FA-I, fast-adapting type I; \( L_{\text{win}} \), number of 10 ms-wide time bins contained within a window. \( *P \leq 0.001 \).
The combined SA-I/FA-I model normal-force and torque estimates from the 15-fold cross-validation for \(L_{\text{win}} = 10\) are shown in Fig. 4, respectively. The number of estimates used to produce the median and 25th–75th percentile estimates for the normal force (Fig. 4A) is five torque levels \(N_{\text{rep}}\); i.e., 30 cases for each of the three normal-force levels. Similarly, the total number of estimates used to produce the median and 25th–75th percentile estimates for the torque estimate (Fig. 4B) is three normal-force levels \(N_{\text{rep}}\); i.e., 18 cases for each of the five torque levels.

This demonstrates that a multiple-regression model, using windows of binned spike counts \((L_{\text{win}} = 10\) bins\) from only 83 afferents (58 SA-I and 25 FA-I) as features, can estimate the normal force and torque (Fig. 4) with relatively small error. The mean MSE for the combined SA-I/FA-I model normal-force estimate (0.045 N\(^2\); Table 1) is significantly smaller \((P < 0.0001; \text{Table 1})\) than that of the baseline permutation model, with \(L_{\text{win}} = 10\) (1.190 N\(^2\); Table 1). There are a number of regions during the normal-force plateau phase (1.1–4.3 s), where the interquartile range of estimates for the three normal-force levels do not overlap (Fig. 4A). Furthermore, during the normal-force loading and unloading phases (0.6–1.1 s and 4.3–5 s, respectively), the estimate has a gradient similar to that of the target. Similarly, the mean MSE for the combined SA-I/FA-I model torque estimate [0.242 (mNm)\(^2\); Table 1] was significantly smaller \((P < 0.0001; \text{Table 1})\) than that of the baseline permutation model, with \(L_{\text{win}} = 10\) [1.716 (mNm)\(^2\); Table 1]. During the torque-plateau phase (2.3–3.8 s), the five torque-plateau levels can be distinguished; however, the estimate seems to decay with time, most likely due to SA-I afferent adaptation, which is not captured by the current model (Fig. 4B). FA-I afferents generally do not fire once the plateau phase is reached.

The contribution of the different afferent types were determined using the weights calculated during cross-validation of the combined SA-I/FA-I models. For the SA-I afferent contribution, the weights for the FA-I afferents were set to zero, and the estimates for the test cases for each fold were recalculated. Similarly, for the FA-I afferent contribution, the weights for SA-I afferents were set to zero, and the estimates for the test cases for each fold were recalculated. The sum of the estimates in Fig. 5, A and B, result in the estimates in Fig. 4A, and the sum of the estimates in Fig. 5, C and D, result in the estimates in Fig. 4B.

In the combined SA-I/FA-I models, the contribution of the SA-I afferents is important during the plateau phases of stimulus, as during these static phases, the FA-I afferents are not responding and therefore, are not contributing to the estimates. During the transient phases of stimulus, large errors can be seen from the SA-I afferent contribution (Fig. 5, A and C). The contribution of the FA-I afferents is observed to counteract the SA-I afferent estimate errors during stimulus transients (Fig. 5, B and D); during loading and unloading of normal force and torque, in most cases where the SA-I afferent contribution has large positive errors, the FA-I afferent contribution can be seen.

![Fig. 4. Combined SA-I/FA-I models (\(L_{\text{win}} = 10\)). A: estimate of normal force for plateau of 1.8, 2.2, and 2.5 N. Dotted line is median estimate; solid line is target. Edges of gray region are the 25th and 75th percentiles. B: estimate of torque for plateau of \(-3.5, -2.0, 0, +2.0,\) and \(+3.5\) mNm.](image)

![Fig. 5. Contribution to combined SA-I/FA-I models (\(L_{\text{win}} = 10\)) of (A) SA-I afferents and (B) FA-I afferents to normal-force estimate for plateau of 1.8, 2.2, and 2.5 N and (C) SA-I afferents and (D) FA-I afferents to torque estimate for plateau of \(-3.5, -2.0, 0, +2.0,\) and \(+3.5\) mNm for combined SA-I/FA-I models (\(L_{\text{win}} = 10\)). See Fig. 4 legend for key of line descriptions.](image)
to have large negative errors and vice versa. Thus in essence, the model here uses the FA-I afferent responses to compensate for the dynamic effects of SA-I afferent responses.

