Cross-validated models of the relationships between neck muscle electromyography and three-dimensional head kinematics during gaze behavior

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Cross-validated models of the relationships between neck muscle electromyography and three-dimensional head kinematics during gaze behavior. J Neurophysiol 107: 573–590, 2012. First published October 12, 2011; doi:10.1152/jn.00315.2011.—The object of this study was to model the relationship between neck electromyography (EMG) and three-dimensional (3-D) head kinematics during gaze behavior. In two monkeys, we recorded 3-D gaze, head orientation, and bilateral EMG activity in the sternocleidomastoid, splenius capitis, complexus, biventer cervicis, rectus capitis posterior major, and occipitalis capitis inferior muscles. Head-unrestrained animals fixated and made gaze saccades between targets within a 60° × 60° grid. We performed a stepwise regression in which polynomial model terms were retained/rejected based on their tendency to increase/decrease a cross-validation-based measure of model generalizability. This revealed several results that could not have been predicted from knowledge of musculoskeletal anatomy. During head holding, EMG activity in most muscles was related to horizontal head orientation, whereas fewer muscles correlated to vertical head orientation and none to small random variations in head torsion. A fourth-order polynomial model, with horizontal head orientation as the only independent variable, generalized nearly as well as higher order models. For head movements, we added time-varying linear and nonlinear perturbations in velocity and acceleration to the previously derived static (head holding) models. The static models still explained most of the EMG variance, but the additional motion terms, which included horizontal, vertical, and torsional contributions, significantly improved the results. Several coordinate systems were used for both static and dynamic analyses, with Fick coordinates showing a marginal (nonsignificant) advantage. Thus, during gaze fixations, recruitment within the neck muscles from which we recorded contributed primarily to position-dependent horizontal orientation terms in our data set, with more complex multidimensional contributions emerging during the head movements that accompany gaze shifts. These are crucial components of the late neuromuscular transformations in a complete model of 3-D head-neck system and should help constrain the study of premotor signals for head control during gaze behaviors.

Gaze orientation is determined by both eye-in-head and head-on-body orientation. Head rotation contributes maximally to very large gaze shifts, but in some behaviors it also contributes to even the smallest gaze shifts (Crawford and Guittion 1997; Oomen and Stahl 2005). Given that many of our exteroceptors are mounted in the head, achieving a deeper understanding of the neurobiology underlying head movements is clearly an important goal. Neck muscles intermittently control head movements and stabilize the head’s orientation (Peterson and Richmond 1988). It has been shown that neck muscle activity correlates with head kinematics (orientation, velocity, and acceleration) in monkeys (Bizzi et al. 1971; Corneil et al. 2001) and humans (Buchthal 1954; Zangemeister et al. 1982). However, neuromuscular control of three-dimensional (3-D) measurements of primate head orientation and the formal mathematical relationships have not been determined. The purpose of this study was to determine how well and what head rotational kinematics can be predicted from neck electromyography (EMG) during 3-D head movement and stabilization using a cross-validation-based stepwise regression procedure. A secondary goal was to infer what neural signals are needed to drive the neck muscles examined for this behavior.

The musculoskeletal architecture of the head-neck system is extremely complex. More than 20 pairs of multilayered neck muscles contribute to head movements and maintaining head posture in a complex multiarticular and seemingly redundant configuration (Peterson and Richmond 1988; Richmond et al. 2001; Richmond and Vidal 1998). Despite synergistic activation of some neck muscles under isometric conditions (Gabriel et al. 2004; Keshner et al. 1989; Vasavada et al. 2002), the redundancy of the neck muscle structure poses a huge problem in inferring the physiological contribution of each muscle from its anatomical configuration: an infinite combination of muscle activations could produce the same head orientation and rotation.

Most comprehensive studies of neck EMG have been performed in cats (Keshner et al. 1992; Richmond et al. 1992; Roucoux et al. 1989; Thomson et al. 1994). Because of the differences between feline and nonhuman primate neck musculature, the generalizability of results between these species is difficult (Richmond et al. 1999, 2001). Unfortunately, many previous neck EMG studies in primates either 1) studied only a limited number of neck muscles (relative to the six pairs examined in the present study) (e.g., Bizzi et al. 1972; Zangemeister et al. 1982) or 2) used surface EMG electrodes that, due to the inherent cross talk from nearby muscles, are only...
able to reliably capture muscle activation in superficial neck muscles (Mayoux-Benhamou et al. 1995). Moreover, most previous neck EMG studies [e.g., Farshadmanesh et al. (2008) and Lestienne et al. (2000) in nonhuman primates and Zange-meister et al. (1982) in humans] often analyzed neck EMG-head kinematics relationships within a limited range of head orientations. For example, in our previous study we attempted to isolate neck EMG at an approximately straight ahead orientation to examine neck EMG-head posture relationships during stimulation and inactivation of the interstitial nucleus of Cajal (INC) (Farshadmanesh et al. 2008). These are not critiques of those previous studies (which had different aims), but rather limitations that we sought to avoid for our aims.

