Relationships among low-frequency local field potentials, spiking activity, and three-dimensional reach and grasp kinematics in primary motor and ventral premotor cortices

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Bansal AK, Vargas-Irwin CE, Truccolo W, Donoghue JP. Relationships among low-frequency local field potentials, spiking activity, and three-dimensional reach and grasp kinematics in primary motor and ventral premotor cortices. J Neurophysiol 105: 1603–1619, 2011. First published January 27, 2011; doi:10.1152/jn.00532.2010.—A prominent feature of motor cortex field potentials during movement is a distinct low-frequency local field potential (lf-LFP) (<4 Hz), referred to as the movement event-related potential (mEP). The lf-LFP appears to be a global signal related to regional synaptic input, but its relationship to nearby output signaled by single unit spiking activity (SUA) or to movement remains to be established. Previous studies comparing information in primary motor cortex (MI) lf-LFPs and SUA in the context of planar reaching tasks concluded that lf-LFPs have more information than spikes about movement. However, the relative performance of these signals was based on a small number of simultaneously recorded channels and units, or for data averaged across sessions, which could mislead information of larger-scale spiking populations. Here, we simultaneously recorded LFPs and SUA from two 96-microelectrode arrays implanted in two major motor cortical areas, MI and ventral premotor (PMv), while monkeys freely reached for and grasped objects swinging in front of them. We compared arm endpoint and grip aperture kinematics’ decoding accuracy for lf-LFP and SUA ensembles. The results show that lf-LFPs provide enough information to reconstruct kinematics in both areas with little difference in decoding performance between MI and PMv. Individual lf-LFP channels often provided more accurate decoding of single kinematic variables than any one single unit. However, the decoding performance of the best single unit among the large population usually exceeded that of the best single lf-LFP channel. Furthermore, ensembles of SUA outperformed the pool of lf-LFP channels, in disagreement with the previously reported superiority of lf-LFP decoding. Decoding results suggest that information in lf-LFPs recorded from intracortical arrays may allow the reconstruction of reach and grasp for real-time neuroprosthetic applications, thus potentially supplementing the ability to decode these same features from spiking populations.

motor cortex; neural signals; neural coding; brain-machine interfaces; neural prosthesis

THE PRIMARY MOTOR CORTEX (MI) and the reciprocally connected ventral premotor area (PMv) appear to form a key part of a network for planning and execution of reach and grasp actions (Godschalk et al. 1984; Matelli et al. 1986; Gentilucci et al. 1988; Rickert et al. 2005; Prabhu et al. 2009). These areas, together with other cortical regions, are thought to participate in the final stages of the computation of grip type and reach parameters when reaching to objects. MI-PMv activity during reach and grasp is of interest at the fundamental level because it reveals cortical transformations related to motor planning and execution. Furthermore, understanding this activity has relevance for neural prosthetic applications, where LFP-based high dimensional control signals could supplement simultaneously recorded spiking that may be used to achieve reach and grasp actions for people with paralysis (Hochberg et al. 2006; Vargas-Irwin et al. 2010).

Among the broad range of field potential types (Bullock 1997), low-frequency local field potentials (lf-LFP) are of interest because they may reflect arriving synaptic drive (Haberly and Shepherd 1973; Rebert 1973; Mitzdorf 1985; Logothetis 2002) that leads to spiking patterns through a not-yet-understood transform. Intracortical recordings in frontal cortex reveal an lf-LFP signal during relatively constrained reach or grasp tasks. This movement-evoked potential (mEP; typically <4 Hz) in monkeys contains information about target direction, velocity, and trajectory for discrete (step-tracking) two-dimensional movements (Mehring et al. 2003; Rickert et al. 2005). Furthermore, grip type can be classified from lf-LFP signals (Asher et al. 2007; Stark and Abeles 2007); specifically, these studies used the activity in a 1–100 Hz LFP band averaged over tens to several hundred milliseconds. Others have described a similar signal called a slow potential (~1 Hz) obtained from extracortical recordings in electrocorticography (ECoG), EEG, and magnetoencephalography (MEG) and related to kinematics of continuous two-dimensional movements (Kelso et al. 1998; O’Suilleabhain et al. 1999; Jerbi et al. 2007; Schalk et al. 2007; Pistohl et al. 2008), three-dimensional hand velocity (Bradberry et al. 2010), and forces (Shibata et al. 1997). These data suggest that the intracortical lf-LFP may reflect local neural processes leading to spiking output and provide useful neural prosthetic command signals. However, previous studies have not determined whether the lf-LFP carries information about three-dimensional reach and grasp as recently found for spiking populations (Vargas-Irwin et al. 2010) and LFP power in much higher-frequency bands (Zhuang et al. 2010) in MI. Mehring et al. (2003) recorded up to eight simultaneously recorded channels in MI and suggested that LFP channels tend to do better than units on average, but the results of Asher et al. (2007) suggested that the unit activity is more informative than LFPs in posterior parietal cortex. Stark and Abeles (2007)
found that the LFPs (1–100 Hz) generally provided similar or better decoding performance than single unit activity in pre-motor cortex, except in predicting discrete reach direction. Although PMv is thought to be a major source of grasp information for MI (Kurata and Tanji 1986; Prabhu et al. 2009; Rizzolatti et al. 1988), the information available about reach and grasp from PMv if-LFP, and its information content relative to MI if-LFP, is also not known. Comparative information about natural reach and grasp information simultaneously in MI and PMv has been difficult to obtain because it requires multichannel recording from multiple arrays (e.g., MI and PMv) while fully capturing kinematics during free reach and grasp movements.

