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RESEARCH ARTICLE

Cortical activity predicts good variation in human motor output

Sarine Babikian[1] · Eva Kanso[1] · Jason J. Kutch[2]

Abstract Human movement patterns have been shown to be particularly variable if many combinations of activity in different muscles all achieve the same task goal (i.e., are goal-equivalent). The nervous system appears to automatically vary its output among goal-equivalent combinations of muscle activity to minimize muscle fatigue or distribute tissue loading, but the neural mechanism of this "good" variation is unknown. Here we use a bimanual finger task, electroencephalography (EEG), and machine learning to determine if cortical signals can predict goal-equivalent variation in finger force output. 18 healthy participants applied left and right index finger forces to repeatedly perform a task that involved matching a total (sum of right and left) finger force. As in previous studies, we observed significantly more variability in goal-equivalent muscle activity across task repetitions compared to variability in muscle activity that would not achieve the goal: participants achieved the task in some repetitions with more right finger force and less left finger force (right > left) and in other repetitions with less right finger force and more left finger force (left > right). We found that EEG signals from the 500 milliseconds (ms) prior to each task repetition could make a significant prediction of which repetitions would have right > left and which would have left > right. We also found that cortical maps of sites contributing to the prediction contain both motor and pre-motor representation in the appropriate hemisphere. Thus, goal-equivalent variation in motor output may be implemented at a cortical level.

Keywords EEG · Motor cortex · Goal-equivalent variability · Finger

Introduction

A key feature of human movement is that task goals can be repeatedly achieved even though the fine details of the movement are never repeated exactly (Bernstein 1967). Increasing evidence suggests that the lack of detailed repeatability in movement (interchangeably called goal-equivalent or task-irrelevant variation), rather than being noise, is actually an intended feature that may promote health by distributing tissue loading and/or minimizing muscle fatigue (Hamill et al. 2012; Lipsitz 2002). Goal-equivalent variation has been referred to as "good" variation and contrasted with "bad" variation, which would lead to motor errors not consistent with the goal of the task (Latash and Anson 2006).

Goal-equivalent variation has been observed in many types of movements and tasks. Such variation has been studied using Uncontrolled Manifold (UCM) analysis in such varied tasks as multi-finger force production, multi-joint reaching, standing, swaying and stepping (Latash 2008). These studies mostly focus on comparing variance across task repetitions in goal-equivalent and non-goal equivalent directions at the level of motor output (e.g., kinematics or endpoint force). Goal-equivalent variation has been shown using electromyography (EMG) to be present

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at the level of muscle commands (Krishnamoorthy et al. 2003). However, the level in the nervous system at which goal-equivalent variation appears has not been established. A subcortical-level hypothesis for goal-equivalent variation is that descending motor commands from the cortex are constant across repetitions of the same task, and goal-equivalent variation across repetitions happens at the level of subcortical or spinal circuitry that coordinates muscle activity (Giszter et al. 1993; Saltiel et al. 2001). An alternative cortical-level hypothesis is that goal-equivalent variation is directly formed at the level of the cortex and is present in descending motor commands (Latash and Huang 2015).

Here we take the novel step of testing these hypotheses and thus localizing goal-equivalent variation in the nervous system; we specifically aim to determine if goal-equivalent variability can be predicted by cortical-level signals. We made synchronous recordings of bilateral finger force and whole-scalp electroencephalographic (EEG) signals while participants repeatedly performed a task that allowed for goal-equivalent variation. We reasoned that if we found cortical-level signals that could predict goal-equivalent variation prior to the start of each repetition, we could reject the subcortical-level hypothesis that descending cortical signals were constant and support the cortical-level hypothesis for goal-equivalent variation in motor output.

Materials and methods

Participant population

We recruited 18 healthy right-handed participants (nine males and nine females) with a mean age 27.4 ± 4.5 years (range 23–41). The studies we describe here were performed at the University of Southern California and approved by the University of Southern California Institutional Review Board. All participants provided informed consent.

