Analysis of the effects of firing rate and synchronization on spike-triggered averaging of multidirectional motor unit torque

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Abstract Spike-triggered averaging (STA) of muscle force transients has often been used to estimate motor unit contractile properties, using the discharges of a motor unit within the muscle as the triggering events. For motor units that exert torque about multiple degrees-of-freedom, STA has also been used to estimate motor unit pulling direction. It is well known that motor unit firing rate and weak synchronization of motor unit discharges with other motor units in the muscle can distort STA estimates of contractile properties, but the distortion of STA estimates of motor unit pulling direction has not been thoroughly evaluated. Here, we derive exact equations that predict that STA decouples firing rate and synchronization distortion when used to estimate motor unit pulling direction. We derive a framework for analyzing synchronization, consider whether the distortion due to synchronization can be removed from STA estimates of pulling direction, and show that there are distributions of motor unit pulling directions for which STA is insensitive to synchronization. We conclude that STA may give insight into how motoneuronal synchronization is organized with respect to motor unit pulling direction.

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1 Introduction

Spike-triggered averaging (STA) is one of the most widely used system identification techniques in motor neuroscience. When estimating motor unit properties, STA involves extracting sections of joint torque based on the timing of discharges of a single motor unit, and then averaging the sections together (Buchthal and Schmalbruch 1970). While the resulting torque transient is reflective of the magnitude and time course of the motor unit twitch, it has also been shown in numerous experimental and theoretical studies that STA of joint torque based on motor unit discharge times is strongly influenced by both mean motor unit firing rate (Calancie and Bawa 1986; Nordstrom et al. 1989) and by synchronization (Taylor et al. 2002; Keen and Fuglevand 2004b). 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 (Datta and Stephens 1990; Deluca et al. 1993; Farmer et al. 1997; Semmler 2002). The distortion of the twitch waveform by firing rate is well understood (Andreassen and Baron 1983; Lim et al. 1995), but the distortion due to motor unit synchronization is less well understood. For example, it has been observed that increases in motor unit firing rate decrease estimates of motor unit peak force, whereas increases in population synchronization likely increase estimates of motor unit peak force (Thomas et al. 1990b; Taylor et al. 2002; Keen and Fuglevand 2004b). Clearly, such confounding distortions make the inter-

pretation of STA estimates for motor unit contractile properties difficult.

Motor unit pulling direction is a very different property. Pulling direction is a multidimensional vector that specifies the relative torque contribution of a motor unit to the various components of torque output. For example, Keen and Fuglevand (2004b) evaluated the pulling direction of motor units in the extensor digitorum communis, a large digital extensor muscle on the dorsal side of the forearm. The pulling direction was a 4-dimensional vector describing the relative amounts of torque generated on each of the digits subsequent to a discharge in a particular motor unit. Thomas et al. (1990a) evaluated the pulling direction of thenar motor units. In this case, the pulling direction was a 2-dimensional vector specifying the relative amounts of torque generated in thumb abduction and flexion subsequent to a discharge in a particular motor unit.

Many other experimental studies have sought to determine the range of pulling directions for the motor units within a muscle or a related group of muscles. We show that whether synchronization distorts STA results is likely to depend on the pulling directions of the weakly synchronized motor units. In particular, STA distortion may occur if weakly synchronized motor units have pulling directions spanning a larger range than the desired directional accuracy of the study. Throughout the paper, motor units that pull in a range of directions greater than the desired accuracy are said to have different pulling directions, while motor units that pull in a range of directions less than the desired accuracy are said to have similar pulling directions.

Here, we develop a framework for analyzing the effects of motor unit firing rate and population synchronization on STA estimates of motor unit pulling direction. We show that when multiple torque components are recorded and simultaneously averaged based on a single motor unit spike train, firing rate distorts all components equally and the correct pulling direction is recovered in the absence of synchronization. Therefore, any distortion of the STA estimate for pulling direction is likely to result from motor unit population synchronization. In other words, STA performed on multidirectional motor unit torque decouples firing rate and synchronization distortion.

We further develop the analysis of synchronization to show that if the set of weakly synchronized motor units all pull in the same direction, STA will still correctly identify the pulling direction of any sampled motor unit. Alternatively, if several motor units with very different pulling directions are even weakly synchronized, STA estimates of pulling direction will be profoundly distorted, with each sampled motor unit producing roughly the same STA estimate for pulling direction. We consider whether synchronization-induced distortion of STA estimates for motor unit pulling direction can be removed. We show, both in the case of uniform synchronization applied to a population of motor units and also in a simple case of non-uniform synchronization motivated by the experiments of Keen and Fuglevand, that the distortion of STA estimates for pulling direction can be removed. It has been shown that pairs of motor units between muscles with very different pulling directions can be weakly synchronized (Bremner et al. 1991a,b,c); we therefore show that there are distributions of motor unit pulling directions for which STA is insensitive to synchronization.

2 Methods

The theoretical framework and assumptions are illustrated in Fig. 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 easily observed in otherwise passive muscle, and does not appear to be as significant when large portions of muscle are active (see for review, Sandercock 2005). Westling et al. (1990) found that individual thenar motor units have straight force trajectories in the flexion/abduction plane of the thumb when activated by intraneural 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 (Stein et al. 1972; Mannard and Stein 1973). However, the steady state force versus firing rate curve is nonlinear and similar for most motor units when firing rate is normalized to the twitch time course (Kernell et al. 1983), suggesting that the motor unit twitch gain is firing-rate dependent (Fuglevand et al. 1993).

The analytical predictions were compared to the numerical model of Fuglevand et al. (1993) for a motor unit population. This model specifies the contractile properties of the set of motor units, as well as the
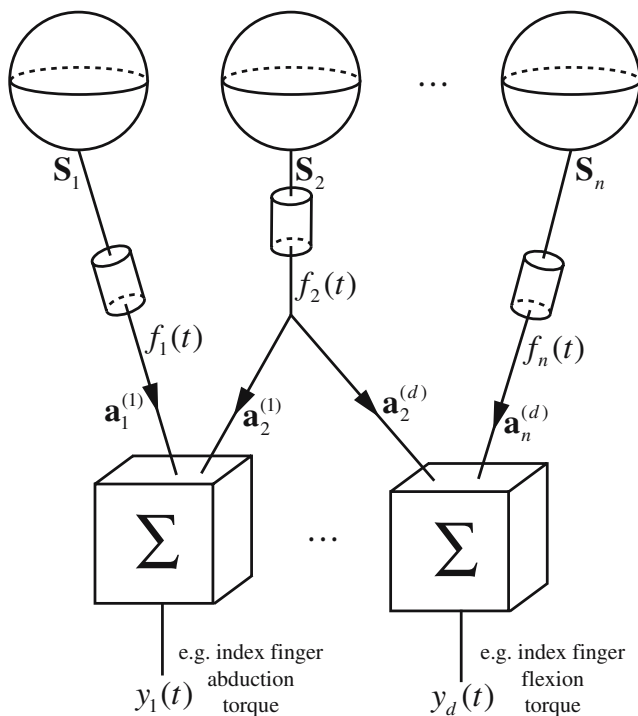
Fig. 1 The modeling framework for spike-triggered averaging. A population of n active motor units generates spike trains $\mathbf{S}_1, \ldots, \mathbf{S}_n$. These spike trains generate continuous-time joint torques $y_1(t), \ldots, y_d(t)$. The spike trains are transformed into continuous-time motor 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 pulling direction which is a multidimensional vector $\mathbf{a}_i$ whose components specify the relative contributions made by motor unit i to the different dimensions of torque output