In this study, we confined our measurements to head rotation, as opposed to translation, which contributes little to gaze at the target distance tested presently (Crané and Demer 1997). Even so, the 3-D head kinematics of head rotation are also complex. In addition to horizontal and vertical components, one also must account for torsional (roll) motion about the naso-occipital axis. Behavioral findings in humans (Glenn and Vilis 1992; Medendorp et al. 1998) and monkeys (Crawford et al. 1999) have shown that during gaze and head stabilization, the head obeys a special form of Donders’ law (Helmholtz and Southall 1924; Medendorp et al. 1999), known as the Fick strategy. This states that if orientation is defined in Fick coordinates (a set of axes nested in the following order: vertical, horizontal, and torsional), then torsion is held near zero (Crawford et al. 2003; Glenn and Vilis 1992; Medendorp et al. 1998). However, head torsion is much more variable than eye torsion during natural behavior, even during relatively stable epochs (Crawford et al. 1999; Glenn and Vilis 1992; Straumann et al. 1991). Moreover, during oblique head motion, head orientation transiently departs from the Fick coordinates (Ceylan et al. 2000; Crawford et al. 1999). It is not known if any of these static or dynamic torsional components are coded by specific muscle synergies. Finally, the Fick constraint results in position-dependent tilts in axes of rotation; it is not known if these are implemented mechanically like the analogous axis tilts in the eye (Demer et al. 1995; Klier et al. 2006; Meng et al. 2005).

The main problem in identifying the relationship between 3-D head kinematics and neck EMG is that standard parametric statistical models (e.g., linear regression) rest on assumptions that likely do not hold here. For example, it is typically assumed that all important sources of variation, excluding purely Gaussian noise, have been identified and accounted for. Unfortunately, the relationship between head kinematics and EMG is highly nonlinear, and the EMG signal itself is only one of a number of variables determining muscle force (Loeb and Gans 1986; Zajac and Gordon 1989). Other variables include muscle length, muscle velocity, morphometry, histochemistry, muscle potentiation, fiber types, fatigue, and elastic/viscous recoil of the head plant, many of which are impossible to measure in a behaving animal.

We therefore required an analytic tool that 1) does not rely on unverifiable parametric assumptions and 2) does not require the measurement of additional physiological parameters. This led us to develop a stepwise regression procedure to relate 3-D head kinematics and neck EMG through cross-validation. Cross-validation is a statistical technique with few underlying assumptions that provides a direct measure of model generalizability (Kohavi 1995). This measure, which is obtained by fitting and testing a model on separate data sets (see METHODS for details), is indicative of how well a model will describe novel data. Results obtained from our technique should both complement and be more reliable than those obtained from other, more assumption-based, parametric models. This technique should identify the EMG-kinematics relationships essential for the final stages of a complete physiological model and also may help to identify the nature of neural control signals that arise from higher levels in the system.

To our knowledge, this is the first study to employ a cross-validation-based approach to examine the relationship between neck EMG and 3-D head kinematics. The data set used for this analysis was derived from two head-unrestrained alert monkeys performing voluntary gaze shifts and fixations. After determining the relationships described above in several possible coordinate systems, we picked the coordinates that provided the best overall fit and then 1) compared our cross-validated results with known functional anatomy of examined neck muscles and 2) examined the different control strategies used during static and dynamic head intervals. Regardless of whether one is looking at neck muscle recruitment (which is effectively a sample of neck motoneurons) or the recruitment of head premotor neurons (which must be related somehow to neck muscle recruitment), our findings reveal the complex ways in which head kinematics variables are reflected in muscle recruitment and perhaps in signals at the premotor level.

METHODS

Surgical Procedures

Eye and head search coils. Two female Macaca mulatta monkeys (M1 and M2) each underwent two surgeries before data collection. During the first surgery, we implanted two search coils in one eye of each animal together with an acrylic skull cap. Gaze orientation recordings were used primarily for training and reward delivery purposes. Before each experiment session, a plastic platform containing two additional search coils was attached to the skull cap to record instantaneous head orientation. All protocols were in accordance with the Canadian Council on Animal Care guidelines on the use of laboratory animals and were preapproved by the York University Animal Care Committee.

EMG electrodes. Two weeks after the first surgery, we implanted chronically indwelling bipolar hook electrodes in the following neck muscles of each animal (6 bilateral pairs, 12 muscles in total; see Fig. 1A): sternocleidomastoid (SCM), splenius capitis (SP), rectus capitis posterior major (RCPmaj), capitulocapitis inferior (OCI), biventer cervicis (BC), and complexus (COM). The electrodes were constructed using Teflon-coated stainless steel wire (AS631; Cooner Wire). They consisted of recording contacts (3 mm long) staggered by 3 mm and were curved obliquely through the muscle perpendicular to the long axis of the muscle fiber fascicles (Loeb and Gans 1986). The wires of the EMG electrodes were attached to a connector embedded within the acrylic skull cap. Surgical details have been published elsewhere (Elsey et al. 2007). The muscles mentioned above, which primarily span the upper cervical vertebrae, were selected because they are accessible and contribute to a wide range of head movements. Among them, RCPmaj, OCI, and SP function as agonists for ipsilateral head rotations and potentially upward head pitches, whereas BC and COM function for upward head pitches and potentially ipsilateral head rotations. SCM generally functions as an agonist for contralateral head turns and downward head pitches, and as a possible antagonist during...
ipsilateral head turns and upward head pitches (Corneil et al. 2001; Richmond et al. 2001).