The stimulus onset (start of normal-force loading) is at 0.6 s. The contributions of the SA-I and FA-I afferents start at ~0.5 s (Fig. 5), that is, 100 ms before the stimulus onset. This is not the case for the final estimate of normal force, where the estimate rises from zero (above the noise level) at approximately the same time as the stimulus onset. This is a direct result of the length of the window used ($L_{win} = 10$, i.e., 100 ms) and the fact that the model uses a 100-ms window to estimate the normal force and torque at the time corresponding to the first bin of the window (see Multiple regression); when the afferent spikes at 0.6 s, this spike will be included in the window starting at 0.51 s and will therefore contribute to the estimate at 0.51 s.

Examples of individual afferent-response patterns. To demonstrate the complexity of the afferent responses and the power of the modeling approach in extracting useful features, this section shows the responses of some individual afferents to the applied stimulus.

There was large variability in response properties between afferents, and each afferent had its own unique response pattern. Raster plots in Fig. 6 exemplify the response patterns of two SA-I afferents and two FA-I afferents. The normal-force and torque model weights assigned for the windowed data from each afferent are also shown, and the locations of the RFCs are included for reference.

The response of SA-I afferent #13 is observed to be scaled to normal force during the loading (0.5–1.1 s) and plateau region (1.1–4.3 s), and during normal-force unloading (4.3–4.6 s), the afferent response is suppressed (Fig. 6A, i). There is little variability in the response to normal force for multiple applications; this can be seen in the normal-force plateau before the application of torque (1.1–1.9 s; Fig. 6A, ii). Furthermore, during the application of torque, an observable difference in response, compared with the background normal-force response, can only be seen in the case of a torque plateau of +3.5 mNm (Fig. 6A, ii). The weights assigned to windowed data from this afferent for the normal-force model and the torque model were positive (Fig. 6A, iii).

The response of SA-I afferent #21 appears to be scaled by normal-force magnitude during the plateau region (Fig. 6B, i). There is, however, a large intertrial variability in the response to normal force, which can be observed during the normal-force plateau before the application of torque (1.1–1.9 s; Fig. 6B, ii). The afferent spiking activity is suppressed when a positive torque is applied and is scaled by torque magnitude when a negative torque is applied (1.9–4.2 s; Fig. 6B, ii). The weights assigned to the windowed data from SA-I afferent #21 for the normal-force model were approximately zero (probably due to the variability), and the weights for the torque model were negative, reflecting the directional sensitivity of this afferent, since the response was scaled by negative torque and inhibited by positive torque (Fig. 6B, iii).

![Fig. 6. Example of individual afferent-response patterns and combined SA-I/FA-I model weights ($L_{win} = 10$). Raster plots for (A) SA-I #13, (B) SA-I #21, (C) FA-I #4, and (D) FA-I #22 for (i) normal-force plateaus of 1.8, 2.2, and 2.5 N for 1 trial with no torque was applied; (ii) torque-plateau values of −3.5, −2.0, 0, +2.0, and +3.5 mNm for 1 trial with a normal force of 2.2 N; (iii) the mean weights across 15-folds for bins within a window for the normal-force (dashed line) and torque models (solid line); and (iv) the RFC indicated by a “+” and 1st contact point of the stimulus applicator indicated by an “X.” Top (X): target values for (i) normal force and (ii) torque as a timing reference for the raster plots.](http://jn.physiology.org/ by 10.220.33.3 on November 2, 2016)
afferent contributes to the torque model only by responding to normal force. Therefore, these responses to normal force must be canceled that encode torque will respond to normal force as well. insensitive to normal force; however, most of the afferents stimuli, has pronounced negative weights in the torque weights assigned to the windowed data from FA-I afferent #22, which does not respond to the torque loading of (0.6–1.1 s). There is no response to normal-force unloading (4.3–4.6 s; Fig. 6C, i) or to torque loading (1.9–2.3 s) or unloading (3.8–4.2 s; Fig. 6C, ii). The response to normal-force loading appears to be scaled by normal-force magnitude. The weights assigned to the windowed data from this afferent for the normal-force and torque models were negative (Fig. 6C, iii), probably to offset large transient responses to normal-force loading from SA-I afferents that have been assigned positive weights in the normal-force and torque models, such as in the case of SA-I afferent #13 (Fig. 6A).