dependence of motor unit firing rate on these properties and on the global level of excitation applied to the motor unit population. Two hundred seconds of simulated data were generated, which typically produced 1,600–3,000 spikes on which to perform STA. Motor unit spike trains were generated independently with a constant coefficient of variation in their interspike interval of 20% (Fuglevand et al. 1993). Synchronization was then applied using the algorithm of (Yao et al. 2000). 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 (Taylor et al. 2002). Under these conditions, the expected width of synchronization peaks was approximately 6 ms. Imposing weak motor unit synchronzation using the algorithm of Yao et al. requires two input parameters: the fraction of reference spikes that would be used to apply synchronization, and the fraction of "alternate" motor units that would have spikes synchronized to the selected reference spike.

The actual amount of synchronization was measured between all active motor unit pairs using the synchronization index (described below). Since the parameters of the algorithm of Yao et al. are not experimentally measurable, they were adjusted by trial-and-error until the average synchronization index across all active motor unit pairs was set to a level that could be compared with experimental measures.

The synchronization index was computed as follows. 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 the synchronization peak. The synchronization index s was the difference between the actual synchronization probability and the synchronization probability when the spike trains were independent. 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 (2001) and the synchronization index of Deluca et al. (1993). We chose to use this synchronization measure for two reasons. First, it has been measured experimentally from several muscles and can be computed directly from the crosscorrelogram (Deluca et al. 1993). Second, unlike the Common Input Strength (CIS), the synchronization index that we used does not depend on reference motor unit firing rate. In the theoretical analysis of synchronization derived below, the synchronization index that we used arises naturally in the equations. STA depends critically on the fraction of synchronized spikes, but not how fast they occur, which would be measured by the CIS.

For some simulations, the synchronization index was varied over the physiological range measured by Deluca et al. (1993), which was 0–25%. In other simulations, the average synchronization index was set to 0.08, which was the average synchronization index measured from the FDI by Deluca et al. (1993). In some simulations, synchronization is applied uniformly across all motor unit pairs, while in other simulations synchronization is limited to motor units with similar pulling directions. When we refer to uniform synchronization, we are referring to uniform with respect to pulling direction. Synchronization is not uniform with respect to motor unit recruitment threshold (Schmied et al. 1994; Datta and Stephens 1990). We did not model the dependence of synchronization on recruitment threshold as we were interested in the effects of synchronization on STA estimates for pulling direction. Thomas et al. (1990a) did not find a clear relation between motor unit peak force and pulling direction. Therefore in our model, peak force, and consequently

recruitment threshold, was distributed uniformly with respect to pulling direction.

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

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

We derive general equations and analyses that apply to an arbitrary distribution of pulling directions. In order to compare simple analytical predictions with numerical simulations, we were interested in how STA would perform in identifying motor unit pulling directions if simultaneously active motor units had pulling directions spanning a broad range; thus the direction vectors during simulation were assumed to continuously span a range of 90°. A broad, continuous range of pulling directions was observed from human thenar motor units using intraneural stimulation (Thomas et al. 1990a); a broad range is also possible for human first dorsal interosseous motor units (Thomas et al. 1986).

To investigate the possibility of pulling direction distributions for which STA would be insensitive to synchronization, a separate set of simulations were performed that involved the simulation of simultaneously active muscles. The pulling vectors (moment arms) for the seven muscles that contribute torque to human metacarpophalangeal (MCP) joint torque were estimated from cadaver measurements by An et al. (1983). These muscles were the first dorsal interosseous (FDI), first palmar interosseous (FPI), first lumbrical (LUM), extensor indicis proprius (EIP), extensor digitorum communis (EDC), flexor digitorum profundus (FDP), and flexor digitorum superficialis (FDS). We used the moment arms that corresponded to a joint flexion angle of 0° and a joint adduction angle of 0°. For these simulations, each motor unit within a muscle was assumed to have the same pulling direction. Since, to our knowledge, no models exists for the recruitment and rate-coding schedule for muscles other than the FDI, we assumed that each muscle had the same schedule as does the FDI model (Fuglevand et al. 1993).

To find the proper excitation for each muscle to achieve the desired force in each muscle, a calibration curve was derived by using various levels of excitation with a model with one-dimensional force output and measuring the resultant average force level. In the case where activating each muscle generated no net torque, we solved for the required average force level of each muscle using quadratic programming (quadprog in MATLAB) so that the minimum total squared force was exerted subject to the constraint that there was no net torque and all muscles were active. Each muscle was given a (potentially) different excitation command, independent spike trains were generated for all motor units in all muscles, weak synchronization was applied using the algorithm of Yao et al. (2000) as above to to all pairs of active motor units both within and across muscles, and finally the force for each muscle was computed, multiplied by the moment arm vector, and summed to generate net joint torque. Bremner et al. (1991a,b,c) estimated the level of synchronization between the FDI and the second dorsal interosseous to be roughly half of the level between motor unit pairs within the FDI. Since the synchronization index of Deluca et al. (1993) was the same as the one that we used, and they found an average synchronization index of 0.08 between FDI motor units, we applied synchronization between motor unit pairs within and across muscles so that the average synchronization index was 0.08. We reasoned that this would provide a worst-case simulation of the distorting effects of synchronization on STA when synchronization spanned multiple muscles.

3 Results

3.1 General equations

It is possible to use the assumptions of Fig. 1 to derive general equations that describe the STA process. Assuming that the motor units in Fig. 1 generate torque in parallel, it is possible to write

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

where $\mathbf{n}(t)$ is a mean-zero independent and identically distributed random vector associated with the measurement uncertainty inherent in observing the output torque vector $\mathbf{y}(t) = [y_1(t), \ldots, y_d(t)]$. 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 force of the ith motor unit at the time of the jth spike, $T_i(t)$ is

the unpotentiated twitch waveform of motor unit i, and N_i is the number of spikes in motor unit i. The twitch gain g_{ji}, which can vary from discharge to discharge, was included to model the nonlinear dependence of twitch gain on firing rate (Fuglevand et al. 1993). Inserting Eq. (3) into Eq. (2), we obtain an equation describing the output torque vector

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

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

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

We are interested in the behavior of the STA process as N_r gets very large, and it is clear by the Law of Large Numbers that the second term in Eq. (5) approaches zero as $N_r \rightarrow \infty$. The first term of Eq. (5) shows that STA is composed of weighted averages of the pulling directions, the weighting functions we will refer to as contribution functions. Contribution functions can be expressed as

