Analysis of the effects of firing rate and synchronization on spike-triggered averaging of neuronal output

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Abstract— Spike-triggered averaging (STA) has been used experimentally to identify multiple features of neuronal output including post-synaptic potentials, whole muscle facilitation, and motor unit output. Using only the most basic assumptions, we develop equations that predict the effects of neuronal firing rate and synchronization on STA. We use exact equations to show that, if the measured neuronal output is multidimensional, then the direction of STA is unaffected by firing rate in the absence of synchronization. We then extend these equations into a framework for analyzing synchronization, and show that under reasonable conditions the analysis of synchronization can be mapped to linear algebra. We consider whether the effects of synchronization can be removed, and if there are neuronal output configurations for which STA is insensitive to synchronization. We conclude that STA can give insight into how neuronal synchronization is organized with respect to neuronal output.

I. INTRODUCTION

Spike-triggered averaging (STA) is one of the most widely used system identification techniques in neuroscience. STA involves extracting sections of a continuous input variable (e.g. visual stimulus) or output variable (e.g. joint torque, post-synaptic potential) based on the observed discharges of a single neuron, and then averaging the sections together. In motor neuroscience, it can be used to explore synaptic connections between neurons [12], [15], demonstrate facilitation of muscle activity by cortical cells [7], and to estimate force generating properties of single motor units [3], [18]. It has been shown in numerous experimental and theoretical studies that STA of joint torque based on motor unit discharge times is strongly influenced by both firing rate [4], [16] and synchronization [19], [10]. Synchronization refers to the increased probability of simultaneous discharge between a pair of motor units relative to chance, and has been studied in many muscles [6]. The distortion of the twitch waveform by firing rate is well-understood [1], [13], but there has been no comprehensive framework that predicts the effects of both firing rate and synchronization. This paper

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is an effort to provide this framework specifically in the case of estimating motor unit properties, and therefore the results will be discussed in these terms. However, the results contained within are applicable to any application of STA where a continuous function of neuronal output is averaged based on neuronal discharge times; it may be possible to replace motor unit twitch by post-synaptic potential or post-spike facilitation, depending on how STA is used.

II. METHODS

The theoretical framework and assumptions are illustrated in Figure 1. The key assumptions of this model were that

1) Motor unit force sums linearly among units, and
2) Force within a single motor unit can be described by the superposition of impulse responses (twitches), though the impulse response gain can vary through time in a stochastic or nonlinear way.

With regard to the first assumption, nonlinear summation of motor unit force is most readily observed in otherwise passive muscle, and does not appear to be physiologically significant when large portions of muscle are active (see [17] for review). Westling et al. [23] found that individual thenar motor units have straight force trajectories in the flexion/abduction plane of the thumb when activated by intra-neural stimulation, suggesting that motor unit action across multiple degrees-of-freedom can be approximated by a single vector. With regard to the second assumption, experiments have shown that the frequency response of motor units is consistent with a second-order, critically-damped linear model [18], [14]. However, the steady state force versus firing rate curve is nonlinear [11], which suggests a time-varying impulse response gain [8].