Overview of experiments

We used a bilateral finger task where participants applied simultaneous left and right index finger forces to repeatedly match the sum of forces to a target feedback force. Participants always matched the target, but there was a variation in left and right forces across repetitions: some repetitions were achieved with higher left force than right, and vice versa. We selected this task because it has been well studied in the literature on goal-equivalent motor output variation (Latash et al. 1998, 2001; Scholz et al. 2003). We used electroencephalography (EEG) to measure cortical signals during repetitions of the task, and employed a machine

learning technique to find out if EEG signals just prior to the start of each repetition were correlated with goal-equivalent force output variations. We selected EEG to leverage prior studies that have developed algorithms to decode the intention of explicit left versus right movements (Blankertz et al. 2008; Pfurtscheller et al. 1997). Our analysis was based on classifying goal-equivalent force output variation (two classes, left > right or right > left) using EEG signals only, and comparing the EEG-based classification with the force-based classes. A successful classification would imply that brain signals associated with each class are in fact distinguishable, and support the brain-level hypothesis for goal-equivalent motor output variation.

Finger force task

Participants performed a bimanual finger force task that involved abducting both index fingers simultaneously against load cells (Measurement Specialties, Hampton, VA) (Fig. 1a). We asked participants to repeatedly use both fingers to match a target total finger force [left force (F_L) + right force (F_R)] of 6 Newtons (N). For simplicity in this study, we chose a single target force level that would be easy to achieve for all healthy young participants, but not so low that it would be difficult to perform reliably in many repetitions: in a preliminary set of three participants (1 female, 2 males, mean age 31), we identified that 6 N was an appropriate force level, and used this force level in the main study cohort of 18 participants, none of which reported discomfort or fatigue. Participants received continuous visual feedback of their current total finger force as well as the fixed 6 N target; however, individual finger force was never provided to the participant as feedback. Each repetition of the task included the following segments chosen based on previous literature (Blankertz et al. 2006; Müller-Gerking et al. 1999): (1) 2 s of rest where nothing was shown on the feedback screen, (2) 2 s of a preparation period in which participants were cued to prepare for the task, and (3) 5 s of force hold. Participants performed a total of 100 repetitions.

We show an example of one participant's force repetitions in Fig. 1b. During each repetition of the task, total force was kept at 6 N (top trace), while individual forces fluctuated. Some repetitions of the task were performed with more left finger force $(F_L > F_R)$, and some were performed with more right finger force $(F_R > F_L)$. To summarize the combination of forces used by the participant on each repetition of the task, we computed separate averages for F_R and F_L across time starting 1 s after the target was displayed (to allow for reaction time and force stabilization) and ending half a second before the target disappeared (to exclude the return to baseline force). A total of 100 combinations of F_R versus F_L along with a 95% covariance ellipse
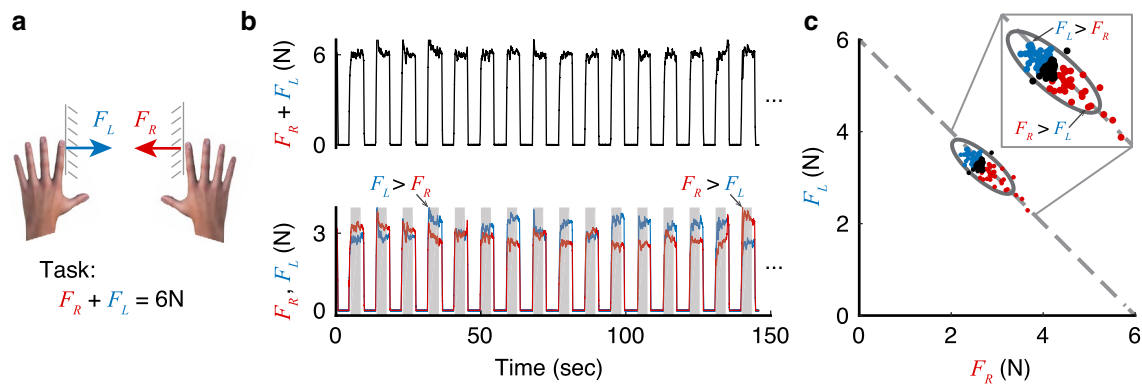
Fig. 1 Experiment setup and force output. **a** The participants place their hands flat on a table and repeatedly exert *left* (F_L) and *right* (F_R) index finger forces simultaneously, while keeping the sum of the two constant at a target force of 6 N. Only the sum of forces is shown to the participants as feedback on a screen, along with the target force level; **b** example of a representative participant's repeated force holds. The *top* trace shows the participant maintained the sum of the two forces at 6 N, while the bottom traces show the *left* (in *blue*) and *right* (in *red*) forces for the same repetitions. Some repetitions of the task were accomplished with a relatively higher *right finger* force, and others with a relatively higher *left finger* force. The interval shaded in *gray* (1 s after the start and 0.5 s before the end of the hold period) is used to determine the time average of individual forces in each repeti-tion; **c** average *right* versus *left* forces during all task repetitions for the same participant with a 95% covariance ellipse representing the variance of the data. The major axis represents the goal-equivalent direction, where the sum of forces is always 6 N, while the minor axis is the non-goal-equivalent direction where the sum of forces would deviate from the target of 6 N. The highest variation is seen in the goal-equivalent direction, while the orthogonal non-goal-equivalent direction has much lower variance. In our analysis we discard repetitions where forces belonged to the middle third portion of the ellipse, shown in black, to only keep repetitions where left and right forces were clearly different. Two classes of repetitions emerge: $F_L > F_R$ (in *blue*) and $F_R > F_L$ (in *red*). (Color figure online)