Here we used dual 96-microelectrode arrays to simultaneously record if-LFPs and the spiking activity of neuronal ensembles in PMv and MI while monkeys performed unconstrained reaching and grasping to capture objects moving in their three-dimensional workspace. We compared three-dimensional hand position (referred to as arm end point) and hand aperture trajectory decoding performance based on either if-LFPs or spiking activity. It was possible to reconstruct grip-aperture, reach speed, and hand position in space from both signals in MI or PMv. Typically, the if-LFP from single channels yielded more information on average about a movement feature than an individual unit on the same array. This implies that the if-LFP provides a useful information signal about reach and grasp kinematics, especially when single units are not informative or not present. However, in our data the best units typically exceeded the best single LFP channels and the spiking ensemble typically gave better performance than using all LFP channels. In addition, we found that the if-LFP could be used to reconstruct the summed ensemble spiking suggestive of a close relationship between the two signals. Studies of the timing between if-LFP and kinematics suggest that the if-LFP carries more information about kinematics during the feedback period than during motor output. Nevertheless, if-LFP could provide a useful signal for neural prosthesis applications either to replace or supplement spike-based decoding.

METHODS

All experiments were performed with approval from the Institutional Animal Care and Review Committee (IACUC) at Brown University.

Behavioral Task

Continuous grasping task. Monkeys C and G performed a continuous grasping task. In this task the monkeys sat in a chair and were trained to reach and grasp various objects (see Fig. 1 of Vargas-Irwin et al. 2010) that were suspended using a string, which the experimenter would swing toward them. The trajectories and speeds of the objects were varied to elicit a variety of different reach-to-grasp movements. The experimenter’s pace in swinging the objects determined the periodicity of the targets. The arrows in the hand-speed spectrograms in Fig. 1, b and c, point to the average frequency (~0.5 Hz) at which the monkey reached toward the objects, which typically matched the frequency at which the objects were presented. Between six and nine objects were used for each session, with 20–40 trials per object.

The monkeys were rewarded for grasping and holding the suspended object for about 0.5–1 s. The reward consisted of ~0.5 ml orange juice delivered using a mouth tube. We simultaneously recorded kinematic data using an infrared optical motion capture system (Vicon Motion Systems, Oxford Metrics Group). This allowed us to obtain a measure of the hand x, y, z position (and corresponding velocity), aperture (and aperture velocity), and hand speed by tracking reflective markers (4 mm in diameter) placed at various positions along the arm and the hand. Details of the reconstruction of kinematics from the markers are available in other publications (Artemiadis et al. 2007; Vargas-Irwin et al. 2010). Hand position was measured as the location of the proximal wrist marker. Aperture was measured as the distance between the distal most markers on the thumb and index finger. For plots showing occupancy of hand in the maximal workspace, please see Fig. 2d of Vargas-Irwin et al. 2010.

Cued reach and grasp (turntable) task. Two monkeys (CL and G) were trained to perform a reaching and grasping task toward a cylindrical object placed on a turntable. The monkeys were head-fixed and sat in a chair facing a turntable setup. The trial timeline was as follows (supplementary Fig. 5b; all supplemental material can be found with the online version of this article). Each trial started in the dark with the monkeys squeezing two hand-switches, one with each hand. After a 2-s delay, the object to be grasped was illuminated. This was then followed by a variable 1- to 2-s delay wherein the monkeys had to continue to hold the hand-switches. After this variable delay, a green light-emitting diode (LED) turned on, which served as a go signal for the monkey to release the hand-switch (chosen as the start of movement time) with its left (monkey CL) or right (monkey G) hand and reach out, grasp (CL, precision grip; G, power grip), and lift the object, while continuing to hold the hand-switch with the other hand. We used QTouch contact sensors (Quantum Research Group, Southampton, UK) on the object and turntable to detect when the monkeys made first contact, and when they began and finished lifting the object, and we recorded these events for aligning the neural activity. Reward was delivered 50 ms (monkey CL) or 250 ms (monkey G) after the end of the lift of the object, followed immediately by the lights being switched off, and an interval of 2 s until the beginning of the next trial. Detailed kinematic data were not reconstructed for this task, and consequently the decoding analysis described below was also not performed for this task.

Data Recording and Preprocessing

Neural recording was performed using two chronically implanted microelectrode arrays (Blackrock Microsystems, Salt Lake City, UT; 4.2 × 4.4 mm; 96 Si electrodes coated with parylene). Details of surgery are similar to those described previously (Sumer et al. 2005), except that two arrays were implanted in monkeys C and G. Arrays were implanted in arm/hand regions of MI and PMv (contralateral to hand used for task) in monkeys C and G (only MI in monkey CL). As shown in supplemental Fig. 1 in Vargas-Irwin et al. 2010, the MI implantation site was rostral to the central sulcus at the level of the genu of the arcuate sulcus. The PMv implantation site was just caudal to the arcuate sulcus at the level of the principal sulcus.

Data acquisition and storage were accomplished using a Cerebus multichannel data acquisition system (Blackrock Microsystems, formerly Cyberkinetics). LFPs (filtered on pre-amp between 0.3 and 500 Hz and sampled at 2 kHz or 1 kHz, 48 recorded channels for monkey C, 96 for monkey G; referred to as raw LFP subsequently to differentiate from filtered LFP) and spiking activity (30 kHz signal thresholded at 4.5 × baseline noise standard deviation followed by extracting 1.6 ms, 48-sample spike waveform) were collected. Collected activity included both single- and multunit. An automatic spike-sorter (Vargas-Irwin and Donoghue 2007) was used to identify single units that were extracted from the thresholded filtered signal.

Data analysis was performed using custom software written in Matlab (Mathworks, Natick, MA), and the Chronux library (http://chronux.org/ and from Observed Brain Dynamics, Partha Mitra and Hemant Bokil, Oxford University Press, New York, 2008). Slow-
potentials or Pf-LFPs were obtained using a Savitzy Golay filter (2nd order, 0.5 s). This is similar to the filter used in Pistolet et al. (2008). Similar results were observed with a Kaiser filter with a 2-Hz cutoff. The data were filtered using zero-phase filtering (filfilt in Matlab) to avoid phase distortions at different frequencies.