The analytical predictions were compared to the numerical model of Fuglevand et al. [8] for a motor unit population. This model specifies the contractile properties (peak force in arbitrary units (au) and contraction time in ms) of the set of motor units, as well as the dependence of motor unit firing rate on these properties and on the global level of excitation applied to the motor unit population. Simulations were performed over 120 s with a time step of 1 ms. Motor unit spike trains were generated independently with a constant coefficient of variation in their inter-spike interval of 20% [8]. Synchronization was then applied using the algorithm of Yao et al. [24]. Spikes selected for synchronization by this algorithm were shifted into exact alignment plus a normal random variable with mean zero and standard deviation of 1.67 ms [19]. Under these conditions, the expected width of synchronization peaks was 6 ms. Synchronization was
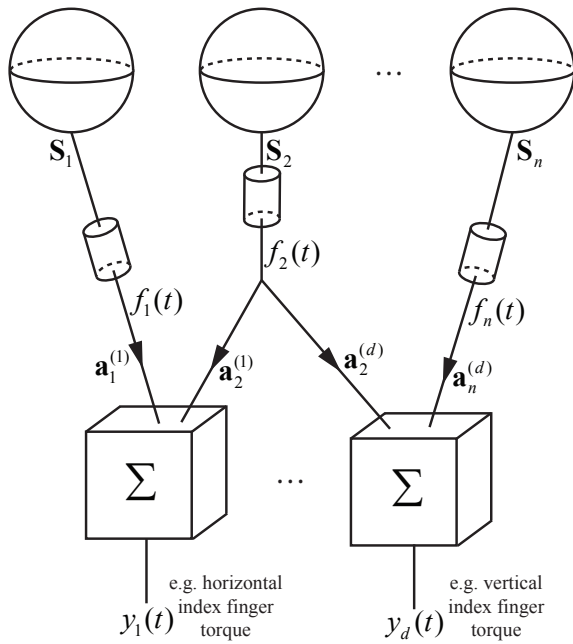
Fig. 1. The modelling framework for spike-triggered averaging. A population of n active motor units generates spike trains $\boldsymbol{S}_1, \ldots, \boldsymbol{S}_n$. These spike trains generate continuous-time joint torques $y_1(t), \ldots, y_d(t)$. The spike trains are transformed into continuous-time motor unit forces $f_1(t), \ldots, f_n(t)$ by time-varying linear transformations. The effect of $f_i(t)$ for some motor unit i may be confined to a single torque dimension, such as motor units 1 and n, or may span multiple torque dimensions such as motor unit 2. This information is encoded in the motor unit's "direction vector" which is a multidimensional vector $\boldsymbol{a}_i$ whose components specify the relative contributions made by motor unit i to the different dimensions of torque output.

measured between all active motor unit pairs using the synchronization index. Given a pair of motor units r and i, with unit r serving as the reference, let the synchronization probability p be the fraction of spikes discharged by unit r for which there is a spike in unit i within 6 ms. The synchronization index s was the difference between the actual synchronization probability and the synchronization probability when the spike trains were independent (prior to the application of the synchronization algorithm). Thus, $s = (p_{\text{actual}} - p_{\text{independent}})$. This synchronization index s was the same as the "extra spikes per trigger" used by Binder and Powers [2] and the synchronization index of DeLuca et al. [6].

We were interested in how STA would perform when multidimensional output torque is averaged based on a single reference spike train. Therefore, each motor unit was additionally described by a two-dimensional direction vector. The direction vector for motor unit i is labelled $\boldsymbol{a}_i$, and is a vector of length 1 that specifies the relative contribution of motor unit i to the two torque outputs. Motor unit i exerted force $f_i(t)$ along direction $\boldsymbol{a}_i$ so that the total torque output was the linear sum

$$\boldsymbol{y}(t) = \sum_{i=1}^{n} f_i(t)\boldsymbol{a}_i \qquad (1)$$

We were interested in how STA would perform in identifying direction vectors *if* they exhibited a broad range; thus the direction vectors were assumed to continuously span a range of 90°, which was observed from human thenar motor units using intraneural stimulation [21]; a broad range is also possible for human first dorsal interosseous motor units [20].

III. RESULTS

A. General Equations

It is possible to use the assumptions of Figure 1 to derive general equations that describe the STA process. Assuming that the neurons in Figure 1 generate output in parallel, it is possible to write

$$\boldsymbol{y}(t) = \sum_{i=1}^{n} f_i(t)\boldsymbol{a}_i + \boldsymbol{n}(t) \qquad (2)$$

where $\boldsymbol{n}(t)$ is a mean-zero i.i.d. random process associated with the measurement uncertainty inherent in observing the output torque vector $\boldsymbol{y}(t) = [y_1(t), \ldots, y_d(t)]$. Using assumption 2 for motor unit force generation, we can write

$$f_i(t) = \sum_{j=1}^{N_i} g_{ji} T_i(t - S_{ji}) \qquad (3)$$

where S_{ji} is the time of the jth spike in the ith motor unit, and g_{ji} is the impulse response gain in the output of ith motor unit at the time of the jth spike, and N_i is the number of spikes in neuron i. Inserting Equation 3 into Equation 2, we obtain an equation describing the output vector

$$\boldsymbol{y}(t) = \sum_{i=1}^{n} \boldsymbol{a}_i \sum_{j=1}^{N_i} g_{ji} T_i(t - S_{ji}) + \boldsymbol{n}(t) \qquad (4)$$