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

Equation (6) shows that the contribution function is an average of a function of two random variables, a random gain and a random shift, over the duration of the STA. 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 Eq. (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 motor units 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

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

We first note that Eq. (7) predicts that, if the spike trains of all motor unit pairs in the population are independent, STA will accurately identify the pulling direction $\mathbf{a}_r$ without being able to accurately identify either the magnitude or time-course of the reference motor unit twitch $T_r(t)$. 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 marginals of the density $f_{ri}(x, g)$. $f_{ri,X}(x)$ is the crosscorrelogram between the spike trains in motor units r and i, with motor unit r serving as the reference. Since we assume no correlation between the spike trains of motor units r and i, $f_{ri,X}(x)$ is a constant function (for some region surrounding $x = 0$ that becomes arbitrarily large as $N_r \rightarrow \infty$) if $i \neq r$. Therefore, if $i \neq r$,

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

Since $f_{ri,X}(x)$ is a constant function, the integral in x is the same value regardless of t. Thus, $C_{ri}(t)$ is a constant function of t if $i \neq r$. Returning to Eq. (5), we can see that

$$\mathbf{z}_r(t) = C_{rr}(t) \mathbf{a}_r + \mathbf{c} \qquad (9)$$

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

Figure 2 illustrates the convergence of STA for pulling direction in the absence of synchronization for the simulated Fuglevand model. Figure 2(a) shows simulation results at 5% maximum as an increasing number of spikes are used for STA. The direction of the STA trajectory converges to the actual motor unit pulling direction, but neither the time course nor the magnitude converges to the corresponding properties of the twitch waveform. Figure 2(b,c) shows simulation results at 15% maximum after 1,500 spikes have been used for STA. The angular error in the STA pulling direction estimate is shown across all 75 active motor units. Figure 2(b) shows results for the standard distribution of peak forces across the motor units; motor units that discharge more rapidly also have smaller peak forces. Equation (9) predicts that increased fir-
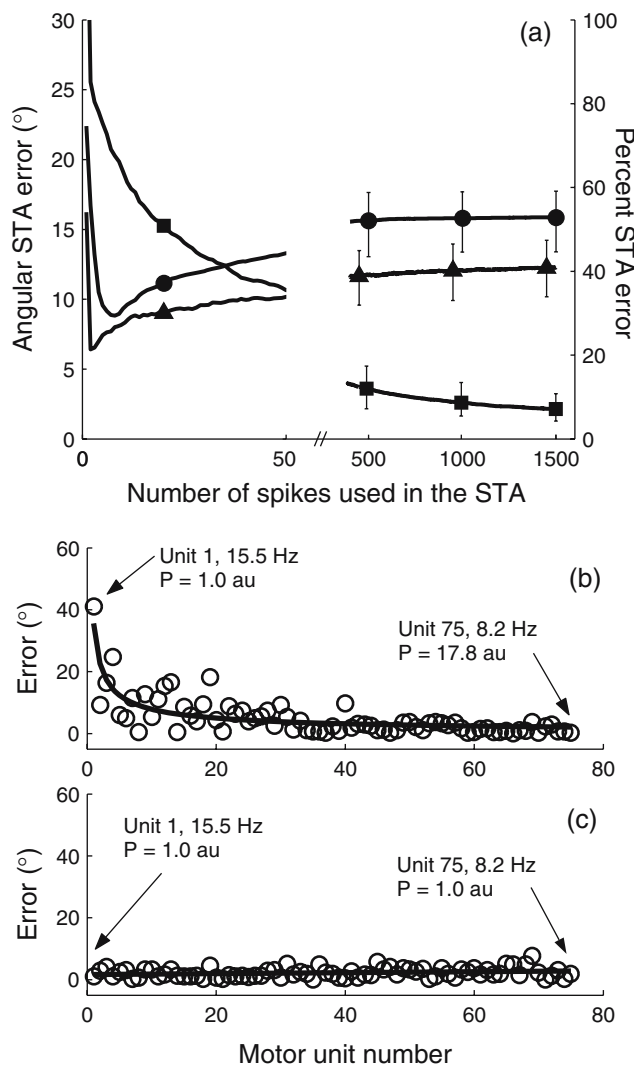
Fig. 2 STA estimates of pulling direction converge in the absence of synchronization whereas estimates of contractile properties do not. (**a**) STA error as a function of the number of number of spikes in the average for a 90° range of pulling directions and an excitation of 5% maximum. *Square curve* corresponds to the *left vertical axis* and shows the angular error in degrees between the line of best fit to the STA trajectory and the true motor unit pulling direction. *Triangle curve* corresponds to the *right vertical axis* and shows the error in percent between the actual contraction time and the average time to peak of the STA waveforms for both torque components. *Circle curve* corresponds to the *right vertical axis* and shows the error in percent between the actual peak force and the peak magnitude of the STA trajectory. *Error bars* indicate best and worst performance over the population of active motor units. (**b**, **c**) Simulations performed at 15% maximum. Each plot shows the angular error in degrees as a function of motor unit number. (**b**) The standard model that contains motor units with peak forces ranging from $P = 1$ arbitrary unit (au) to $P = 17.8$ au. Notice that lower force motor units that are firing at a faster rate have more error than the larger units firing at a slower rate. (**c**) Modified model that contains motor units all having peak force $P = 1$. Notice that STA identifies the correct pulling direction for all motor units independent of firing rate

ing rate can not distort STA trajectory direction, so Fig. 2(c) shows results from a modified model in which all motor units have the same peak force. Notice that the STA trajectory direction now converges to the correct pulling direction for all motor units, indicating that increased firing rate is not the source of distortion seen during increased excitation. Equation (8) predicts the distortion of STA for low force motor units when higher force motor units are simultaneously active. If $N_r < \infty$, there will be residual non-uniformity in the crosscorrelogram between motor unit pairs. If unit i is a higher force motor unit and unit r is a lower force motor unit, the convolution in the computation of $C_{ri}(t)$ will amplify the non-uniformity of the crosscorrelogram $f_{ri,X}(x)$ because the convolution depends on the twitch waveform $T_i(t)$ of the larger force motor unit.

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 distribution of pulling directions to the distribution of STA trajectories. This linear map can be visualized by the following matrix

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

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

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

Next, consider a population of motor units, potentially expressing weak synchronization, that all have the

same pulling direction **a** . The STA trajectory for motor unit can be written

$$\mathbf{z}_i(t) = \left(\sum_{j=1}^{n} C_{ij}(t) \right) \mathbf{a} \tag{11}$$

which points in the correct direction regardless of synchronization. Therefore synchronization-induced distortion of STA will depend critically on how synchronization is organized with respect to pulling direction. Finally, we would expect that if many motor

units with very different pulling directions were synchronized, the effects of synchronization would compound and profoundly distort the distribution of STA trajectories relative to independent spike trains.