Decoding

Kinematic data were downsampled from 240 Hz to 24 Hz by linear interpolation. Pf-LFP data were downsampled from 2 kHz to 24 Hz. For the results in the paper (excluding supplementary Fig. 1), the kinematic parameters were filtered with a 2 Hz low-pass filter similar to that applied on the LFP signal. Optimal lags corresponding to the maximum cross-correlation obtained were used. This process was repeated 100 times for each signal, and then used this signal to decode the kinematics (or summed spiking). This process was repeated 100 times for each area. The maximum of the cross-correlation obtained was used to decode reach and grasp kinematics from the Pf-LFP. The state-space model was given by:

$$x_{k+1} = A x_k + e_k$$

$$y_k = H x_k + w_k$$

where $$x_k$$ is a given kinematic variable, $$k$$ indexes time (41.7 ms time steps). $$P_{k-1}$$ corresponds to the Pf-LFP amplitude as measured on the 18th electrode (2 kHz signal linearly interpolated down to 24 Hz to match downsampled kinematics). $$A$$ and $$H$$ are the state and observation matrices, respectively, and $$e_k \sim N(0, Q)$$ and $$w_k \sim N(0, R)$$ are the state and observation Gaussian noise, respectively. Parameters in state-space and the Kalman filter solutions were estimated and computed using an algorithm described earlier (Wu et al. 2004). Both the kinematic states and the Pf-LFP observations were normalized by mean subtraction and dividing by the standard deviation.

The decoding was cross-validated by using the data from n-1 objects within a session for training and testing on the trials that were not used for training (leave-one-object-out classification).

Relationship to Spiking

To test the relationship between LFP and spiking, we evaluated the ability to decode the total summed population spiking from the simultaneously recorded Pf-LFP. We computed the total number of spikes across all units in 41.7-ms bins (defined as summed spikes) and then attempted to decode this quantity using a Kalman filter with Pf-LFP observations. The approach was otherwise the same as used for kinematic decoding.

Bootstrap Estimate for Significance

To obtain confidence intervals for the cross-correlation, we phase-randomized the Pf-LFP signal (by taking the Fourier transform, randomizing the phases, and then taking the inverse Fourier transform of the signal), and then used this signal to decode the kinematics (or summed spiking). This process was repeated 100 times for each session across each area. The maximum of the cross-correlation obtained using this procedure across sessions is reported in the black bars in figures such as Figs. 4a and 7b. For decoding using individual units, significance was gauged by comparing the decoded kinematic signal with a phase-randomized version of the kinematic signal. The confidence bounds for root mean squared error were estimated by plotting the range of the root mean squared error of the kinematics (or summed spiking) decoded using the phase-randomized LFP signal.

Performance of n-Best Units/Channels

To examine the improvement obtained by progressively adding additional Pf-LFP channels (or spiking units) to the pool used for decoding using Kalman filter, we first selected the best channel (or unit) among the total number of channels (or units). We then selected the best two channels (or units) including the already selected channel (or unit) that improved the most on the first channel (or units). Next we selected the best three channels (or units) including the already selected best two channels (or units) that improved the most over those two channels (or units), and so on, until the maximum number of channels (or units) was reached. Thus at each step the channel (or unit) that contributed the most independent information was added to the existing pool of channels (or units). Channel selection was performed on the test data.

For the average-case analysis (Fig. 6, c and d), we picked n input channels (or units) at random instead of picking the best n channels (or units) for 100 draws at each input number.

RESULTS

LFP During Reach and Grasp Actions

The LFP recordings in MI and PMv were obtained from two monkeys in two sessions, each performing the continuous grasping task (48 channels in monkey C; 96 channels in monkey G; supplementary Table 1 lists the number of units recorded during each session). The monkeys reached and grasped different objects that were suspended in front of them (see METHODS for details). Figure 1a shows representative traces of the kinematics (here hand-speed), the raw LFP (0.3–500 Hz), and the slow-frequency filtered LFP (0.3–2 Hz) recorded in MI and PMv in monkey C. At a descriptive level, the raw LFP traces illustrate a correspondence between reach kinematics and the LFPs. Each reach is accompanied by a cycle in the LFP of a similar duration (~2 s). This correlation can be further appreciated in Fig. 1, b and c, which shows that the MI and PMv LFP signals and the hand-speed signal have peaks in the same frequency range (around 0.5 Hz, depicted by arrows; note that monkey G, Session 2, MI spectra in the low frequency range was noisy). Finally, the sum of the spikes recorded in all units in each area also cycles in parallel with the reach speed and LFP (Fig. 1a).

Decoding of Reach and Grasp Using Pf-LFP

We next used decoding methods to evaluate the relationship between behavioral variables and neural signals. First, we tested the ability to reconstruct reach and grasp kinematics from the Pf-LFP. We reconstructed aperture, aperture velocity, three-dimensional position (x, y, and z), three-dimensional velocity (x, y, and z-velocity) and reach-speed using the Pf-LFP signal decoded with a Kalman filter (with many-fold cross-validation). Figure 2, a and b and c and d, respectively, show examples of three-dimensional trajectory decoding in monkey G and monkey C from two sessions. Overall, the Pf-LFP does well at reconstructing the general shape of the movement.

The two- or three-dimensional trajectories in Fig. 2 do not completely convey the quality of reconstruction of the details of kinematic parameters. To ascertain how well the Pf-LFP captured the details of kinematic parameters we plot in Fig. 3 the decoded (under cross-validation) aperture (gray) for two different objects, along with the original aperture (black) (Session 2, monkey G, PMv). Note that the shape and the amplitudes of the aperture are distinct for the two objects, and the decoded aperture matches these distinctions, even though no Pf-LFP data for each particular object were used in training the corresponding Kalman filter. The figure also plots similar comparisons for hand-speed, z-position, and z-velocity.
Figure 4a summarizes the results of the decoding of all nine kinematic parameters from each monkey for each session. Here we established a significance threshold (black bars), using a bootstrap procedure that tested the ability to decode these kinematic variables using a \( \text{lf-LFP} \) signal with its phases randomized (for details see METHODS). For this figure, in each session we chose the area (MI or PMv) that gave the best cross-correlation. Full decoding results, presented in Table 1, are often quite similar in MI and PMv. We merely plot the best area for ease of visualization. Aperture, aperture velocity, z-position, z-velocity, hand-speed, and y-velocity could be decoded with a mean cross-correlation of between 0.6 and 0.8. X-position, x-velocity, and y-position could be decoded with a mean cross-correlation of between 0.4–0.6. Decoding performance for each kinematic measure varied in each monkey. Thus aperture and y-position were better decoded in monkey G compared with monkey C (mean CC in monkey G for aperture: 0.78, y-position: 0.66; mean CC in monkey C for aperture: 0.51, y-position: 0.27), whereas the reverse was true for hand-speed (mean CC in monkey G: 0.57; mean CC in monkey C: 0.78).
Another method of quantifying decoding accuracy employs root mean squared (rms) error, which corresponds to the mean distance between the neurally reconstructed and the true measured kinematic trajectory. The average of the rms error across sessions for the different kinematic parameters was ~10% of the range of the kinematic parameter (Fig. 4b; supplementary Fig. 1b plots significance estimates; see Table 1). To examine the influence of filtering of kinematics on decoding performance, we measured the decoding performance for kinematic parameters without using a low-pass filter.