for one participant are shown in Fig. 1c. The major axis of the covariance ellipse represents the goal-equivalent direction along which all combinations do not affect the task of producing 6 N of total finger force. The orthogonal direction is the non-goal-equivalent direction. To identify repetitions of the task that were clearly different in the combination of F_R and F_L used by the participant, we removed force repetitions belonging to the middle third portion of the covariance ellipse (shown in black in Fig. 1c), to discard right and left forces that were almost equal. We identified the two remaining groups of force hold repetitions as two classes, $F_L > F_R$ (shown in blue) and $F_R > F_L$ (shown in red).

Electroencephalography

Along with force signals described above, we simultaneously recorded 64-channel whole-scalp electroencephalography (EEG) using a flexible cap according to the International 10–20 system (ANT Neuro, Enschede, The Netherlands). EEG signals were preprocessed to remove artifacts related to eye blinks and muscle activity using independent component analysis implemented in EEGLAB (http://www.sccn.ucsd.edu/eeglab). Subsequent analyses were performed on a subset of 27 EEG electrodes that span the sensorimotor area of the cortex, which is common practice in EEG-based classification studies (Blankertz et al. 2008; Müller-Gerking et al. 1999; Ramoser et al.

2000). Unilateral left- versus right-hand movements have been successfully predicted based on EEG signals from the 500 milliseconds (ms) prior to movement onset (Blankertz et al. 2006; Müller-Gerking et al. 1999), with EEG signals band-pass filtered from 7 to 30 Hz to include both alpha- and beta-bands. We applied this same algorithm to predict whether a given repetition of our bimanual finger task belonged to the $F_L > F_R$ class or the $F_R > F_L$ class using only the EEG signals during this 500-ms pre-movement period.

Machine learning for EEG analysis

Numerous studies have successfully predicted unilateral right-hand versus left-hand movement intention from EEG signals using a machine learning technique combining the signal processing method called common spatial patterns (CSP) (Dornhege 2007; Fukunaga 1990; Lemm et al. 2005), and the classification method linear discriminant analysis (LDA) (Blankertz et al. 2006, 2007, 2008; Dornhege et al. 2006; Ramoser et al. 2000). Pre-movement EEG signals of hand movement intention exhibit an event-related desynchronization, i.e., a decrease in power, of alpha and/or beta rhythms on the contralateral hand motor area; that is, the power (or equivalently, the variance) of the band-passed EEG signals is lower on the contralateral side, and consequently relatively higher on the ipsilateral side. Therefore, the features used in the classification of

left- versus right-hand movement intention are composed of the EEG variances (powers) at the electrodes.

Following this technique, we used only EEG signals to predict whether each repetition of the task belongs to the class $F_L > F_R$ or $F_R > F_L$. For each participant, we used leave-one-out cross-validation (LOOCV) as an initial test of classifier validity, forming a training set on all but one task repetition, testing on the remaining repetition, and repeating the process so that all task repetitions are held out. The CSP technique uses EEG signals from the training repetitions, and determines spatial filters [we used two spatial filters per class as in prior work (Blankertz et al. 2008)] such that the filtered EEG signals from the two classes are optimally distinguishable based on EEG variance. Then, the class of the held out test repetition, whose EEG signals are projected with the above filters, is predicted from EEG data only using an LDA classifier function that outputs a numerical value associated with either one of the classes. Spatial patterns from each class can be visualized on the scalp and represent a measure of brain activation during repetitions of the task belonging to each class.