Applying STA involves knowing the spike times $\boldsymbol{S}_r$ from a reference motor unit r, and then averaging the output based on these spike times. Applying this process to Equation 4, we find that the STA trajectory $\boldsymbol{\sigma}_r(t)$ based on motor unit r is

$$
\begin{aligned}
\boldsymbol{\sigma_r}(t) &= \frac{1}{N_r} \sum_{k=1}^{N_r} \boldsymbol{y}(t + S_{kr}) \\
&= \sum_{i=1}^{n} \boldsymbol{a}_i \underbrace{\frac{1}{N_r} \sum_{k=1}^{N_r} \sum_{j=1}^{N_i} g_{ji} T_i(t + S_{kr} - S_{ji})}_{C_{ri}(t)} \\
&\quad + \sum_{k=1}^{N_r} \boldsymbol{n}(t + S_{kr}) \\
&= \sum_{i=1}^{n} C_{ri}(t)\boldsymbol{a}_i + \frac{1}{N_r} \sum_{k=1}^{N_r} \boldsymbol{n}(t + S_{kr}) \qquad (5)
\end{aligned}
$$

We are interested in the behavior of the STA process as N_r gets very large, and it clear by the Law of Large Numbers that the second term in Equation 5 approaches zero as $N_r \to \infty$. The first term of Equation 5 shows that STA is composed of weighted averages of the direction vectors,

the weighting functions we will refer to as *contribution functions*. Contribution functions can be expressed as

$$C_{ri}(t) = \frac{1}{N_r} \sum_{k=1}^{N_r} \sum_{j=1}^{N_i} \underbrace{g_{ji}}_{\text{random gain}} \; T_i(t + \underbrace{S_{kr} - S_{ji}}_{\text{random shift}}) \quad (6)$$

We denote the random gain g and the random shift x. For a given motor unit pair (r, i), there is a map $(k, j) \rightarrow (x, g)$ generating a locus of $N_r N_i$ points in the (x, g) plane. We convert Equation 6 into an integral by letting $f_{ri}(x, g)$ denote the fraction of shift-gain pairs per unit area from the spike trains of neurons r and i observed in the rectangle with lower left corner at (x, g), horizontal side length Δx, and vertical side length Δg. The integral expression for $C_{ri}(t)$ is

$$C_{ri}(t) = N_i \int_0^\infty \int_{-\infty}^\infty g T_i(t + x) f_{ri}(x, g) dx dg \quad (7)$$

We first note that Equation 7 predicts that, if the spike trains of all motor unit pairs in the population are independent, STA will accurately identify the direction of a_r without being able to accurately identify either the magnitude or time-course of $T_r(t)$. To show this fact, we note that if the spike trains of motor units r and i are independent, then $f_{ri}(x, g) = f_{ri,X}(x) f_{ri,G}(g)$ where $f_{ri,X}(x)$ and $f_{ri,G}(g)$ are fractions of points per unit length. Since there is no correlation between the spike trains of motor units r and i, $f_{ri,X}(x)$ is a constant function. Therefore,

$$C_{ri}(t) = N_i \int_0^\infty g f_{ri,G}(g) dg \int_{-\infty}^\infty T_i(t + x) f_{ri,X}(x) dx \quad (8)$$

Thus, $C_{ri}(t)$ is a constant function of t if $i \neq r$. Returning to Equation 5, we can see that

$$\boldsymbol{\sigma}_r(t) = C_{rr}(t) \boldsymbol{a}_r + c \quad (9)$$

$C_{rr}(t)$ does not necessarily have the same magnitude or time-course as $T_r(t)$, but nonetheless $\boldsymbol{\sigma}_r(t)$ points in the direction of $\boldsymbol{a}_r$.