Fig. 2. Examples of reconstructed 3-dimensional hand end point trajectories (actual in thick black; reconstructed in thin gray) from each of the 4 data sessions. Star indicates start location of the trajectory. a and b correspond to a trajectory each from sessions 1 and 2, respectively, from monkey C. c and d correspond to a trajectory each from sessions 1 and 2, respectively, from monkey G. Axes are in normalized units (mean subtracted and divided by standard deviation for each dimension for display purposes).
on the kinematics (supplementary Fig. 1a). The results were generally comparable for most parameters but slightly worse for aperture velocity, x-velocity, and y-velocity. Of note is the difference in hand-speed decoding performance for monkey G between filtered and unfiltered kinematics. Monkey G’s movements were faster (reduced peaks for hand-speed spectra in Fig. 1c) than monkey C’s (Fig. 1b). The decoding performance for monkey G for filtered kinematics is better than that for unfiltered kinematics, suggesting that the If-LFP does better at decoding the slower frequency component of the kinematics. These results also suggest that the qualitative results plotted for decoded hand-speed in Fig. 3 for monkey G can be improved on in monkey C.

Comparison Between Individual If-LFP Performance and Individual Unit Performance

Both MI and PMv contain neurons that encode kinematic parameters related to reach and grasp (Georgopoulos et al. 1986; Kurata and Tanji 1986; Rizzolatti et al. 1988; Vargas-Irwin et al. 2010, and thesis), but the relative quality of decoding these variables using spiking or LFP has not been established. We compared the decoding performance of individual units versus the decoding performance of the If-LFP measured on the same electrode array for each kinematic parameter. We first examined the distribution of cross-correlation (between observed and decoded kinematics) values obtained by using each If-LFP channel individually versus using each unit individually. We found that the median cross-correlation obtained using the If-LFP was almost always (31/36 comparisons) higher than that obtained using any one unit, for all kinematic parameters tested across sessions across monkeys (Fig. 5, a and b; supplementary Fig. 2, a and b). We next decoded a selected kinematic variable (1 from each monkey) where the pooled If-LFP performed optimally (monkey C: hand-speed using MI array; monkey G: z-velocity using PMv array). The rationale was to examine whether the pooled If-LFP across channels can do better than the pooled units across the electrodes (similar to a comparison in Mehring et al. 2003). We compared the improvement in decoding performance when progressively adding units versus progressively adding If-LFP channels (Fig. 6, a and b). As shown in this figure, although the median single-channel If-LFP cross-correlation is better than the median unit cross-correlation, the best unit across the entire group of channels typically does better than the best If-LFP channel for that variable (also see Table 2). Furthermore, as the best units or channels are added to the pool, the performance of the pool of best n units stays above the performance of the pool of best n channels, with the performance saturating at around 20 best units or best channels. However, it is interesting to note that after a certain number of channels are added, the pool of If-LFP channels can begin to do better than the single best unit.

We found that the pooled and best single channel If-LFP decoding does not exceed that of equivalent decoding using spiking neurons (Fig. 6, a and b). By contrast Mehring et al. (2003) reported that decoding based upon a population of LFP channels exceeds that from a population of units (compare our Fig. 6b with their Fig. 3a). The difference may be due to the fact that their curves represent the cross-correlation for the average case, i.e., when LFPs or units are recorded across days.

Fig. 3. Reconstruction of kinematic parameters using If-LFP for two objects (obj). Decoded (gray) and original (black) aperture, hand-speed, z-position, and z-velocity for a 15-s long subsection for reaches and grasps to 2 different objects by monkey G during session 2 (PMv If-LFPs were used).
and their performance is computed for a randomly subsampled ensemble from the combined pseudo-population, whereas our curves were constructed using a greedy or best-case algorithm. We examined this question by redoing the analysis reported in Fig. 6, a and b, according to the averaging approach taken by Mehring et al. (2003). We picked 100 random subsets of LFP channels or units and computed their average decoding performance for each session for each kinematic parameter plotted (open markers: monkey C; filled markers: monkey G; squares: MI; circles: PMv). Bars represent mean (across 2 sessions in each of the 2 monkeys) cross-correlation for each of the 9 kinematic parameters. Black bars represent the maximal range of the cross-correlation that was observed by using a phase-randomized $lf$-LFP signal (see METHODS) for decoding the same kinematics for all the sessions (100 iterations $\times$ 4 sessions). b: assessing the decoding performance using root mean squared error (RMSE) is reported for the area that gave the best cross-correlation value for that session. Supplementary Fig. 1b plots the bootstrap significance estimates for the root mean squared errors.

**Relationship Between $lf$-LFP and Local Spiking**

Because FPs can reflect dendritic (and hence synaptic) current flow, the $lf$-LFP could reflect the total local input giving rise to spiking output in a given region (Rebert 1973; Mitzdorf 1985; Logothetis 2002). To directly test the idea whether the $lf$-LFP is related to the local summed spiking we examined whether the local summed spiking (as recorded on the array) could be reconstructed from the $lf$-LFP signal. Figure 7a shows examples of Kalman filter decoded summed spiking using the $lf$-LFP signal in each monkey. The mean cross-correlation between original and decoded summed spiking was between 0.71 and 0.88 for the different sessions (except monkey G, session 2, MI on account of noisier recordings), with a root mean squared error of around 10% (Fig. 7b, Table 3a). This suggests that the $lf$-LFP is a close correlate of summed spiking. However, this needs to be considered along with the analysis of optimal timing between these signals for decoding (lags), discussed in the next section.