Overview of CSP and LDA

EEG data from a single task repetition are encoded in a $C \times T$ matrix $X = [x(t),\ x(t+1),\ \dots, x(t+T-1)]$ by concatenating $C \times 1$ vectors $x(t)$ which are the multi-channel EEG data at a specific time point t, T is the total number of time points in one repetition, and C is the number of EEG channels. The CSP algorithm is performed on $C \times n_1 T$ matrix S_1 and $C \times n_2 T$ matrix S_2 formed by concatenating all n_1 training examples of the $F_L > F_R$ class, and all n_2 training examples of the $F_R > F_L$ class, respectively. Matrices S_1 and S_2 are used in the CSP algorithm to determine a single matrix W (whose columns are spatial filters) such that $W^T S_1$ and $W^T S_2$ are uncorrelated across channels, which leads to easier distinguishing of the two classes. W is arranged such that the columns are ordered according to eigenvalue; filters on the left end of W correspond to those most important for predicting the $F_L > F_R$ class, and filters on the right end of W correspond to those most important for predicting the $F_R > F_L$ class. $W^T S_1$ and $W^T S_2$ are then used to calculate linear weights β_j and bias β_0 of the LDA classifier using Fisher's Linear Discriminant Analysis (Hastie et al. 2005).

A test sample X from a repetition not used in training can then be classified using LDA:

$$f = \sum_{j=1}^{J} \beta_j \log \left(w_j^T X X^T w_j \right) + \beta_0,$$

where w_j are the filters determined earlier with CSP, and J is the total number of filters used.

We follow common practice of feature extraction in EEG classification studies and extract the two most important spatial filters from either end of the W matrix (a total of four) (Blankertz et al. 2008) to be used in the projection of signals in X; therefore, in our case $J = 4$.

In contrast to prior studies that use EEG to construct brain–machine interfaces (BMI) and assess single-subject performance by quantifying classification accuracy, we wanted simply to ensure that there was a statistically significant relationship (across multiple participants) between the EEG-based classifier output and the force-based class for the repetition, regardless of classification accuracy. We, therefore, used a linear mixed-effects (LME) model to quantify the association between force-based repetition class and EEG-based classifier output. The LME model of the EEG-based classifier output (y) contained a fixed-effects term for force-based repetition class (x_i, $i = 1$ for $F_L > F_R$ and 2 for $F_R > F_L$), as well as for participant j a random intercept (u_{0j}) and random slope (u_{1j}) to capture participant-specific dependencies:

$$y_j = \beta_0 + \beta_1 x_{ij} + u_{0j} + u_{1j} x_{ij} + \epsilon_{ij}$$

We examined the p value for the fixed-effect of force-based repetition class on EEG-based classifier output, and considered $p < 0.05$ as evidence for a statistically significant relationship between cortical activity and goal-equivalent variation in finger forces. In addition to the LME model, we implemented a receiver operating characteristic (ROC) analysis of test data to assess the performance of the classifiers at various threshold settings. For each participant, we created an ROC curve using all leave-one-out classifier outputs for that participant, and estimated the area under the curve (AUC) as a measure of classifier performance. We then used all participants' classifier outputs to plot the overall ROC curve and obtain an estimate of the overall AUC.
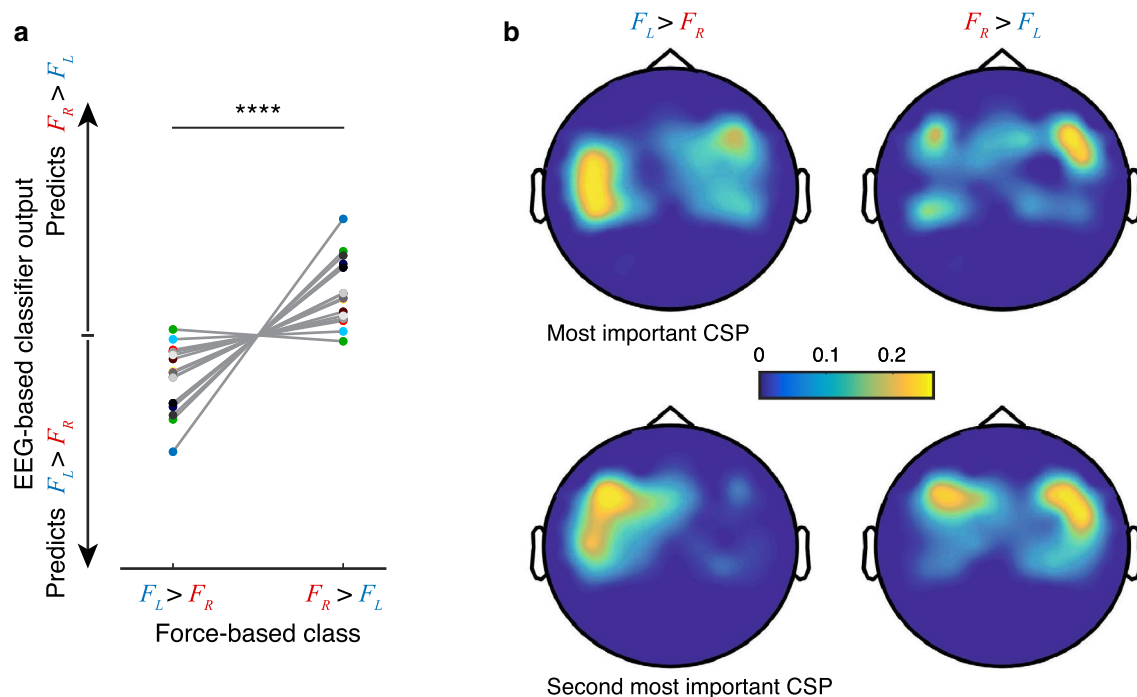
Results

We found that all 18 participants achieved the task with a significantly higher variance of repeated forces along the goal-equivalent direction than the non-goal-equivalent direction. In Fig. 2a, we show the 95% covariance ellipses of all 18 participants, along with the goal-equivalent line. Some participants have more elongated ellipses than others, but the relative variance along the goal-equivalent direction is always greater than in the orthogonal direction, as illustrated in Fig. 2b. The ratios of goal-equivalent variance to the sum of both non-goal-equivalent and goal-equivalent variances in all participants for the chosen force level of 6 N were significantly greater than 0.5 ($p < 0.0001$).

Our LME model indicated that force-based repetition class had a significant effect on EEG-based classifier output
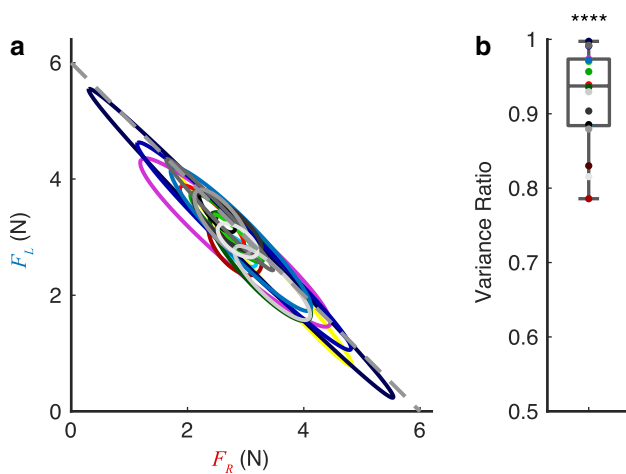
Fig. 2 Covariance ellipses and force variance ratio of 18 participants. **a** 95% covariance ellipses of all participants. The covariance ellipse of each participant was constructed using the average *left* and *right* forces from all repetitions of the task (see Fig. 1c). The overlapped ellipses show that all participants maintained a relatively higher variation in the goal-equivalent direction than in the non-goal-equivalent direction; **b** *boxplot* of the ratio of goal-equivalent force variance to the sum of goal-equivalent and non-goal-equivalent variance. The ratio was significantly greater than 0.5 ($p < 0.0001$, ****)

($p < 0.0001$). Figure 3a illustrates the EEG-based classifier output of each participant averaged across repetitions from each class, compared with actual force-based classes. The *x*-axis represents the label of force-based classes, while the *y*-axis is the LDA classifier output f, a linear combination of the natural log of channel variances of spatially filtered EEG data. The EEG-based classifier was trained to produce lower values for training repetitions for which $F_L > F_R$ compared to training repetitions for which $F_R > F_L$. Our results showed that test repetitions for which $F_L > F_R$ were consistently associated with lower EEG-based classifier output than for $F_R > F_L$. For each participant, a positive slope from $F_L > F_R$ to $F_R > F_L$ indicates a successful prediction of the two classes.