Even weak synchrony between motor unit pairs may significantly complicate the use of STA, so the remainder of the paper is devoted to analytical tools for predicting the effects of synchronization on STA. When considering the entire set of active motor units, STA should be viewed as a time-varying linear map from the set of directions $\{a\}$ to the set of STA trajectories $\{\boldsymbol{\sigma}(t)\}$. This linear map can be visualized by the following matrix

$$\begin{bmatrix} \boldsymbol{\sigma}_1(t) \\ \boldsymbol{\sigma}_2(t) \\ \vdots \\ \boldsymbol{\sigma}_n(t) \end{bmatrix} = \begin{bmatrix} C_{11}(t) & C_{12}(t) & \cdots & C_{1n}(t) \\ C_{21}(t) & C_{22}(t) & \cdots & C_{2n}(t) \\ \vdots & \vdots & \ddots & \vdots \\ C_{n1}(t) & C_{n2}(t) & \cdots & C_{nn}(t) \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \boldsymbol{a}_2 \\ \vdots \\ \boldsymbol{a}_n \end{bmatrix} \quad (10)$$

We can write this equation compactly as $\boldsymbol{\Sigma}(t) = \boldsymbol{C}(t)\boldsymbol{A}$. If the motor unit population output $\boldsymbol{y}(t)$ is d-dimensional, then $\boldsymbol{A}$ is a $n \times d$ matrix with the ith row equal to $\boldsymbol{a}_i$ (represented as a row vector). $\boldsymbol{\Sigma}(t)$ is also a $n \times d$ matrix with the $\boldsymbol{\sigma}_i(t)$ trajectory represented as the ith row of $\boldsymbol{\Sigma}(t)$. We call $\boldsymbol{C}(t)$ the contribution matrix, $\boldsymbol{A}(t)$ the distribution of direction vectors, and $\boldsymbol{\Sigma}(t)$ the distribution of STA trajectories.

From the general equations, we are able to make one comment about the effect of synchronization. Note that all terms in the integral expression for $C_{ri}(t)$ (Equation 7) are positive. Therefore, the set $\boldsymbol{\Sigma}(t)$ are linear combinations of the set $\boldsymbol{A}$ with positive coefficients, so $\boldsymbol{\Sigma}(t)$ must be in the interior of $\boldsymbol{A}$. Thus, STA can only produce an underestimate for the range of direction vectors $\boldsymbol{A}$.

B. Uniform approximation for synchronization analysis

The purpose of this section is to show that, under certain conditions, the analysis of synchronization can be mapped to linear algebra. The conditions underlying this analysis is that the set of active neurons can be approximated as homogenous in discharge statistics and that there is one impulse response $T(t)$ common to all neurons. By comparison to a simulated model of a motor unit population, we will show that the homogenous approximation well-describes the full simulated system in which motor units can have different firing rates and motor unit impulse response properties are different among the populations of units. Presumably, the quality of approximation comes from the fact that differences in motor unit properties are averaged out in the STA process. The homogenous approximation retains the synchronization structure of the motor unit pairs, and generates a simple framework for analyzing different synchrony configurations.

The simulation of contribution functions strongly suggests that the linear scaling of contribution function magnitude by the synchronization index: $C_{ri}(t) \approx s C_{rr}(t) + c$, where c is an arbitrary constant. Figure 2 compares $C_{ri}(t)$ and $C_{rr}(t)$ both in an example (A), and across a range of synchronization probabilities and firing rates (B). The results of these simulations suggest that $C_{ri}(t) \approx s C_{rr}(t) + c$ is an appropriate approximation for a pair of motor units with identical properties under the conditions of relatively low variability in the discharge statistics (i.e. $CV \approx 0.2$).