In contrast, FA-I afferent #22—an afferent with a similar receptive field location to FA-I afferent #4 (Fig. 6D, iv, and Fig. 6C, iv, respectively)—is observed to respond to normal-force loading and unloading, as well as torque loading and unloading (Fig. 6D, i and ii). The response to normal-force loading appears to be scaled by normal-force magnitude; however, the response to normal-force unloading does not appear to be scaled (Fig. 6D, i). The response to torque loading (1.9–2.3 s) appears to be scaled to torque magnitude when torque is positive, and the afferent is less sensitive when torque is negative (Fig. 6D, ii). The afferent also responds in a scaled fashion when negative torque is unloaded (Fig. 6D, ii). The weights assigned to the windowed data from FA-I afferent #22 for the normal-force model were close to zero, and the weights for the torque model were negative (Fig. 6D, iii).

FA-I afferent #22, which does not respond to the torque stimuli, has pronounced negative weights in the torque model. This is because the torque model is required to be insensitive to normal force; however, most of the afferents that encode torque will respond to normal force as well. Therefore, these responses to normal force must be canceled in the torque model. The negative torque model weights assigned to this afferent appear to be doing just that, as the afferent contributes to the torque model only by responding to normal force without response to torque. Similarly, the torque model contributions from SA-I afferents may cancel out the normal-force effect by having positive and negative weights. This approach would work very efficiently, because a roughly similar number of afferents are expected to be scaled by positive and negative torque (Birznieks et al. 2010).

Further analysis of the individual afferent responses and model weights was beyond the scope of the current work; however, the observations made above indicate that there is a wealth of information that could be extracted from afferent responses using the linear regression model.

**SA-I-only models.** To investigate whether the population of SA-I afferents could estimate the stimulation parameters on their own, the SA-I-only models were trained using only the spike trains from 58 SA-I afferents in the feature matrix, and the target values were the same as for the combined SA-I/FA-I models; i.e., the target for each window was the value of the stimulation parameter at the start of the window.

The SA-I-only model estimates for normal force and torque are shown in Fig. 7, A and B. The normal-force and torque estimates (Fig. 7, A and B, respectively) are similar to those of the combined SA-I/FA-I model (Fig. 4, A and B, respectively); however, in each case, the combined SA-I/FA-I model outperforms the SA-I-only models. The MSE of the normal-force and torque estimates of the combined SA-I/FA-I model and the SA-I-only model are presented in Table 2. One-way ANOVA was performed to compare the mean MSE for 15 folds of both models and to determine whether the inclusion of FA-I responses in the combined SA-I/FA-I models results in a significant performance improvement compared with the SA-I-only models. The P values of the ANOVA are reported in Table 2. For normal force, the MSE increased significantly in the SA-I-only model compared with the combined SA-I/FA-I model (P < 0.01), but the difference in MSE for torque was insignificant (P > 0.05).

**DISCUSSION**

The neural decoding problem. Solving the neural decoding problem is important for our understanding of the fundamentals of neural coding mechanisms as well as for the design of neural prosthetic devices (Donoghue 2002). A number of studies investigating the neural decoding problem use regression methods, typically multiple linear regression in the time or frequency domain (Bensmaia and Miller 2014; Nicolelis 2001; Serruya et al. 2002; Wessberg et al. 2000). Most of these studies investigate neural decoding in the cortex for the purpose of brain-machine interface applications or for controlling prosthetics.

**Table 2.** **MSE of normal-force and torque estimates (mean and SD for 15 folds) of different models**

<table>
<thead>
<tr>
<th>Model</th>
<th>Normal-force MSE, N^2</th>
<th>Torque MSE, (mNm)^2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean for 15 folds SD</td>
<td>Mean for 15 folds SD</td>
</tr>
<tr>
<td>Combined SA-I/FA-I, L_{win} = 10</td>
<td>0.045 0.013</td>
<td>0.242 0.056</td>
</tr>
<tr>
<td>SA-I only, L_{win} = 10</td>
<td>0.061 0.014</td>
<td>0.284 0.078</td>
</tr>
<tr>
<td>1-Way ANOVA, P</td>
<td>0.0026*</td>
<td>0.1039</td>
</tr>
</tbody>
</table>

*P ≤ 0.01.