The ROC analysis indicated an overall AUC of 0.72 across all participants. Figure 4 shows the individual ROC curves of cross-validated test data for each participant (individual AUC values reported in Table 1), as well as an overall ROC curve using all classifier outputs from all participants. The classifier output from each leave-one-out cross-validation run of each participant was first normalized using means and standard deviations of training data


Fig. 3 EEG-based prediction of force output and averaged common spatial patterns (CSP). **a** EEG-predicted classes versus force-based classes of all 18 participants. The *x*-axis represents the class labels based on the true force data, while the *y*-axis is the classifier output, which is a linear combination of the natural log of EEG channel variances using LDA weights. For each participant, the classifier outputs of repetitions from each class ($F_L > F_R$ and $F_R > F_L$) were averaged and joined by a line. Most participants show a clear distinction between the two classes as indicated by a positive slope of the line. Linear mixed-effect modeling demonstrated a significant effect of force-based repetition class on EEG-based classifier output ($p < 0.0001$, ****); **b** the most important (*top row*) and second most important (*bottom row*) common spatial patterns (CSP) used for the EEG-based classification of repetitions where $F_L > F_R$ (*left*) and repetitions where $F_R > F_L$ (*right*), averaged across 18 participants. Enhanced EEG amplitudes are seen in the *left-hand* motor area when F_L is greater (*top left*). Similarly, EEG amplitudes are higher in the *right-hand* motor area when F_R is greater
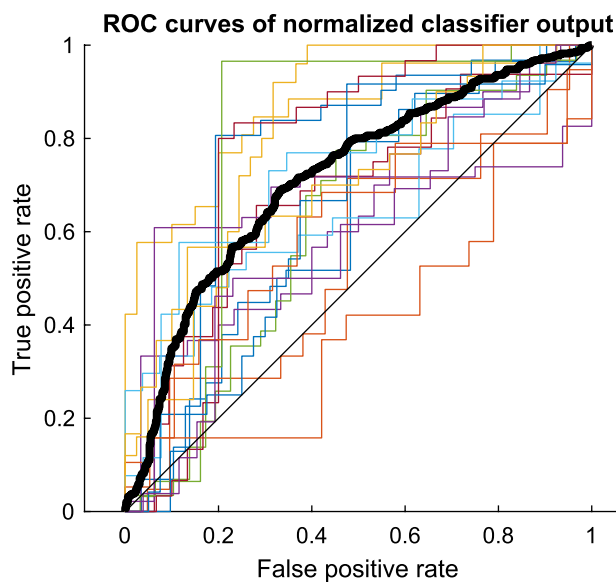
Fig. 4 Individual ROC curves of all participants and overall ROC curve across all participants. The *colored lines* represent each individual participant's ROC curve derived from the normalized outputs of all leave-one-out cross-validated classifiers. The *bold black curve* is the overall ROC across all participants, and is determined using all participants' normalized classifier outputs. The area under the curve (AUC) of the overall ROC curve is 0.72. (Color figure online)

Table 1 AUC values and number of repetitions in each class for each participant

Participant	AUC	Number of repetitions in each class: $F_L > F_R / F_R > F_L$
1	0.6278	29/29
2	0.5374	21/21
3	0.8519	33/33
4	0.6367	30/30
5	0.6181	31/31
6	0.6475	27/27
7	0.6748	32/32
8	0.7586	31/31
9	0.4100	19/19
10	0.8117	33/33
11	0.6576	31/31
12	0.7931	29/29
13	0.7234	26/26
14	0.7622	30/30
15	0.6469	32/32
16	0.5956	19/19
17	0.7211	30/30
18	0.5843	26/26

classifications; to ensure classifier outputs were directly comparable across leave-one-out classifiers and across participants. In a subsequent sensitivity analysis, we removed repetitions that belonged to only half of the middle third portion of the covariance ellipse in Fig. 1c, and obtained an overall AUC of 0.68, slightly lower than our reported value for the current analysis.