The homogenous approximation allows the contribution function matrix to be represented by the product of a single function of time $C(t)$, and a symmetric time independent matrix $\boldsymbol{C}_H$ ("H" for "homogenous"):

$$\begin{bmatrix} \boldsymbol{\sigma}_1(t) \\ \boldsymbol{\sigma}_2(t) \\ \vdots \\ \boldsymbol{\sigma}_n(t) \end{bmatrix} = C(t) \begin{bmatrix} 1 & s_{12} & \cdots & s_{1n} \\ s_{12} & 1 & \cdots & s_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ s_{1n} & s_{2n} & \cdots & 1 \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \boldsymbol{a}_2 \\ \vdots \\ \boldsymbol{a}_n \end{bmatrix} \quad (11)$$

where s_{ri} is the synchronization index between the motor unit pair (r, i). In this case we will write $\boldsymbol{\Sigma} = \boldsymbol{C}_H \boldsymbol{A}$, because t is no longer relevant to the direction of the STA trajectories in $\boldsymbol{\Sigma}$. Thus, the uniform approximation maps the changes in STA induced by synchronization into the structure of a matrix.

The special case of particular interest that we analyzed is that of a homogenous set of motor units with uniform synchronization index s applied between all motor unit pairs and a uniform distribution of direction vectors $\boldsymbol{A}$ with two-dimensional direction vectors. The homogenous contribution matrix $\boldsymbol{C}_H$ has $s_{ri} = s$ for $i \neq r$, so we will denote it $\boldsymbol{C}_H^{(s)}$. Suppose that a set of n active motor units have a set
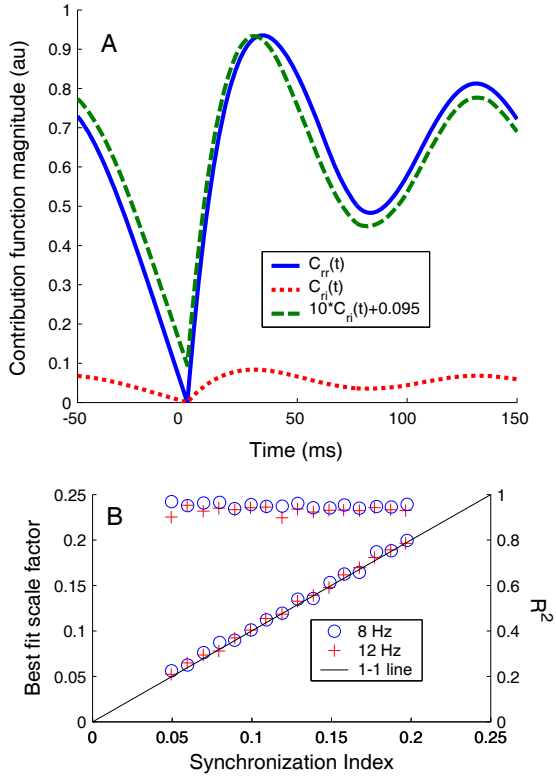
Fig. 2. Contribution functions scale linearly with synchronization. A. Example of determinant functions derived from a pair of simulated motor units discharging at 10 Hz, inter-spike interval coefficient of variation 0.2, peak force 1 au, contraction time 50 ms, with a 10% synchronization index. Notice that $C_{rr}(t)$ is 10 times $C_{ri}(t)$ (alternatively $C_{ri}(t)$ is 0.1 times $C_{rr}(t)$). B. Empirical evaluation of the proposed relation $C_{ri}(t) \approx s C_{rr}(t) + c$ over a range of synchronization indices for discharge rates of 8 and 12 Hz, which is a typical range of rates for STA experiments. The goodness of the approximation is evaluated by least-squares fitting $C_{ri}(t)$ to a linear function of $C_{ri}(t)$. The scale factors are shown with the left axis and conform very well to the 1-1 line. The goodness of fit is evaluated using the R^2 coefficient as shown by the right axis; the R^2 values are greater than 0.9 indicating a good similarity in shape between $C_{ri}(t)$ and $C_{rr}(t)$.