We tested these hypotheses by simulating the Fuglevand model and the results are shown in Fig. 3. Figure 3 shows that the distribution of STA trajectories represents the underlying distribution of pulling directions when spike trains are independent, the distribution of STA trajectories is profoundly altered when synchronization is uniform with respect to pulling
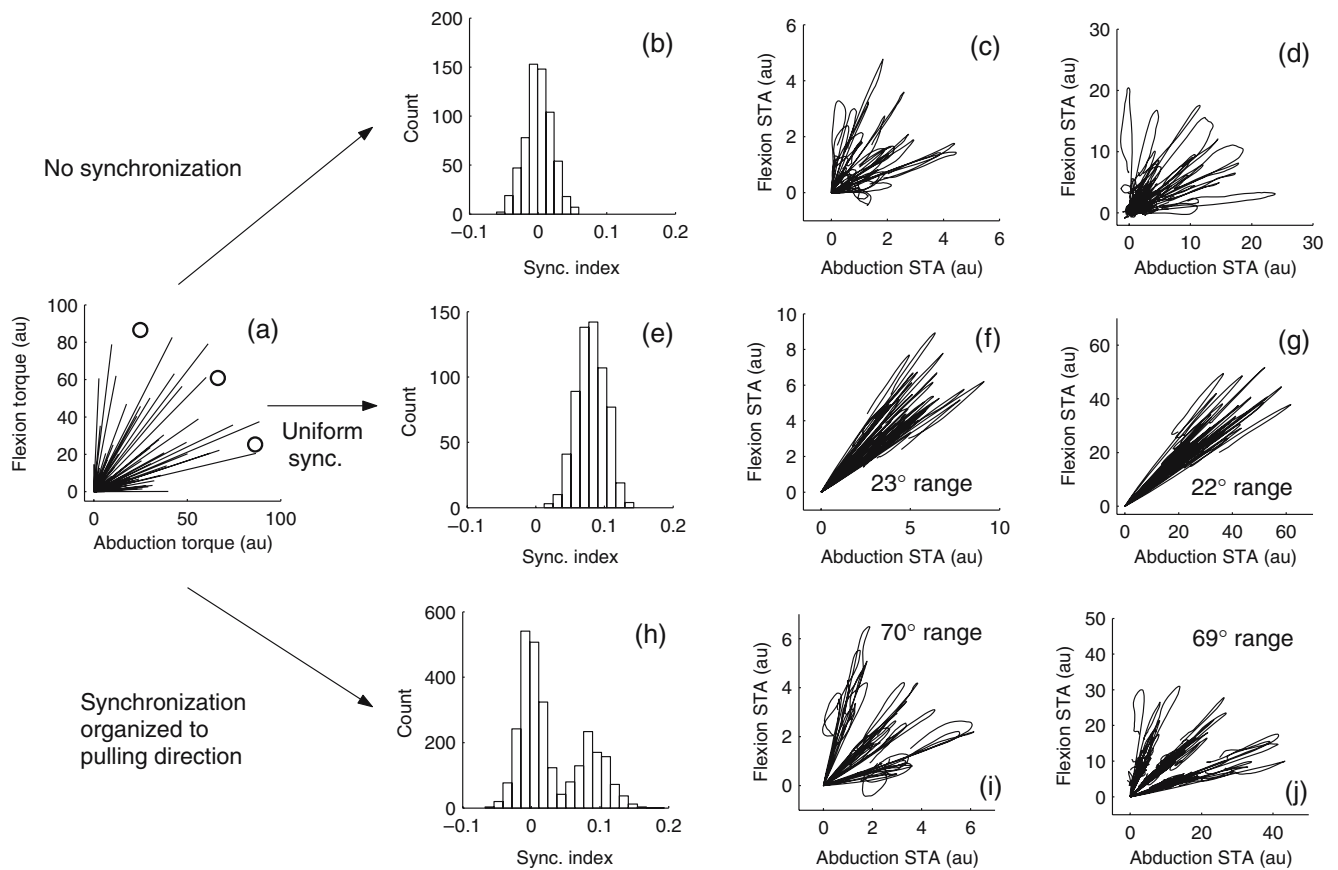
Fig. 3 The effect of synchronization on STA estimates for motor unit pulling direction. (**a**) The assumed underlying distribution of pulling directions for the set of potentially active motor units. *Circles* become relevant in h–j. (**b–d**) Evaluation of STA trajectories without motor unit synchronization. (**b**) Distribution of synchronization indices between all active motor unit pairs (shown for 5% of maximum; distribution at 15% maximum was similar). (**c**) The STA trajectory from 0 to 100 ms post-spike for each active motor unit at 5% of maximum. (**d**) The STA trajectory for from 0 to 100 ms post-spike for each active motor unit at 15% of maximum. (**e–g**) Evaluation of STA trajectories with synchronization applied uniformly to all motor unit pairs. (**e**) Distribution of synchronization indices between all active motor unit pairs (shown at 5% of maximum; distribution at 15% maximum was similar), with a mean of 0.08 consistent with the measurements of Deluca et al. (1993) from the FDI muscle. (**f**) The STA trajectory from 0 to 100 ms post-spike for each active

motor unit at 5% of maximum with uniform synchronization. (**g**) The STA trajectory from 0 to 100 ms post-spike for each active motor unit at 15% of maximum with uniform synchronization. (**h–j**) Evaluation of STA trajectories with non-uniform synchronization. Three groups of motor units were formed by finding the set of active motor units with pulling directions closest to each of the three directions indicated by the *circles* in a. Synchronization was only permitted within the motor unit groups, resulting in synchronization organized with respect to motor unit pulling direction. (**h**) Distribution of synchronization indices between all active motor unit pairs (shown at 15% of maximum; distribution at 5% maximum was similar), showing peaks corresponding to intra- and inter-group synchronization. (**i**) The STA trajectory from 0 to 100 ms post-spike for each active motor unit at 5% of maximum with non-uniform synchronization. (**j**) The STA trajectory from 0 to 100 ms post-spike for each active motor unit at 15% of maximum with non-uniform synchronization

direction, and that the distortion is limited if synchronization occurs between motor units with similar pulling directions.

3.2 Homogenous approximation for synchronization analysis

The purpose of this section is to show that, under certain conditions, synchronization can be analyzed using linear algebra. The conditions underlying this analysis are that the set of active motoneurons can be approximated as homogenous in discharge statistics and that there is one impulse response $T(t)$ common to all motor units. By comparison to the Fuglevand motor unit population model, we will show that the homogenous approximation well describes STA applied to the full system in which motor units can have different firing rates and motor unit twitch properties are different among the population of motor 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 synchronization configurations.