To visualize patterns of brain activations during each class of repetitions we mapped average spatial patterns, CSPs, from each class onto the 27 electrode locations on the scalp (Fig. 3b). The top and bottom rows represent the most important and second most important patterns associated with the most important and second most important spatial filters, respectively, that were used to predict EEG-based classes. Left and right columns represent the patterns for the two classes, $F_L > F_R$ and $F_R > F_L$, respectively. The CSP patterns illustrate the amount of EEG variance at each electrode, which played an important role in the discrimination between classes. Both the most important and second most important patterns displayed laterality on the sensorimotor areas, i.e., a relatively higher EEG variance on the left hemisphere during repetitions belonging to class $F_L > F_R$, and vice versa.

Discussion

We observed a goal-equivalent variability in individual forces during repetitions of the finger force task in all of our participants. This result is consistent with previous studies with similar multi-finger tasks (Latash et al. 1998, 2001): when two or more fingers of a hand applied forces that matched to the sum of forces of all employed fingers, a variability in individual forces is seen over repetitions while keeping the sum of forces constant. Other types of movement repetitions, e.g., a sit-to-stand task (Scholz and Schöner 1999) or walk to run transitions (Seay et al. 2006), have also been associated with goal-equivalent variability such as at the level of joint configurations. We additionally found that pre-movement EEG signals could make significant predictions of goal-equivalent force variation. We observed spatially distinct cortical patterns associated with the goal-equivalent variability: a relatively higher EEG variance was localized on the left when higher left finger force was applied, and vice versa. We conclude that goal-equivalent variability is not entirely generated by subcortical circuitry, and that the cortex may be involved in coordinating muscle activity in a goal-equivalent way.

While our study is the first to examine the predictive power of cortical signals associated with automatic variations in goal-equivalent motor output in a bimanual task, our results are consistent with previous work predicting hand choice during voluntary unimanual tasks. The

lateralization in brain activity that we determined to be predictive of goal-equivalent motor output variation is consistent with previous studies of EEG-based prediction of unilateral hand movement intention (Müller-Gerking et al. 1999; Ramoser et al. 2000). These studies found that during the imagination and preparation of left-hand movements, CSP patterns indicate a high EEG variance localized on the left-hand motor area, with low variance on the right (Müller-Gerking et al. 1999; Pfurtscheller et al. 1997; Ramoser et al. 2000). This pattern switches to a higher variance on the right-hand motor area during repetitions involving the right hand. The ipsilateral concentration of EEG variance is interpreted as arising from event-related desynchronization of EEG signals (i.e., decrease in amplitude) on the contralateral sensorimotor area, often accompanied by event-related synchronization on the ipsilateral side (Pfurtscheller and Aranibar 1979; Pfurtscheller and Neuper 1997; Pfurtscheller et al. 1997). Our CSP patterns during the bilateral finger task also reveal a relatively higher EEG variance on the left hemisphere when relatively higher left force than right was applied, and higher variance on the right when relatively higher right force than left was applied. We interpret this finding as evidence that task repetitions with relatively higher left finger force were associated with more activity in right motor cortex, and task repetitions with relatively higher right finger force were associated with more activity in left motor cortex.

Previous research has revealed brain-level circuitry that could plausibly implement goal-equivalent variation in motor output as either feedforward planning or a sensory feedback strategy. A purely feedforward planning strategy for goal-equivalent motor output variation for this task would suggest that nonlinear dynamics in intracortical circuits during task preparation may converge on different solutions to the task before movement onset (Churchland et al. 2006). Variation in motor output generated during feedforward planning may arise from fundamental fluctuations in neural firing rate at the level of the brain that then propagate through networks, as has been observed for cerebellar neurons (Joshua and Lisberger 2014; Medina and Lisberger 2007), visual neurons (Softky and Koch 1993; Stein et al. 2005), and motor neurons (Churchland et al. 2006). Alternatively, goal-equivalent motor output variation could be generated by cortical circuits that are integrating sensory feedback about downstream factors, such as muscle fatigue (Kouzaki and Shinohara 2006) or tissue discomfort (Singh et al. 2010), and adjusting motor output to trade-off among muscles to minimize the effects of these factors. Future studies can begin to disambiguate these alternatives by manipulating muscle fatigue or skin nociception (e.g., exerting finger force on a rough surface), and determining if these manipulations affect cortical signals associated with predicting goal-equivalent variation.