of direction vectors that span an angular range of θ. The angular range of STA trajectories θ' is given by

$$\tan \frac{\theta'}{2} = \frac{1-s}{1-s+ns} \tan \frac{\theta}{2} \qquad (12)$$

To investigate the usefulness of this approximation, we simulated the Fuglevand motor unit population model and compared the range of STA trajectories to that predicted by Equation 12. The results of this comparison are shown in Figure 3. Both the full simulated model and the uniform approximation predict a rapid collapse in the range of STA directions relative to the range of force directions in the presence of synchronization applied uniformly across motor units with different force directions. The analytical equation of Equation 12 makes an accurate approximation when there are 36 active motor units, and a slightly less accurate by reasonable prediction when 75 motor units are active. Presumably, the uniform approximation provides a good "rule-of-thumb" because the STA process averages out
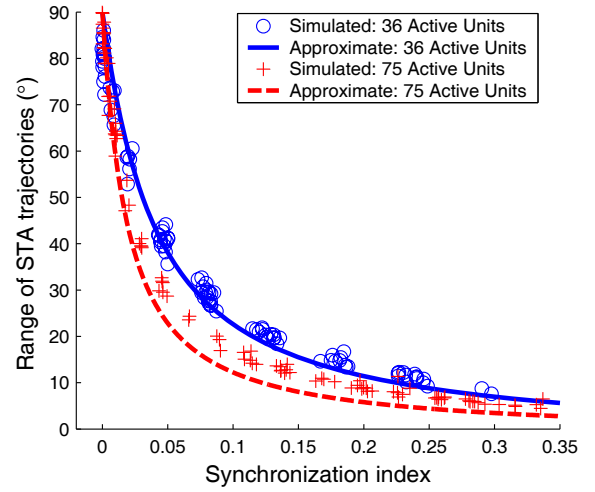

Fig. 3. Range of STA directions for simulated motor unit model and homogenous approximation with uniform synchronization. At 5% of maximum, the model predicts 36 active motor units, firing rate ranging from 8.07 Hz to 9.82 Hz, peak force ranging from 1.03 au to 3.98 au, and contraction time ranging from 64 ms to 89 ms. At 15% of maximum, the model predicts 75 active motor units, firing rate ranging from 8.17 Hz to 15.5 Hz, peak force ranging from 1.03 au to 17.78 au, and contraction time ranging from 45 ms to 89 ms. Uniform synchronization was applied at various levels, and STA was performed on the two-dimensional output force based on the spike times from all active units. Notice the sharp collapse in the range of STA trajectories relative to the 90° range force directions, as synchronization increases. The approximate curves shown were derived from Equation 12. Notice that both the full simulated model and the analytical reduction based on the assumption of homogenous motor units predict sharp collapse of STA trajectories with increasing synchronization. The homogenous approximation with uniform synchronization makes very accurate predictions at 5% maximum, and slight less accurate but acceptable predictions at 15% maximum, which is a reasonable limit to the level at which STA would be performed experimentally at present.

differences in firing rate, peak force, and contraction time among motor units.

C. STA Invertibility

The collapse of STA trajectories illustrated in Figure 3 provides a worst-case scenario for the corrupting effects of synchronization. If synchronization is limited to pairs of motor units with similar direction vectors, the set of STA trajectories will be minimally-distorted with respect to the set of direction vectors. Nonetheless, it is logical to ask whether or not the synchronization effects on STA can be inverted: that is, given a set of STA trajectories and the structure of the contribution matrix, can the underlying distribution of direction vectors be recovered. This question is equivalent to determining whether or not the contribution matrix is invertible.

Again, we consider a synchronization index s applied uniformly to all motor unit pairs. In this case, we can explicitly write down the eigenvalues of the contribution matrix:

$$\lambda_1 = (n-1)s + 1 \quad \text{and} \quad \lambda_2, \ldots, \lambda_n = 1 - s \qquad (13)$$

Notice that since the synchronization index satisfies $0 \leq s \leq 1$, so all eigenvalues are positive unless all pairs are perfectly

synchronized and $s = 1$. Physiological synchronization is never this large across a population of motor units, and therefore the contribution matrix is invertible in this case. The range of STA trajectories θ' can be directly inverted to the range of direction vectors θ using Equation 12.