Another method of evaluating the relationship between $lf$-LFP and spiking is to compute the extent to which they are phase-locked. We therefore performed a preliminary analysis to explore whether the spiking activity was phase-locked to the $lf$-LFP in monkey C (supplementary Fig. 6). We found that a large number of units in PMv ($n = 135$) and MI ($n = 54$) were significantly phase-locked to the $lf$-LFP (circular distribution of spike-phases relative to $lf$-LFP was significantly different from a uniform distribution).
Table 1. Summary of decoding performance using the Kalman filter

<table>
<thead>
<tr>
<th>Kinematic parameter</th>
<th>MI</th>
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<td></td>
<td>CC</td>
<td>RMSE</td>
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</tr>
<tr>
<td>C</td>
<td>0.8</td>
<td>0.78</td>
<td>0.07</td>
<td>0.06</td>
</tr>
<tr>
<td>G</td>
<td>0.76</td>
<td>0.69</td>
<td>0.06</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Table shows peak cross-correlation (CC) and root mean squared error (RMSE) of original and decoded kinematics in two monkeys in two sessions using lf-LFP from all recorded local field potential (LFP) channels from two areas. MI, primary motor cortex; PMv, ventral premotor; Vel, velocity.

Analysis of Optimal Lags

The above analyses used lags of between $-833.33$ ms and $+833.33$ ms to find a cross-correlation peak between decoded kinematics and original kinematics. However, previous studies have used deterministic (predictive) lags where the neural signal precedes the kinematic signal to make a case for applicability to brain-machine interfaces (Mehring et al. 2003; Pistohl et al. 2008). We next imposed a deterministic lag on the cross-correlation peak (where the kinematics decoded using the lf-LFP signal could only precede the original kinematics). We found that the decoding accuracy (Fig. 8a) was worse compared with that in Fig. 4a with nondeterministic lags, suggesting that sensory feedback from movement contributed to the quality of reconstruction. However, most of the cross-correlations remained statistically significant after removing lag activity, indicating that some of the lf-LFP reflects drive associated with generation of movement.

We next evaluated the optimal lags (before and after movement) for each parameter for each area in each session (Fig. 8b). The typical lags were around 100–300 ms (original kinematics precede lf-LFP decoded kinematics) for all decoded parameters, except for x-position where they were observed to be over 400 ms. Figure 8c shows that there was no significant difference between the optimal lags for MI versus those for PMv ($P > 0.94$), suggesting that both areas simultaneously show maximal information about kinematics in the lf-LFP.

The previous plots tell us about the optimal lags for the entire pool lf-LFP channels, but individual channels (or units as in Fig. 5) within the pools could have different optimal lags. This in turn could correspond to different levels of information about the kinematic parameter preceding or succeeding the movement. To study this question, we compared the optimal lags for individual channels and individual units. Figure 9 (and supplementary Fig. 4) plots the distribution of observed optimal lags for the lf-LFPs and the units (for all the kinematic parameters). Although there were many units and channels that had a negative lag (neural signal preceded kinematics), the median optimal lag for both units and channels was positive (kinematics preceded neural signal), suggesting that kinematic feedback-related information contributes both to the unit and lf-LFP signal. The optimal lags for decoding summed spiking in both areas were $+83.3$ ms in monkey C and $+41.7$ ms in monkey G, which indicates that the lf-LFP best predicted the summed spiking in the past, even while containing significant information about summed spiking in the future (Table 3b). In summary, the temporal relationship between the variables studied here demonstrates that kinematics precedes summed spiking, which in turn precedes the lf-LFP. However, the lf-LFP still contains information about kinematics before movement, which could potentially be used for brain-computer interface (BCI) applications.

Intrinsic Oscillation or Event-Related Potential?

An unresolved issue so far with the use of the lf-LFP here (and as a slow potential in other studies, see Table 4) is whether the signal is an intrinsic oscillation or related to the rhythmic or repetitive movements (as in the mEP) performed. As an initial analysis, we compared the lf-LFP signals in the
Fig. 5. Comparison of individual units vs. individual channel decoding performance. a: distribution of cross-correlations when using individual units (gray) vs. using individual lf-LFP channels (open). Inverted triangles represent the corresponding medians of the distributions. For all comparisons, the medians were significantly different ($P < 10^{-7}$, Kruskal-Wallis test) (monkey G, session 1, PMv array). b: similar to a, but for monkey C, session 2, MI array. For all comparisons, the medians were significantly different ($P < 10^{-5}$, Kruskal-Wallis test; except x-position, where $P < 0.02$).
continuous reaching task with those in a discrete task where each reach and grasp movement was cued in one monkey (see METHODS; data presented below are from 1 session in 1 monkey, although multiple sessions were recorded from 2 monkeys with qualitatively similar results).

Supplementary Fig. 5a shows raw traces (0.3–500 Hz) of the LFP recorded simultaneously on two different microelectrodes from ventral premotor cortex and primary motor cortex (MI) of monkey G as it performed a cued grasping task (see METHODS) with an instructed delay on four trials. A consistent lf-LFP (1 Hz) was observed around the time of movement onset (corresponding to the release of a hand-switch) in both areas. On the PMv channel shown here, this signal started with an initial negativity just before the release of the hand-switch, followed by an increase leading to a positivity just after the end of lift, and finally a gradual return to baseline. In the MI channel shown here, the positivity occurred more quickly after the negativity. The return to baseline suggests that the signal is an evoked potential and not related to an intrinsic rhythm as such.

In addition, we observed that the dominant frequency of the lf-LFP or slow potential was generally slower (1 Hz), compared with the typical frequency of the mEP (2 Hz) (Donchin et al. 2001; Rickert et al. 2005). This might be attributable to the lower frequency limit of the differences in bandpass filter settings (1–150 Hz in their studies vs. 0.3–1 Hz for this figure). To test this further, we compared the result of filtering the lf-LFP signal from MI using a 1–150 Hz bandpass filter instead of a 0.3–1 Hz filter in a monkey performing a center-out task (supplementary Fig. 5b). We observe that the time course of the signal was then faster, matching the time course of previously reported mEP signals.