The simulation of contribution functions strongly suggests the linear scaling of contribution function magnitude by the synchronization index: $C_{ri}(t) \approx sC_{rr}(t) + c$, where c is an arbitrary constant. Figure 4 compares $C_{ri}(t)$ and $C_{rr}(t)$ both in an example (a), and across a range of synchronization indices and firing rates (b). The results of these simulations suggest that $C_{ri}(t) \approx sC_{rr}(t) + c$ 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. inter-spike interval coefficient of variation ≈ 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 $\mathbf{C}_H$ (H for homogenous):

$$\begin{bmatrix} \mathbf{z}_1(t) \\ \mathbf{z}_2(t) \\ \vdots \\ \mathbf{z}_n(t) \end{bmatrix} = C(t) \underbrace{\begin{bmatrix} 1 & s_{12} & \cdots & s_{1n} \\ s_{12} & 1 & \cdots & s_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ s_{1n} & s_{2n} & \cdots & 1 \end{bmatrix}}_{\mathbf{C}_H} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \vdots \\ \mathbf{a}_n \end{bmatrix} \quad (12)$$

where s_{ri} is the synchronization index between the motor unit pair (r, i). In this case we will write $\mathbf{Z} = \mathbf{C}_H \mathbf{A}$, because $C(t)$ is common to all components of $\mathbf{Z}$, and is thus no longer relevant to the direction of the STA trajectories. Thus, the homogenous approximation maps
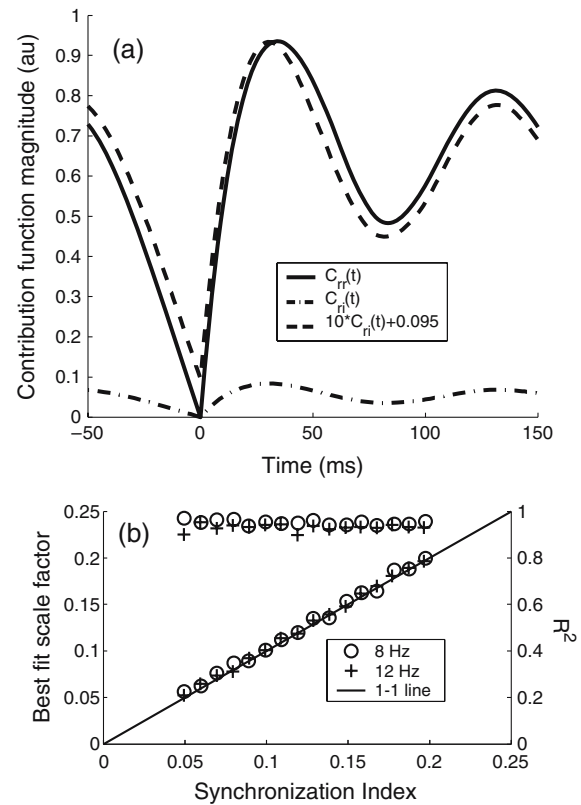
Fig. 4 Contribution functions scale linearly with synchronization. (**a**) Example of contribution functions derived from a pair of simulated motor units discharging at 10 Hz, inter-spike interval coefficient of variation 0.2, peak force 1 arbitrary unit (au), contraction time 50 ms, with a 10% synchronization 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 $C_{ri}(t) \approx sC_{rr}(t) + c$ 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 $C_{rr}(t)$. 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 $C_{rr}(t)$

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 two-dimensional pulling directions $\mathbf{A}$. The homogenous contribution matrix $\mathbf{C}_H$ has $s_{ri} = s$ for $i \neq r$, so we will denote it $\mathbf{C}_H^{(s)}$. Suppose that a set of n active motor units have a set of 2-dimensional pulling directions that span an angular range of θ. The angular range of STA trajectory directions θ' is given by

$$\tan \frac{\theta'}{2} = \frac{1 - s}{1 - s + ns} \tan \frac{\theta}{2} \quad (13)$$

which is derived in the Appendix.

To investigate the usefulness of the homogenous approximation, we simulated the Fuglevand motor unit population model and compared the range of STA trajectory directions to that predicted by Eq. (13). The results of this comparison are shown in Fig. 5. Both the full model and the homogenous approximation predict a rapid collapse in the range of STA directions relative to the range of pulling directions in the presence of synchronization applied uniformly across motor units with different pulling directions. Equation (13) 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 homogenous approximation provides a good "rule-of-thumb" because the STA process averages out differences in firing rate, peak force, and contraction time among motor units.

Fig. 5 Range of STA directions for the simulated Fuglevand 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 to 9.82 Hz, peak force ranging from 1.03 arbitrary units (au) to 3.98 au, and contraction time ranging from 64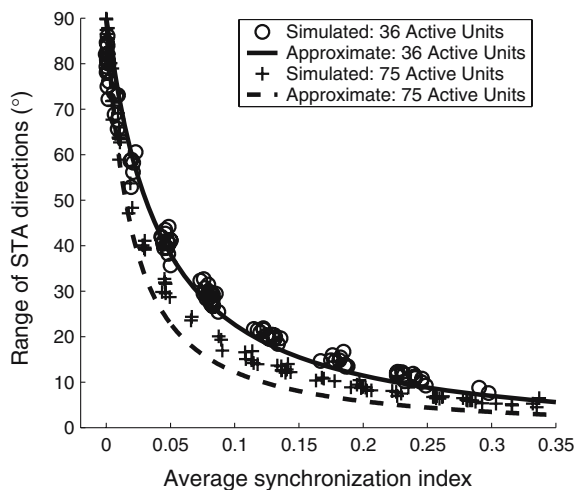 to 89 ms. At 15% of maximum, the model predicts 75 active motor units, firing rate ranging from 8.17 to 15.5 Hz, peak force ranging from 1.03 au to 17.78 au, and contraction time ranging from 45 ms to 89 ms. Uniform synchronization was applied at various levels, and STA was performed on the two-dimensional torque based on the spike times from all active units. Notice the sharp collapse in the range of STA trajectories relative to the 90° range pulling directions as synchronization increases. The approximate curves shown were derived from Eq. (13). Notice that both the full model and the homogenous approximation predict a 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

3.3 STA invertibility

The collapse of STA trajectories illustrated in Fig. 5 provides a worst-case scenario for the corrupting effects of synchronization. If synchronization is limited to pairs of motor units with similar pulling directions, the distribution of STA trajectories will be much less distorted with respect to the distribution of pulling directions. 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 pulling directions 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:

$$\lambda_1 = (n-1)s + 1 \quad \text{and} \quad \lambda_2, \ldots, \lambda_n = 1 - s \qquad (14)$$

Notice that since the synchronization index satisfies $0 \le s \le 1$, 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 pulling directions θ using Eq. (13).

Keen and Fuglevand (2004a,b) described non-uniform synchronization with respect to pulling direction in a population of motor units. They showed that motor unit pairs in different compartments of the extensor digitorum communis muscle expressed different levels of synchronization. Motor unit pairs within a compartment expressed the highest synchronization levels, while pairs in adjacent compartments expressed less but significant synchronization (Keen and Fuglevand 2004a). They also showed that while intraneural stimulation of motor units produced force on a single finger, STA gave the impression that motor units generated force on multiple fingers (Keen and Fuglevand 2004b).