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Decoding in the case of tactile input would involve the extraction of all stimulation parameters, including, but not limited to, all three dimensions of force and torque and the region of interaction on the finger, as well as the curvature, compliance, and texture of the stimulating object and the friction of the interface. There are no previous studies demonstrating continuous decoding of tactile input.

Behavioral studies concerning dexterous manipulation have demonstrated that torque about the axis normal to the grasp surface strongly influences the normal force required for grasp stability and that sensorimotor programs adjust grip force according to the total load, comprising both tangential forces and torques (Goodwin et al. 1998; Kinoshi et al. 1997). Therefore, the understanding of the encoding of normal force and torque is essential for revealing sensorimotor control mechanisms involved during object manipulation.

In previous work, classification and regression of force and torque-plateau levels depended on a priori knowledge of possible stimulus combinations and stimulus-onset times. Furthermore, validation of these methods was performed with only a subset of the stimulus, during which normal force was held constant, and torque was loaded (Birznieks et al. 2010; Fu et al. 2012; Redmond et al. 2010a, b). Classification, as such, is a far less difficult task than estimating the stimulation parameters continuously throughout the entire stimulation period (during which multiple stimulation parameters are changing simultaneously), using a single, fixed-parameter model.

The regression approach adopted here is superior to the classification approach, as it can estimate a continuum of values for normal force and torque; classification, on the other hand, may only classify the stimulation parameters into a known and fixed number of classes. The current approach has been demonstrated to estimate accurately normal force and torque for stimulus combinations that have not been encountered by the model during training and does so without the need for retraining and therefore, can continuously estimate the stimulus parameters in a real-time fashion. This is the first study achieving this by extracting information from the tactile afferent responses. The estimation of normal-force and torque parameters from tactile afferent data is a step toward the complete decoding of tactile afferent signals into a full stimulus description. This achievement is comparable with and may have future implications similar to influential work, demonstrating the ability to extract information from cortical motor neurons that lead to the development of brain-machine interfaces.

There exist a number of alternative pattern recognition and modeling techniques that could be used in place of the least-squares, multiple-regression technique used here. However, regression is a simple and widely known technique, and the intrinsic properties of a linear model applied to binned windows make it a very powerful, yet relatively straightforward, tool for estimating stimulus parameters. One of the expected benefits of regression, compared with more advanced techniques, is that the regression weights derived from these models can be interpreted more easily to understand how individual afferents contribute.

The raster plots in Fig. 6 illustrate the complex response patterns exhibited by the SA-I and FA-I afferents, which the regression model must combine to estimate the stimulus parameters. Some afferents were observed to provide a significant contribution to the model of one but not the other stimulus parameter. For example, in the torque model, an afferent that only encodes torque may be assigned a large weight, and in the normal-force model, the same afferent may be assigned a weight of zero; this is the case for SA-I afferent #21 (Fig. 6B). Other afferents were observed to contribute to the encoding models of individual stimulus parameters to different extents.

Examination of the model weights has also revealed a mechanism for how the static magnitude of one parameter (for example, normal force) could be signaled by the population of afferents, regardless of the changing, superimposed stimuli (for example, torque), which is likely to evoke a response in the same population of afferents. For example, to estimate normal force from two afferents, where the first afferent responds to normal force but is also influenced by the application of torque, and the second afferent responds to normal force but to a lesser degree than torque, the second afferent would be assigned a negative weight to cancel the effect of superimposed torque on the response of the first afferent to normal force. In this manner, the regression model combines the complex response patterns of individual afferents in a population to recover the stimulus features.