D. Synchronization-insensitive direction vectors configurations

The previous section highlighted that if synchronization is uniform and known, its effects can be inverted without the need for a specific linear model. Although there are experimental examples of non-uniform synchronization where the synchronization structure is known [9], in general the structure of synchronization with respect to direction vectors may not be known. Therefore, it is appropriate to ask whether there are special direction vector distributions $\boldsymbol{A}_{SI}$ that are insensitive to synchronization. For simplicity, we ask this question in the case of the homogenous approximation with synchronization index s applied uniformly to all motor unit pairs acting in two dimensions of torque output, though this analysis can be readily extended to more complicated synchronization configurations with higher dimensional outputs.

To look for synchronization insensitive force directions sets, we need to look at the fixed point structure of the contribution matrix $\boldsymbol{C}_H^{(s)}$. That is, does there exist a set of direction vectors $\boldsymbol{A}$ for which $\boldsymbol{C}_H^{(s)}\boldsymbol{A} = \lambda\boldsymbol{A}$. The application of $\boldsymbol{C}_H^{(s)}$ to the cth column of $\boldsymbol{A}$ results in the cth column of the STA trajectory matrix $\boldsymbol{\Sigma}$. In order for a direction vector set $\boldsymbol{A}$ to be insensitive to synchronization, the columns of $\boldsymbol{A}$ must be linear combinations of the eigenvectors of $\boldsymbol{C}_H^{(s)}$ with common eigenvalues. Interestingly, $\boldsymbol{C}_H^{(s)}$ has $n - 1$ repeated eigenvalues (see Equation 13). Linear combinations of eigenvectors with the same eigenvalue are also eigenvectors, so a synchronization-insensitive matrix $\boldsymbol{A}$ of direction vectors must have columns in the span of the eigenvectors of $\boldsymbol{C}_H^{(s)}$ that are associated with $\lambda_2, \ldots, \lambda_n$. This set of eigenvectors can be represented as the columns of matrix $\boldsymbol{V}$:

$$\boldsymbol{V} = \begin{bmatrix} -1 & \cdots & -1 \\ & \boldsymbol{I}_{n-1} & \end{bmatrix} \quad (14)$$

where $\boldsymbol{I}_{n-1}$ is the $n - 1$-dimensional identity matrix. As an example, if the output vector $\boldsymbol{y}(t)$ is two-dimensional, we can generate synchronization insensitive force direction distribution by taking two linear combinations of the columns of $\boldsymbol{V}$. If these two linear combinations are labelled $\boldsymbol{v}_1$ and $\boldsymbol{v}_2$, then we form synchronization insensitive direction vector distribution $\boldsymbol{A}_{SI}$ by looking at the *rows* of the following matrix

$$\boldsymbol{A}_{SI} = \begin{pmatrix} | & | \\ \boldsymbol{v}_1 & \boldsymbol{v}_2 \\ | & | \end{pmatrix} \quad (15)$$

Figure 4 shows an example of a synchronization insensitive force direction distribution in two degrees-of-freedom and the corresponding distribution of STA trajectories for a
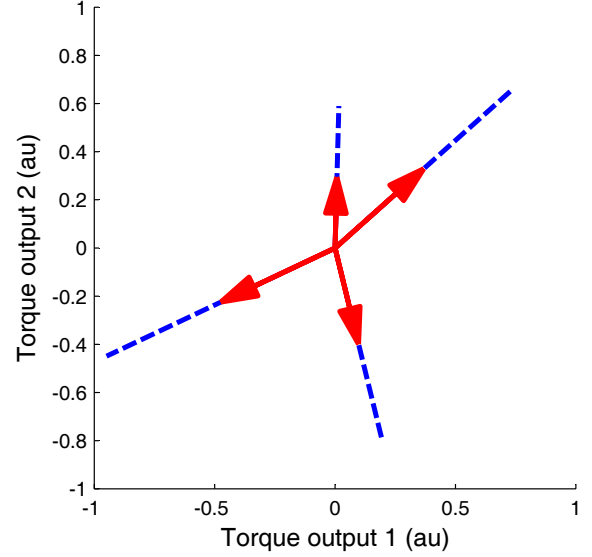