We consider whether the effect of synchronization can be removed in this case of non-uniform synchronization. We suppose that there are two compartments of motor units; one group only exerts torque on the index finger while the second group only exerts torque on the middle finger. Motor unit pairs in this population express synchronization index s_w within the same compartment, while the motor unit pairs express synchronization index s_b between compartments. If we make the homogenous approximation for this system, the

STA system can be expressed with block contribution matrix as

$$
\mathbf{Z} = \begin{bmatrix} 1 & & \boxed{s_w} & & & \\ & \ddots & & & \boxed{s_b} & \\ \boxed{s_w} & & 1 & & & \\ & & & 1 & & \boxed{s_w} \\ & \boxed{s_b} & & & \ddots & \\ & & & \boxed{s_w} & & 1 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \vdots \\ \mathbf{a}_1 \\ \mathbf{a}_2 \\ \vdots \\ \mathbf{a}_2 \end{bmatrix} \quad (15)
$$

where $\mathbf{a}_1$ is the pulling direction of a compartment 1 motor unit and $\mathbf{a}_2$ is the pulling direction of a compartment 2 motor unit. If we assume that each compartment has n active motor units, a contribution function matrix of this form has $2n - 2$ eigenvalues $\lambda_1 = 1 - s_w$ and 2 eigenvalues $\lambda_2 = (n-1)s_w + 1 + ns_b$ and $\lambda_3 = (n-1)s_w + 1 - ns_b$. λ_1 and λ_2 are clearly greater than zero because s_w is not near 1 (synchronization is weak). λ_3 can be rewritten as $\lambda_3 = n(s_w - s_b) + 1 - s_w$ which is greater than 0 under the experimental observation that $s_w > s_b$. Therefore, the contribution matrix for this simple non-uniform synchronization configuration has no eigenvalues equal to zero, and is therefore invertible.

3.4 Synchronization-insensitive direction vector distributions

The previous section highlighted the finding that if synchronization is known, its effects may 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 (Keen and Fuglevand 2004a), 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 pulling direction distributions $\mathbf{A}_{SI}$ for which STA is synchronization insensitive (SI). 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 and higher dimensional torque outputs. We conclude the section by studying a specific example of muscle pulling vectors measured experimentally by An et al. (1983), and show that, if the muscles are appropriately activated to produce zero net torque, STA may be synchronization-insensitive for these pulling vectors.

To look for pulling vector sets for which STA is synchronization insensitive, we need to look at the fixed point structure of the contribution matrix $\mathbf{C}_H^{(s)}$. That is, does there exist a set of direction vectors $\mathbf{A}$ for which $\mathbf{C}_H^{(s)}\mathbf{A} = \lambda\mathbf{A}$. The application of $\mathbf{C}_H^{(s)}$ to the cth column of $\mathbf{A}$ results in the cth column of the STA trajectory matrix $\mathbf{Z}$. In order for a direction vector set $\mathbf{A}$ to be insensitive to synchronization, the columns of $\mathbf{A}$ must be linear combinations of the eigenvectors of $\mathbf{C}_H^{(s)}$ with common eigenvalues. Interestingly, $\mathbf{C}_H^{(s)}$ has $n - 1$ repeated eigenvalues (see Eq. (14)). Linear combinations of eigenvectors with the same eigenvalue are also eigenvectors, so a synchronization-insensitive matrix $\mathbf{A}$ of pulling vectors must have columns in the span of the eigenvectors of $\mathbf{C}_H^{(s)}$ that are associated with $\lambda_2, \ldots, \lambda_n$. This set of eigenvectors can be represented as the columns of matrix $\mathbf{V}$. As an example, if the torque vector $\mathbf{y}(t)$ is two-dimensional, we can generate a pulling vector distribution for which STA is synchronization insensitive by taking two linear combinations of the columns of $\mathbf{V}$. If these two linear combinations are labelled $\mathbf{v}_1$ and $\mathbf{v}_2$, then we form the pulling vector distribution $\mathbf{A}_{SI}$ for which STA is synchronization insensitive by looking at the *rows* of the following matrix

$$
\mathbf{A}_{SI} = \begin{pmatrix} | & | \\ \mathbf{v}_1 & \mathbf{v}_2 \\ | & | \end{pmatrix} \quad (16)
$$

Since any two linear combinations of the eigenvectors in $\mathbf{V}$ yields a valid $\mathbf{A}_{SI}$, STA may be insensitive to synchronization for many pulling vector distributions. Therefore, it is useful to ask if, given a pulling vector distribution $\mathbf{A}$, is it possible to compute the "nearest" $\mathbf{A}_{SI}$ for which STA would be insensitive to synchronization? For simplicity, we consider this question in the context of the homogenous approximation with uniform synchronization. Given a contribution matrix $\mathbf{C}_H^{(s)}$ and a pulling vector distribution $\mathbf{A}$, we first compute the eigenvalue matrix $\mathbf{V}$ as above. For any non-zero matrix $\mathbf{M}$, $\mathbf{A}_{SI} = \mathbf{VM}$ is guaranteed to produce STA directions that are synchronization-insensitive. We would like to find $\mathbf{M}$ such that the overdetermined system $\mathbf{A} = \mathbf{VM}$ is solved in a least-squares sense. The resultant $\mathbf{A}_{SI} = \mathbf{VM}$ will have STA directions insensitive to synchronization and will be the nearest possible distribution to the starting distribution $\mathbf{A}$ in the least squares sense. An example of $\mathbf{A}_{SI}$ computed in this way for $\mathbf{A}$ measured experimentally by An et al. (1983) assuming equal force generated by each muscle is shown in Fig. 6(g–h).

Figure 6 shows simulation results for the muscle pulling vectors measured by An et al. (1983). All graphs except Fig. 6(d) have the same axes and units, which is shown in the upper left of the figure to be the four directions of torque production at the MCP joint with

arbitrary units. Figure 6(a) shows the measured pulling vectors. Figure 6(b) shows the predicted distribution of STA directions using the homogenous approximation with uniform synchronization (index=0.08) assuming that all muscles generate the same force. Figure 6(c) shows the simulated STA trajectories with each muscle contributing 5% of its maximum force. Figure 6(d) shows the distribution of synchronization indices for this simulation across all active motor units (within and between muscles). Figure 6(e) shows the predicted STA directions using the homogenous approximation with