These results suggest that the lf-LFP (or slow potential) and the mEP may be related to the same underlying neural processes: the lf-LFP described here may just be the continuous, repeated realization of the mEP. Supplementary Fig. 5 suggests that the observed low-frequency signal is an event-related potential, and not an oscillation intrinsic to these cortical areas. The oscillatory nature of the signal observed in other tasks seems to arise from the repeated movements during those tasks.

DISCUSSION

Lf-LFPs and Motor Control

The present study demonstrates that the lf-LFP can be used to decode end-point position, velocity, and aperture during three-dimensional reaching and grasping by able-bodied monkeys. Decoding performance based on lf-LFPs significantly extends previous results in two-dimensional tracking tasks based on using EEG or ECoG (Schalk et al. 2007; Pistohl et al. 2008), indicating that by sampling from many channels, higher dimensional kinematics can also be decoded using the lf-LFP signal. Although it was possible to reconstruct kinematics with substantial accuracy (0.6–0.8 maximum cross-correlation for most parameters) from lf-LFPs (Fig. 4), the decoding performance based on spike counts was typically better and more consistent across sessions (i.e., when compared with Vargas-Irwin et al. 2010, the average maximum value of the cross-correlation function between true and reconstructed kinematics was usually higher when decoding from spikes than when decoding from lf-LFPs; in addition, the across-session variability in the maximum cross-correlation value was lower for spikes than for lf-LFPs). More sophisticated algorithms applied to lf-LFP decoding may outperform spike-based decoding, or at least help it achieve even better performance, and this may

Fig. 6. Best-case and average-case decoding performance. a: comparison of improvements in individual unit (thin gray) vs. individual channel (thick black) decoding performance when using a greedy procedure (monkey C, MI, Hand-speed). b: monkey G, PMv, z-velocity. Dashed lines represent the median of the cross-correlation when using individual units (thin gray) or individual (thick, black) channels for that kinematic parameter for that session. c and d: average-case decoding compared with best-case decoding. c and d are similar to a and b but picking 100 random subsets of LFP channels or units and computing their average decoding performance instead of using the greedy procedure. Error bars plot ± 1 SE. c: monkey C, MI, hand-speed. d: monkey G, PMv, z-velocity.
be examined in future work. Furthermore, in closed loop applications, error correction based on feedback may improve performance.

Spiking signals, which are only available from penetrating microelectrodes, provide a command signal that has been used by monkeys (Serruya et al. 2002; Taylor et al. 2002; Carmena et al. 2003; Velliste et al. 2008) and also by paralyzed humans (Hochberg et al. 2006) to control virtual cursors and physical devices, such as a robotic arm. Intracortical BCIs (iBCIs) also record LFPs, which may also serve as an alternative or as a supplementary source of control (Pesaran et al. 2002; Andersen et al. 2004; Donoghue 2008; Waldert et al. 2009), but the utility of these signals was not clear. A recent study by Fujii and colleagues (Chao et al. 2010) used ECoG in primates to successfully decode three-dimensional position and joint kinematics. Our results are complementary to theirs: 1) we focus on the LF-LFP band, whereas they use all frequency bands up to 150 Hz; 2) ECoG has a different spatial sampling of neuronal signals because it uses bigger electrodes (1 mm exposed) that are spaced over large parts of the cortex (32 or 64 channels, 3.5 mm apart), whereas we used 100 microelectrodes (<0.1 mm exposed) 0.4 mm apart; and 3) we decoded grasp aperture in addition to three-dimensional position and velocity.

**Quality of Reconstructions Using LF-LFP**

The state matrix in the Kalman filter model already incorporates prior knowledge about temporal correlations in hand kinematics and aperture during decoding. Given the rhythmic feature of the performed reach and grasp kinematics, this prior knowledge could by itself lead to substantial correlation coefficients even in the case of a noninformative LFP signal. However, the fact that measured correlation coefficients were well above the upper confidence bound for chance correlations obtained via the phase-randomization procedure suggests that there is a true statistical dependence between LF-LFPs and kinematics (Fig. 4a). One could still argue that this

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**Table 2. Summary of individual LF-LFP channel versus individual unit decoding performance**

<table>
<thead>
<tr>
<th>Kinematic Parameter</th>
<th>Session 1</th>
<th>Session 2</th>
<th>Monkey C</th>
<th>Monkey G</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fraction of Significant Channels</td>
<td>Fraction of Significant Units</td>
<td>Median Channel</td>
<td>Median Unit</td>
</tr>
<tr>
<td>Aperture</td>
<td>0.96</td>
<td>0.93</td>
<td>0.88</td>
<td>0.99</td>
</tr>
<tr>
<td>X-Pos</td>
<td>0.94</td>
<td>0.92</td>
<td>0.84</td>
<td>0.98</td>
</tr>
<tr>
<td>Y-Pos</td>
<td>0.92</td>
<td>0.99</td>
<td>0.81</td>
<td>0.98</td>
</tr>
<tr>
<td>Z-Pos</td>
<td>0.99</td>
<td>0.99</td>
<td>0.96</td>
<td>0.99</td>
</tr>
<tr>
<td>Hand-speed</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
</tr>
<tr>
<td>Ap-Vel</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
</tr>
<tr>
<td>X-Vel</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
</tr>
<tr>
<td>Y-Vel</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
</tr>
<tr>
<td>Z-Vel</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
</tr>
</tbody>
</table>

Shown here are fraction of significant channels/units, median cross-correlation, and best channel/unit cross-correlation for each parameter for each session for each monkey (for the area that yielded better overall cross-correlation: MI in monkey C, PMv in monkey G). Pos, position.
dependence between $l$-LFPs and kinematics resulted simply because the $l$-LFP oscillation is time-locked to movement onset. In that case, and given the similar frequency content of $l$-LFP and kinematics (Fig. 1, b and c), one could expect some above chance level decoding, especially in terms of rhythmic kinematics. Although we cannot entirely rule out this possibility in our reach and grasp data, the fact that we were able to decode position and velocity in different coordinate frames, as well as grasp aperture kinematics above chance, during a task where the movement goal was haphazardly moved throughout the workspace makes this interpretation unlikely (Fig. 3).