Previous research has also revealed that spinal-level circuitry could plausibly generate goal-equivalent variability, and our study does not necessarily reject the possibility that in addition to cortical signals, some of the variability may be encoded by the spinal circuitry. Spinal reflex circuits are unlikely to generate coordinated activity during bimanual goal-equivalent tasks where one hand applies higher force and the other applies lower force (Mutha and Sainburg 2009). However, this type of opposing bilateral coupling is present in central pattern generators (CPG) encoded at a spinal level (Grillner and Wallen 1985). Therefore, goal-equivalent variation could plausibly be generated entirely at the spinal level by the timing of a constant descending command serving to bias CPG-like oscillatory circuitry into a right-dominant or left-dominant stable state. It is also possible that cortical and subcortical-level processes both contribute to goal-equivalent variation. For example, while pre-movement EEG signals predicted which hand applied relatively higher force than the other, the origin of the actual amount of variability within a class was not addressed in this study. While cortical signals may decide on which hand applies relatively higher force, the variability within a class could also be produced at a subcortical level. Additionally, while we excluded force data where the two forces were almost equal for the purpose of the classification technique, the small variations in the middle portion of the ellipse in Fig. 2c are still important variations, and may possibly be generated by other cortical and/or spinal level contributions. A limitation of our current approach is that we do not quantify cortical and subcortical contributions to goal-equivalent variability relative to each other.

Pre-movement EEG was successful in classifying goal-equivalent variability using alpha- and beta-band modulations over the sensorimotor area, but our study is limited in that other frequency modulations of EEG signals, as well as other cortical and subcortical regions may additionally contain important predictors of goal-equivalent variability. Pre-movement alpha- and beta-band desynchronizations of EEG have been very useful in predicting left/right-hand movement intention and type of intended action (Heinrichs-Graham and Wilson 2016; Pfurtscheller and Aranibar 1979; Turella et al. 2016), as well as distinguishing between hand and foot movement intention (Müller-Gerking et al. 1999). Lower frequency modulations of pre-movement EEG, such as the Bereitschaftspotential or readiness potential—a slow negative shift in the DC potential on the contralateral M1—may also be used in predicting laterality in self-paced movement intentions (Blankertz et al. 2006; Shibasaki and Hallett 2006). In addition to sensorimotor modulations of the EEG signal, other cortical and subcortical brain areas could additionally reveal interesting features associated with variability. Future studies can address these

limitations by analyzing other frequency modulations in EEG, and using fMRI to assess whole-brain predictors of goal-equivalent variability.

Many studies suggest that goal-equivalent variability is important for human health and motor performance. Goal-equivalent variability has been shown to be beneficial in avoiding overuse injuries (Hamill et al. 2005; Lipsitz 2002) and minimizing fatigue (Singh et al. 2010). A decrease in this variability leads to decreased functional ability and overuse injuries (Hamill et al. 2005; Lipsitz 2002). Low goal-equivalent variability has been found in patients with knee pain (Hamill et al. 2005), runners with low back pain (Seay et al. 2011) and lower extremity injuries (Hamill et al. 1999), and elderly individuals vulnerable to falls (Lipsitz 2002). Varying motor output in the goal-equivalent space may also be an important component of exploration during motor learning (Deeny et al. 2009; Latash and Anson 2006; Shim et al. 2005; Todorov and Jordan 2002; Yang and Scholz 2005) and adapting to changes in task demand (de Freitas and Scholz 2010). While our study used a single target force level to study goal-equivalent variability, future studies can explore learning and difficulty of task by mapping out cortical contributions to goal-equivalent variation as a function of multiple levels of target force.

Goal-equivalent variability requires coordinated activity among a set of muscles. We have recently shown that automatic coordination of muscles, even across multiple body segments, likely involves activation and functional connectivity of specific motor cortical regions (Asavasopon et al. 2014; Rana et al. 2015). We have also shown that the motor cortical regions that may coordinate this muscle activity become dysfunctional in chronic pain (Kilpatrick et al. 2014; Kutch et al. 2015; Woodworth et al. 2015). Given that chronic pain and fatigue are common comorbidities (Clauw and Chrousos 1998), and goal-equivalent motor variation could act as a fatigue mitigation strategy, our current results suggest future research on the link between motor cortical dysfunction and the fatigue associated with chronic pain.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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