uniform synchronization (index=0.08) assuming that muscles are appropriately activated to generate no net torque. Figure 6(f) shows the simulated STA trajectories with each muscle contributing an appropriate force level to achieve no net torque (the average contribution was 5% of each muscle's maximum). Notice that the homogenous approximation with uniform synchronization accurately predicts the simulated STA when each muscle is generating the same force, but does not accurately predict the synchronization-insensitivity under conditions of no net torque. Figure 6(g) shows
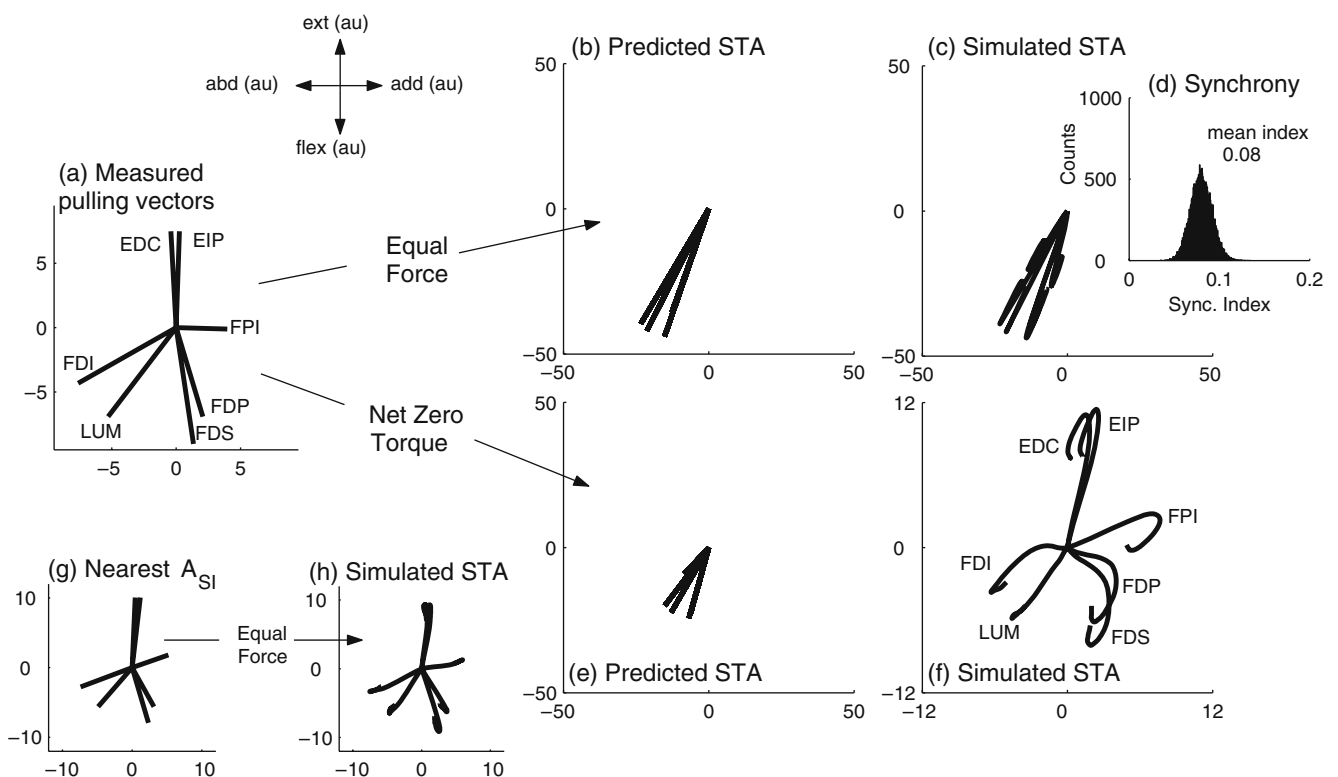
Fig. 6 Analysis of STA synchronization insensitivity of the muscle pulling directions measured by An et al. (1983). Each plot (with the exception of d) has the same axes and same arbitrary units (au), shown in the upper left. (**a**) Moment arms measured by An et al. (1983) for muscles controlling the human second metacarpophalangeal (MCP) joint (see text for abbreviations used). (**b–d**) STA results assuming equal force generated by each muscle and uniform weak synchronization between all motor unit pairs with synchronization index of 0.08. (**b**) STA directions predicted by the homogenous approximation with uniform synchronization for the case of equal force exerted by all muscles. (**c**) Numerical simulation results of STA trajectories for all active motor units for the case of equal force exerted by all muscles. (**d**) The distribution of the synchronization index across all active motor unit pairs had a mean of 0.08, which we expect to be an overestimate for the synchronization that can occur between motor units in different muscles. (**e–f**) STA results assuming muscle forces are chosen so that the net torque about the MCP joint is

zero. Muscles forces were chosen using quadratic programming to minimize total squared muscle force while requiring that the force in each muscle was larger than a small positive amount. (**e**) STA directions predicted by the homogenous approximation with uniform synchronization. (**f**) Numerical simulation results of STA trajectories for net zero torque. The distribution of the synchronization index between motor unit pairs during the net zero torque simulation was identical to the distribution shown in d. (**g–h**) Analysis of the least-squares nearest distribution of pulling vectors to those measured by An et al. for which STA is insensitive to synchronization assuming equal force in all muscles. (**g**) The nearest distribution of pulling vectors to the vectors in a for which STA is synchronization insensitive assuming equal force in all muscles. (**h**) Simulated STA trajectories for the equal activation of muscles with the pulling vectors shown in g. The net zero torque case examined had an average excitation of 5% maximum, so 5% maximum was also used for the case of equal force

the nearest distribution (in the least-squares sense) of pulling vectors to the vectors in Fig. 6(a) for which STA is insensitive to synchronization when all muscles contribute equal amounts of force. Figure 6(h) shows simulated STA trajectories for the distribution of pulling vectors shown in Fig. 6(g). These results suggest that synchronization-insensitive STA might be successfully applied experimentally if the subject were required to co-contract to generate zero net torque.

4 Discussion

This paper presents a simple framework for the analysis of the effects of firing rate and synchronization on the STA of joint torque based on motor unit discharges. If the joint torque output is multidirectional, and motor units discharge independently, STA trajectories are unaffected by firing rate and correctly represent the pulling direction 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 (Thomas et al. 1990b; Keen and Fuglevand 2004b). 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.

We analyzed the effects of synchronization on STA estimates of motor unit pulling direction and showed that even weak synchronization applied to motor units with different pulling directions could significantly alter STA estimates of pulling direction. We constructed our synchronization analysis based on an approximation that motor units were homogenous in contractile properties and firing statistics. This approximation is only justified by comparison to the simulation of the Fuglevand motor unit population model with non-homogenous motor units. Even under conditions of weak uniform synchronization across motor units with different pulling directions, STA would indicate that all motor units pull in approximately the same direction. We showed that synchronization-induced distortion could be removed both for uniform synchronization and a specific case of non-uniform synchronization. Lim et al. (1995) considered whether firing-rate distortion of STA estimates of contractile properties could be removed. Removal of firing rate distortion requires the

assumption of a particular model for the twitch waveform. The removal of synchronization-induced distortion does not require a specific twitch waveform because its effects are common to the multiple dimensions of torque output. Finally, we showed that there are distributions of motor unit pulling directions for which STA is insensitive to synchronization.

Our analysis may also be applicable to STA of postsynaptic membrane potential based on extracelluar spike recording (Komatsu et al. 1988; Matsumura et al. 1996) or STA of muscle activity based on cortical spikes (Fetz and Cheney 1980). The framework that we developed is based on the assumptions illustrated in Fig. 1. If post-synaptic potentials combine under approximately linear spatio-temporal summation, then the same equations apply. If the time-varying postsynaptic potentials from two neurons were simultaneously recorded, it may be appropriate to denote these variables $y_1(t)$ and $y_2(t)$ as in Fig. 1. If these potentials were simultaneously averaged based on the spike train $\mathbf{S}_r$ from a reference neuron r, pulling direction $\mathbf{a}_r$ would have the interpretation as the relative actions of neuron r on the output neurons 1 and 2. Our analysis would be useful in predicting the effects of synchronized inputs on the estimation of $\mathbf{a}_r$.