Relative Performance of $l$-LFP Versus Unit Recordings

To our knowledge, this is the first study to compare decoding performance between units and $l$-LFP from arrays in motor cortical areas in monkeys performing a rich, complex task. Our results indicate that for single intracortical electrodes, on average the $l$-LFP will give better decoding performance than the average performance of any one unit recorded on those electrodes. However, across an array of 96 electrodes, sampling from a small cortical region (4 $\times$ 4 mm$^2$ of MI arm area, or PMv), the best unit overall will provide better decoding than the best $l$-LFP channel from that same sample. Furthermore, our results show that the units considered as a population for decoding do better than the pooled $l$-LFP (also see results from Vargas-Irwin et al. 2010). This difference likely reflects the nature of the recorded signals. The LFP is a function of summed currents across many neurons in an area (although synchronous spikes may also contribute), whereas spiking is a specific signal generated by single neurons that encode the exact output of that single cell.

We also performed a comparison of the best-case (using the best $n$ input $l$-LFP channels or units) and average-case (using any random $n$ input channels or units) approaches to attempt to
resolve the discrepancies between our result and those of Mehring et al. 2003. We found that it was possible to have instances where the LF-LFP outperformed units especially when we considered the average performance across a small number of channels or units. However, the best-case approach outperformed the average-case approach, and units outperformed LF-LFPs with greater numbers of inputs. These results suggest that the best-case approach may lead to a better characterization of the information that can be extracted from the neural signals.

Another reason for contrasting results with previous studies may be that we examined a larger number of simultaneously recorded units and LFPs within a session. The nature of a population code suggests that larger populations of spiking neurons will do better than smaller ones when drawing from this type of sample. For MI these populations may need only reach tens of neurons to show considerable encoding success (e.g., Vargas-Irwin et al. 2010). Nevertheless, a global LFP signal capturing multiple aspects of arm end point could exceed the information contained in the firing of a hypothetical single cell that was mainly correlated with the velocity of a single joint. In addition, our improvements could be partly due to the information in correlations between the unit activities or between the LF-LFPs measured on different electrodes that are afforded by simultaneous recording. Overall, the relative success of LF-LFP decoding of reach and grasp kinematics in this complex task suggests this signal may be useful for BCI applications, but this conjecture remains to be tested directly in paralyzed patients.

Unequal distributions of neurons coding different kinematic parameters will cause a different LF-LFP signal via their spatial averaging around any electrode in the array. We exploit this when using the LF-LFP for decoding. These results are promising for more global, surface FP recording methods such as ECoG, MEG, EEG, and fMRI, which admittedly use a coarser sampling resolution than our 400-micron spaced electrodes, in decoding three-dimensional kinematics but may point to some limitations in using the LF-LFP versus using spiking activity. Nevertheless, the relationship between ECoG and intracortical LFP, the relative differences in information from intracortically obtained FPs, and other factors like the influence of sensor geometry remain to be established.

### Relative Performance of MI and PMv

We found that there was no consistent difference between the decoding performances for PMv versus those for MI. This is surprising because earlier results have suggested that PMv neurons are preferentially associated with finger and grasp movements (Rizzolatti et al. 1988), although proximal movement representations have also been reported (Kurata and Tanji 1986). Also surprising was the finding that the optimal lags for decoding when using the LF-LFP signal were not significantly different between MI and PMv (Fig. 6c), as might be expected from a model where premotor cortex prepares the movement signals to be computed into motor commands by MI. These results argue against a differentiation of MI and PMv based on proximal movements and distal movements, respectively, at the level of FP signals during naturalistic reach and grasp actions.

### Relationship of LF-LFP to Spiking and Encoded Variables

Here we showed that the LF-LFP in primary motor and ventral premotor cortices could predict total spiking activity in each of these areas. The LF-LFP is thought to be associated with synaptic inputs into an area, whereas spiking activity reflects its output. The ability to reconstruct spiking from the LF-LFP at both positive and negative time-lags indicates that this FP might reflect current flow caused both by local as well as external spiking. Recent studies have found that the LF-LFP amplitude and high-frequency-LFP power can decode spiking activity and visual stimulus information in primary visual cortex (Belitski et al. 2008; Rasch et al. 2008). However, to the best of our knowledge this is the first example of decoding total spiking activity using LF-LFP in motor cortex.

Does the LF-LFP merely reflect the synaptic current or could it serve a more mechanistic process? An intriguing possibility is the idea of phase of firing coding where the spiking relative to the LF-LFP phase may provide additional information about kinematics, similar to other studies in auditory and visual cortices (Lakatos et al. 2008; Montemurro et al. 2008). Furthermore, recent theoretical work has suggested that such coding could be important for sequence learning (Masquelier et al. 2009). We found that many spiking units have significant phase-locking to the LF-LFP (supplementary Fig. 6), but we have not explicitly tested whether this carries additional information. Future work may examine whether phase-locking can be used to improve decoding performance.

### Mechanism of Movement Generation by Spikes and LF-LFPs in MI and PMv

We found that the optimal lags for decoding were such that neural activity (LF-LFP channels or units based decoding) succeeded kinematics, implying that kinematic feedback dominates these neural signals. However, both LF-LFPs and units also carried significant predictive information about kinematics, linking this LFP signal to both motor output as well as sensory feedback (also see Vargas-Irwin et al. 2010, where single-unit decoding performance for the same data was examined using strictly predictive lags). At least one previous study has also reported better decoding using both spikes and LFP with acausal lags (neural signal succeeding kinematics; for example, see Fig. 3c in Mehring et al. 2003). By contrast,
other studies have found that the maximal information in spiking about a kinematic parameter is usually before movement (Paninski et al. 2004; Wang et al. 2007). For example, a previous study from our laboratory (Paninski et al. 2004) used information tuning curves and reported lags of 100 ms with spiking preceding velocity, but the study also demonstrated widely distributed (both positive and negative) lags for position in a two-dimensional pursuit tracking task. Moran and colleagues (Wang et al. 2007) used an indirect optimal linear estimator (indirect OLE)-based decoding approach and have reported that the optimal cortical representation of velocity across a population preceded veridical hand velocity by 122 ms, whereas the representation of position preceded actual position by 81 ms in an overtrained three-dimensional reaches to fixed targets.