This work is just the first step. By analyzing the model weights, the regression model can be used to understand better information content in the tactile afferents. The weights may be analyzed, and the contribution of different afferents could be assessed depending on the afferent type, the receptive field location, or some other response properties. The interpretation of the model weights may be intuitive, such as in the example given above for combining contributions of SA-I afferent #13 and FA-I afferent #4, or may require more sophisticated assessment methods, but nevertheless, this demonstrated approach will reveal new information about how interactions between different stimulus parameters could be disentangled for complex population responses. In the case of encoding more numerous concurrent stimulus parameters, more complex interaction effects may be revealed, and thus the model will provide a tool to observe new sensory-analysis mechanisms and test specific hypotheses for how afferent input is processed by the brain. A more detailed analysis of the weights was beyond the scope of this particular study.

Model performance. Throughout the stimulus, the estimates of normal force and torque follow the target values reasonably well. This is true when only a normal force is applied (normal-force loading and normal-force plateau before the torque-loading phase) and also when both normal force and torque are applied (torque loading, plateau and unloading phase, and torque reversal). This demonstrates that the combined SA-I/FA-I models are able to decode the afferent responses in the presence of multiple, independently changing stimulus parameters.

The robustness of the modeling approach is further evident in the normal-force and torque estimates during the overlap between the torque reversal and the normal-force unloading (4.3–4.6 s) when both the torque and normal force are changing simultaneously. During this time, the combined SA-I/FA-I models reasonably estimate the normal force and torque, indicating that even in the presence of multiple, simultaneously changing stimulus parameters, the model is able to decode the afferent responses.
The model was evaluated using a cross-validation procedure to assess how performance will generalize to an independent data set (Duda et al. 2001). In the 15-fold cross-validation approach taken here, for each fold, all six repetitions of a normal-force and torque combination were left out for training, and this stimulus combination was then used to test the model. In other words, for each fold, the stimulus combination in the testing set was not encountered during the model training. This validation approach demonstrates the versatility of the modeling approach—the model is able to estimate instantaneous normal force and torque when the model was not exposed to the stimulus combination during training.

The feature vectors for the regression model represent the responses of an ensemble of afferents, generated by combining responses from independently recorded afferents. This means that correlated noise is unlikely to be represented by the afferent responses, which normally limit the ability of upstream processes to average out noise (Faisal et al. 2008). With the use of an ensemble, however, a different type of experimental noise was introduced, due to the variability of the stimulus application. At this stage, it is difficult to determine, however, how the absence of correlated noise and the presence of trial-to-trial variability would affect the models’ ability to decode stimulus parameters.

Effect of window size. The smallest estimate error is observed for $L_{win} = 10$ (i.e., 100 ms window). A trend can be seen in Table 1, where for longer windows, the model estimate error is smaller. The stimulation protocol here has large periods of static force and/or torque (e.g., plateau phases of normal force and torque), which may account for better performance in a model with longer windows, as variation in firing rates is averaged out over a longer window, when the force/torque is static. However, it is expected that there is an upper limit to the window size, beyond which the effect of averaging out variation in firing rates would become disadvantageous. Since the model continuously outputs instantaneous values of the stimuli, averaging over longer periods of time would take into account response properties not relevant for a particular mechanical event and would deteriorate model performance, particularly during the dynamic phases of stimulation. Furthermore, for sensorimotor control, the availability of information in possibly shorter time provides great advantage. Further investigation is required to determine the ability of this approach to generalize to other stimulation protocols using more dynamic force and torque waveforms.

SA-I afferents. In the current approach for estimating the normal force and torque, the SA-I afferents are essential during the static phases of the stimulus, as the FA-I afferents are not responding at these times. In the combined SA-I/FA-I models, large errors observed in the contribution of the SA-I afferents (Fig. 5, A and C) during the transient phases of the stimulus are counteracted by the contribution of the FA-I afferents (Fig. 5, B and D). This may allow larger weights to be assigned to SA-I afferents with large transient responses to changing normal force and possibly linear responses to different levels of static normal force. In the case where the transient response of such an SA-I afferent was not counteracted, the weight for the afferent may be lower to minimize overall MSE, as large errors during stimulus loading/unloading may outweigh the benefit of smaller errors during the stimulus plateau.

In the SA-I-only models (Fig. 7), the estimate of normal force and torque is similar to those of the combined SA-I/FA-I models (Fig. 4). The SA-I-only models do not exhibit the large errors during loading and unloading of normal force and torque that are observed in the SA-I contribution to the combined SA-I/FA-I models (Fig. 5, A and C). This indicates that the weights were reassigned to decrease the error during stimulus transients, which may also affect the estimate error during stimulus plateau regions.