Fig. 4. An example of a synchronization insensitive direction vector distribution for $n = 4$ active neurons. The lines are a distribution of direction vectors generated by taking linear combinations of the eigenvalues of $\boldsymbol{C}_H^{(s)}$. The arrows are the corresponding STA directions generated by putting the set of direction vectors through the transformation $\boldsymbol{C}_H^{(s)}$ with a uniform synchronization index $s = 0.5$.

uniform synchronization index of $s = 0.5$. The direction vector distribution is constructed by taking linear combinations of the eigenvectors with identical eigenvalues. For more complicated structure in the contribution matrix, the existence and structure of synchronization insensitive force direction distributions can still be analyzed by looking at its eigenvalues and eigenvectors.

IV. DISCUSSION

This paper presents a simple framework for the analysis of the effects of firing rate and synchronization on STA joint torque based on motor unit discharge. If the joint torque output is multidimensional, and motor units discharge independently, STA trajectories are unaffected by firing rate and correctly represent the direction vector of the motor unit being studied. This observation is significant because it decouples the effects of firing rate and synchronization on STA. When STA is applied to estimate motor unit twitch contractile properties, firing rate leads to the underestimation of peak force while synchronization leads to the overestimation of peak force [22]. These competing effects make the interpretation of STA waveforms difficult. However, our analysis framework would suggest that any distortion of the direction of STA trajectories from averaging multiple dimensions of joint torque would result from synchronization, not firing rate.

Keen et al. [10] compared STA of multiple dimensions of joint torque based on spikes from extensor digitorum (ED) motor units with intraneural stimulation of ED motor units. They found that intraneural stimulation produced torque on primarily one finger while STA showed torque on multiple

fingers. The authors conclude, based on previous work [9], that synchronization was the primary cause of distortion. Our results agree with this conclusion. However, STA would not have been distorted relative to the underlying distribution of direction vectors unless there were synchronizing pathways between motor units that had very different direction vectors. Binder and Powers [2] showed that common input to a pair of motoneurons may need to be quite strong to produce experimentally observed levels of synchronization. It remains to be seen whether these inputs are strong enough to prevent the central nervous system from exploiting the differences in direction vectors that exists among motor units within the ED.

The strong effects of relatively weak synchronization seen in Figure 3 caution against STA being used as a direct measure of motor unit direction vectors. However, STA can be very useful in more subtle ways. Preliminary observations from our laboratory suggest that the first dorsal interosseous (FDI), which contributes torque to both horizontal and vertical movement of the index finger about the MCP joint, may have a $53°$ range of STA trajectory directions in the vertical/horizontal torque plane (N.L. Suresh, unpublished observations). Using Equation 12 and assuming that the muscle has between 36 and 75 active units when STA measurements were made, we predict that the FDI could have had a $90°$ range of direction vectors with a 0.027 uniform synchronization index, or a $60°$ range of direction vectors with 0.005 uniform synchronization index, or perhaps anything in between. However, these synchronization indices are much less than literature values for the FDI. Deluca et al. [6] observed a 0.08 synchronization index from the FDI, which is smaller than values reported elsewhere [5].

The most direct explanation of this discrepancy is that synchronization is not uniform with respect to direction vectors. If motor units with similar direction vectors are more likely to synchronize than units with different direction vectors, the collapse of STA trajectory directions will not be nearly as dramatic. STA is simultaneously indicating that FDI motor units both span a sizable range of direction vectors, and that motor units with different direction vectors receive less common input than those with the similar direction vectors. Therefore, STA is potentially useful for studying how motor unit synchronization is organized with respect to motor output.

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