We next address why our results (better prediction with lf-LFP or units succeeding kinematics) might indicate a richer representation during feedback or the time at which proprioceptive information arrives in MI and PMv compared with those of Paninski et al. (2004) and Wang et al. (2007). First, we speculate that the naturalistic three-dimensional task with varied end point locations we use may require more feedback compared with a two- or three-dimensional step-tracking movement. Thus a reliance on high sensory feedback may provide better representation of the movement during the postmovement feedback period. However, this does not account for the observation of Mehring et al. (2003) in their two-dimensional task. We are currently performing further experiments with fixed targets in three-dimensional space, where we hypothesize a reduced role for feedback and, consequently, a better decoding of kinematic parameters before versus after movement. Second, the rostral parts of the primary motor cortex (on the gyrus) where our arrays were implanted receive most of their input from deep (muscle and joint)
Peripheral afferents and lack the abundance of corticomotoneuronal cells found in more caudal portions, which have a stronger input from cutaneous afferents (Rathelot and Strick 2006, 2009). Third, the feedback role of the \( \ell f \)-LFP is highlighted by the mEP's reported absence in a deafferented patient (Kristeva et al. 2006). Consistent with this result is the observation that the mEP is direction-selective after movement-onset in parietal cortex (Asher et al. 2007), indicating its dominance by sensory feedback. These observations highlight the importance of differences in tasks, recorded subregions within cortical areas, and signals (\( \ell f \)-LFP or spikes) in examining issues of motor control.

The early (premovement) components of the \( \ell f \)-LFP and spiking activity are significantly informative about kinematics; however, we find that the late components carry more information. These late components might reflect spiking activity and field potentials generated by local spiking or via corticocortical loops between motor cortical areas (such as MI) and parietal cortical areas (such as area 5). We found that the \( \ell f \)-LFP best decoded local summed spiking in the past (in MI and PMv), even though it could decode local summed spiking in the future. This indicates that the \( \ell f \)-LFP is not exclusively a motor input signal related to remotely generated spikes or a consequence of locally generated spikes, but is simultaneously related to both processes. Thus our results suggest that \( \ell f \)-LFP, spiking, and kinematics are not related to each other with strictly causal links but are instead part of a dynamical interplay that leads to the generation of continuous movements.

Not an Artifact

A concern of LFP signals is the possibility of recording non-neural artifacts. We rule out this possibility based on three lines of evidence. First, the mean cross-correlation and optimal lags were different on different channels, suggesting a difference in the amplitude and timing of the \( \ell f \)-LFP signal across channels. By contrast a global artifact would appear simultaneously on all channels. Second, a principal component analysis showed that 10 orthonormal bases (principal components) were required to account for 99% of the variance in \( \ell f \)-LFP signals, suggesting some degree of independence between the \( \ell f \)-LFP channels (supplementary Fig. 7). Finally, \( \ell f \)-LFP signals have been widely described in other studies, and as such the arguments made there against an artifactual cause for this signal apply here as well (for examples see Hwang and Andersen 2009).

Conclusion

We found that the \( \ell f \)-LFP signal can decode three-dimensional reach and grasp parameters in MI and PMv, with no

Table 4. Comparison of results of \(<1\)-Hz signals in previous studies with current study

<table>
<thead>
<tr>
<th>Method</th>
<th>Task</th>
<th>Observation</th>
<th>Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Schalk et al.</td>
<td>ECoG tracing a circle at 6.3-s period</td>
<td>Local motor potential (LMP)</td>
<td>Can decode 2-dimensional cursor position and velocity</td>
</tr>
<tr>
<td>O’Suilleabhain et al.</td>
<td>EEG wrist tracking at 1 Hz</td>
<td>EEG phase locked to wrist speed</td>
<td>Can decode 3-dimensional hand velocity</td>
</tr>
<tr>
<td>Bradberry et al.</td>
<td>EEG center-out reaches</td>
<td>(Decoding study)</td>
<td></td>
</tr>
<tr>
<td>Jerbi et al.</td>
<td>MEG trackball at 2 Hz</td>
<td>MEG phase locked to hand speed</td>
<td></td>
</tr>
<tr>
<td>Current Study</td>
<td>Intracortical LFP</td>
<td>Main task: Continuous reaching and grasping at (-2\text{--}3) s period [Supplementary: (i) Reaching and grasping turntable task with long ITI (ii) Center out reaches (-500) ms] (i) Slow potential entrained to repeated movements (ii) A slow potential around movement onset</td>
<td>Carries 3-dimensional position, velocity and aperture information</td>
</tr>
</tbody>
</table>

ECoG, electrocorticography; MEG, magnetoencephalography.
consistent differences in the form of kinematic information between the two areas. The lf-LFP decoding performance was more consistent across different electrodes on an array within a session (higher median r values) than the spiking activity, however, the best units performed better than the best individual lf-LFP channel, and when pooled together the population of units outperformed the lf-LFP signal, demonstrating that spiking is a richer source of kinematic information at this scale. It was possible to decode population spiking (summed spiking of all units) from the lf-LFP, thus linking the two signals. Our data suggest that lf-LFP appears to reflect currents generated by sensory feedback (based on decoding by the later components), and by local activity (based on decoding of the summed spiking), and by external signal sources (based on predictive decoding). Thus the lf-LFP cannot simply be considered as the arrival of input to drive movement related activity but a sum of local, motor, and sensory feedback signals. The kinematic information before movement in the intracortical lf-LFP signal should render them useful for BCI applications, potentially adding to the number of signals that can be obtained from penetrating electrodes.

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DISCLOSURES

Conflict of interest disclosure for John P. Donoghue: prior Chief Scientific Officer and director, stock holdings, Cyberkinetics Neurotechnology; company ceased operations in 2009.

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