The difference in contribution of the SA-I afferents to the combined SA-I/FA-I models and to the SA-I-only models highlights an intriguing neurophysiological question concerning how the dynamic component of the SA-I afferent responses may be compensated to signal instantaneous force/torque amplitude without overshoot. The models reveal one of the possible neural mechanisms for this by combining inputs from afferents with different response properties or even from different afferent types (SA-I and FA-I). For example, the response of SA-I afferent #13 is observed to be scaled to the normal-force magnitude; however, it exhibits a large transient response during the normal-force loading (Fig. 6A, i), whereas the FA-I afferent #4 responds with a large transient response during the normal-force loading and does not respond at any other time during stimulation (Fig. 6C, i). SA-I afferent #13 is assigned a positive weight (Fig. 6A, iii), and FA-I afferent #4 is assigned a negative weight (Fig. 6C, iii) for the normal-force model. The combination of the contribution of afferents in this way would result in an estimate that is scaled by normal force with little or no overshoot during normal-force loading. For the normal-force model, this combined contribution would require further combination with other afferents to reduce the effect of the scaled responses to positive torque observed in SA-I afferent #13 (Fig. 6A, ii), as detailed in the first section of DISCUSSION.

The SA-I-only models can estimate normal force and torque with only a small increase in error compared with the combined SA-I/FA-I models (Table 2). This is in agreement with reports by Birznieks et al. (2010), who showed that a Parzen classifier, trained with the cumulative spike counts from the population of SA-I afferents, could distinguish normal-force levels, torque magnitude, and torque direction. Redmond et al. (2010b) also showed that when performing optimization of the afferent subset (from an original afferent set of 58 SA-I and 23 FA-I) for normal-force plateau-level classification, only 16 SA-I and one FA-I afferents were required, again using cumulative spike count from the start of torque-loading phase.

FA-I afferents. The mean MSE for 15 folds of the combined SA-I/FA-I model for the normal-force estimate is 73% of the mean MSE for 15 folds of the SA-I-only model for normal force (Table 2), indicating that the FA-I afferents contribute significantly ($P < 0.01$) to the estimate. For torque, the mean MSE for 15 folds of the combined SA-I/FA-I model is 85% of the mean MSE for 15 folds of the SA-I-only model (Table 2), indicating that the FA-I afferents improve the estimate of torque, however insignificantly ($P > 0.05$). As discussed above, the contribution of the FA-I afferents in the combined SA-I/FA-I models was counteracting the transient responses of the SA-I afferents.

A requirement of the analysis approach described here is that afferents respond during static stimuli; therefore, an alternative analysis approach is needed for FA-I afferents to provide...
expected to provide deeper insight into critical features of various stimulus features from the population responses to weights can reveal hypothetical mechanisms for disentangling model weights. It has also been demonstrated how the model contributed of individual afferents within a population to estimation of additional independent tactile parameters, such as shear to recover continuous stimulus features. The ability of the FA-I afferents to provide continuous estimates of the stimulus prescription here requires afferents to respond during static stimuli; therefore, an alternative analysis approach is necessary for FA-I afferents to provide continuous estimates of the stimulus parameters on their own.

For the first time, it has been demonstrated how the responses from a population of tactile afferents may be decoded to recover continuous stimulus features. The ability of the model to generalize to other stimulation protocols and extraction of additional independent tactile parameters, such as shear force, requires further exploration. Future work will investigate the contributions of individual afferents within a population to the output of the multiple-regression models by analyzing the model weights. It has also been demonstrated how the model weights can reveal hypothetical mechanisms for disentangling various stimulus features from the population responses to complex stimuli, regardless of the interaction effects. This is expected to provide deeper insight into critical features of receptor properties and their relevance to encoding tactile information during object manipulation.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: H.K., I.B., and S.J.R. conception and design of research; I.B. performed experiments; H.K., I.B., and S.J.R. analyzed data; H.K., I.B., and S.J.R. interpreted results of experiments; H.K. prepared figures; H.K. and S.J.R. drafted manuscript; H.K., I.B., and S.J.R. edited and revised manuscript; H.K., I.B., and S.J.R. approved final version of manuscript.

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