Keen and Fuglevand (2004b) compared STA of multiple dimensions of joint torque based on spikes from extensor digitorum communis (EDC) motor units with intraneural stimulation of EDC 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 (Keen and Fuglevand 2004a), that synchronization was the primary cause of the distortion. Our results agree with this conclusion. However, STA would not have been distorted relative to the underlying distribution of pulling directions unless there were synchronizing pathways between motor units that had very different pulling directions. Binder and Powers (2001) 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 common inputs are strong enough to prevent the central nervous system from exploiting the differences in pulling directions that exists among motor units within the EDC.

The strong effect of relatively weak synchronization seen in Figs. 3 and 5 cautions against STA being used as a direct measure of motor unit pulling direction. However, STA can be very useful in more subtle ways. Preliminary observations from our laboratory suggest that the first dorsal interosseous (FDI), which con-

tributes torque to both abduction and flexion of the index finger about the MCP joint, may have a 53° range of STA trajectory directions in the abduction/flexion torque plane. Using Eq. (13) 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 pulling directions with a 0.027 uniform synchronization index, or a 60° range of pulling directions 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. (1993) observed an average 0.08 synchronization index from the FDI, which is smaller than values reported elsewhere (Datta and Stephens 1990). Given a 90° range of pulling directions with a synchronization index of 0.08 and 5% MVC activation (36 active units), we would predict a range of STA directions of 27°. Given the same conditions with 15% MVC activation (75 active units), we would predict a range of 15°. If the range of pulling directions is smaller than 90° and the synchronization index was uniform at 0.08, the range of STA directions would likely be even smaller.

The most direct explanation of this discrepancy is that synchronization is not uniform with respect to pulling direction. If motor units with similar pulling directions are more likely to synchronize than units with different pulling directions, the collapse of STA trajectory directions will not be nearly as dramatic (see Fig. 3(h–j)). STA is simultaneously indicating that FDI motor units may both span a sizable range of pulling directions, and motor units with different pulling directions may receive less common input than those with similar pulling directions.

STA is potentially useful for studying how motor unit synchronization is organized with respect to motor output. The framework developed in this paper demonstrates how STA trajectories are generated by an interaction between motor unit pulling directions and crosscorrelograms between motor unit pairs. Since performing STA in a multidirectional setting removes firing rate distortion, it allows the direct examination of how synchronization is organized with respect to pulling direction. A broad distribution of STA trajectories observed from a motor unit system implies both that the active motor units have a broad distribution of pulling directions, and that there is very limited synchronization between motor units with different pulling directions. This analysis may aid in the interpretation of STA studies, and may give significant clues about how descending pathways are organized to control movement.

Appendix

Here we derive Eq. (13), which relates the angular range of STA trajectories to the angular range of two-dimensional pulling directions using the homogenous approximation with uniform synchronization. We suppose that n active motor units, each pair of motor units being uniformly synchronized with synchronization index s, exhibit a range of pulling directions θ. Given the homogenous contribution function matrix with uniform synchronization

$$\mathbf{Z} = \begin{bmatrix} 1 & s & \cdots & s \\ s & 1 & \cdots & s \\ \vdots & \vdots & \ddots & \vdots \\ s & s & \cdots & 1 \end{bmatrix} \mathbf{A} \tag{17}$$

we need to determine what angular range θ' is exhibited by the rows of $\mathbf{Z}$ given that the rows of $\mathbf{A}$ exhibit a range of θ. We observed in computer simulations that the same range of θ' was observed regardless of whether $\mathbf{A}$ had n rows with directions uniformly distributed over a range of θ, or $n/2$ rows at one angle and the other $n/2$ rows at an angle of θ from the first set. We visualize this transformation from pulling direction to STA direction as:

$$\begin{bmatrix} \mathbf{z}_1 \\ \vdots \\ \mathbf{z}_{\frac{n}{2}} \\ \mathbf{z}_{\frac{n}{2}+1} \\ \vdots \\ \mathbf{z}_n \end{bmatrix} = \begin{bmatrix} 1 & & s & & \\ & \ddots & & & s & \\ s & & 1 & & & \\ & & & 1 & & s \\ & s & & & \ddots & \\ & & & s & & 1 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \vdots \\ \mathbf{a}_{\frac{n}{2}} \\ \mathbf{a}_{\frac{n}{2}+1} \\ \vdots \\ \mathbf{a}_n \end{bmatrix} \tag{18}$$

Given that

$$\mathbf{a}_1, \ldots, \mathbf{a}_{\frac{n}{2}} = \begin{bmatrix} \cos \frac{\theta}{2} & \sin \frac{\theta}{2} \end{bmatrix} \text{ and}$$

$$\mathbf{a}_{\frac{n}{2}+1}, \ldots, \mathbf{a}_n = \begin{bmatrix} \cos \frac{\theta}{2} & -\sin \frac{\theta}{2} \end{bmatrix} \tag{19}$$

it is clear that

$$\mathbf{z}_1, \ldots, \mathbf{z}_{\frac{n}{2}} = \mathbf{u} \quad \text{and} \quad \mathbf{z}_{\frac{n}{2}+1}, \ldots, \mathbf{z}_n = \mathbf{v} \tag{20}$$

where $\mathbf{u}$ and $\mathbf{v}$ are single two-dimensional vectors. The angular range θ' of the STA directions will be the

angle between **u** and **v**. We can write down **u** and **v** explicitly as

$$u_1 = \cos\frac{\theta}{2} + s\left(\frac{n}{2}-1\right)\cos\frac{\theta}{2} + s\frac{n}{2}\cos\frac{\theta}{2}$$

$$u_2 = \sin\frac{\theta}{2} + s\left(\frac{n}{2}-1\right)\sin\frac{\theta}{2} - s\frac{n}{2}\sin\frac{\theta}{2}$$

$$v_1 = \cos\frac{\theta}{2} + s\left(\frac{n}{2}-1\right)\cos\frac{\theta}{2} + s\frac{n}{2}\cos\frac{\theta}{2}$$

$$v_2 = -\sin\frac{\theta}{2} - s\left(\frac{n}{2}-1\right)\sin\frac{\theta}{2} + s\frac{n}{2}\sin\frac{\theta}{2} \quad (21)$$

Vectors **u** and **v** are of the form $\mathbf{u} = [\alpha, \beta]$ and $\mathbf{v} = [\alpha, -\beta]$ where

$$\alpha = (1 - s + ns)\cos\frac{\theta}{2}$$

$$\beta = (1-s)\sin\frac{\theta}{2} \quad (22)$$

We also have

$$\tan\frac{\theta'}{2} = \frac{\beta}{\alpha} \quad (23)$$

Substituting Eq. (22) into Eq. (23) gives the desired result.

$$\tan\frac{\theta'}{2} = \frac{1-s}{1-s+ns}\tan\frac{\theta}{2} \quad (24)$$

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