Experimental Task

At the beginning of each experimental session, the animal was placed in a dark room and was required to fixate a white cross, which was back-projected at the center of a black screen in front of the animal. To encourage the animals to make eye and head movements similar to their natural gaze behavior, and to obtain a wide range of head orientations, we trained the animals to fixate one of nine peripheral targets that appeared as white dots in a random order within a 60° × 60° grid on a black screen (1 center; 4 up, down, left, and right, each 30° from center; and 4 in between, each 42° from center; see Fig. 1B). When 1) the animal fixated a target for a minimum of 500 ms, 2) the animal’s gaze and head orientations were within computer-controlled visual fixation windows (around every target; gaze, 10° diameter; head, 20° diameter), and 3) the head speed was ≤10°/s, a juice reward was delivered. Each target remained visible for 6–10 s and then extinguished, and a new target was presented on the screen. The animals were allowed to make voluntary head movements during intertrial intervals and beyond the required range. These data were also included in the analysis of both static and dynamic intervals (see below).

Data Collection

Eye and head coil signals were digitized at 10-kHz sampling rate and then downsampled offline by a factor of 10 to 1 kHz. Eye and head quaternions, which represent the orientations of the eye and head relative to the stationary laboratory frame, were calculated from the coil signals (Crawford et al. 1999; Farshadmanesh et al. 2007; Tweed et al. 1990). Recorded EMG signals were first differentially amplified at a head stage that was plugged directly into the EMG connector (20× gain) and then bandpass filtered (20 Hz–17 kHz). Finally, the processed EMG signals were fed into a signal processing unit (Plexon; 50× gain; bandwidth, 100 Hz–4 kHz) and were digitized at 10 kHz for later offline analysis.
Data Selection

Recorded EMG signals were first rectified and integrated into 1-ms time bins with the use of a previously described method (Bak and Loeb 1979; Corneil et al. 2001). Since during normal gaze behavior, head orientation usually changes at a slower rate relative to the eye orientation, we further integrated our head orientation data into 10-ms time bins. To exclude task-irrelevant head movements (e.g., head movements due to drinking the juice reward), all the data 500 ms before and 1,000 ms after the juice reward was delivered were removed before the analysis. In the remaining data set, we defined static and dynamic intervals as follows. Note that even during static intervals, the head was not completely still, as in natural gaze behavior. Therefore, in the current study we compared “relatively stationary” vs. “clearly moving” head intervals.

Static intervals. To determine intervals where head orientation was stable following the completion of a previous head movement, we used a criterion of head speed \( \leq 10^\circ/\text{s} \) (see Fig. 1, B–E, for an illustration). We henceforth call these “static intervals.” In addition, a minimum length of 300 ms for each static interval was added to the data selection criteria to ensure that a stable posture was obtained. Only the first 200 ms of data from each interval were used to avoid contractions that might result from subjects preparing for a subsequent movement. With the use of these criteria, data selection for each animal was performed using a custom-built algorithm developed for MATLAB (The MathWorks). In total, 1,505 and 2,033 nonoverlapping static intervals were selected in animals M1 and M2, respectively.

Dynamic intervals. Head speed \( > 10^\circ/\text{s} \) was the main criterion to consider it as moving. We henceforth call these “dynamic intervals.” From each movement interval, one 10-ms bin was chosen randomly to obtain values for 3-D head orientation, head velocity, and head acceleration. Our logic in taking a single time point from each movement interval was that 3-D head kinematics values obtained in this manner from one movement interval would be independent from those selected from any other interval. In contrast, multiple points within one interval could not be assumed to be independent and might not provide additional information in the model fitting procedures. To determine the neuromuscular lag between EMG signal and subsequent head movement and find the point (prior to the randomly selected point within each movement) at which EMG is best correlated with subsequent head movement, we further integrated our head orientation data into 10-ms time bins. To exclude task-irrelevant head movements (e.g., head movements due to drinking the juice reward), all the data 500 ms before and 1,000 ms after the juice reward was delivered were removed before the analysis. In the remaining data set, we defined static and dynamic intervals as follows. Note that even during static intervals, the head was not completely still, as in natural gaze behavior. Therefore, in the current study we compared “relatively stationary” vs. “clearly moving” head intervals.

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Stepwise Regression Procedure

When the relationship between variables is complex and no a priori model exists, regression analysis can be used in a stepwise fashion for model determination. Adding model terms will always increase the variance explained by a model (i.e., will increase \( R^2 \)), but the resulting model will be more complex and may not generalize as well. Thus a selection criterion is required to determine when the increase in \( R^2 \) is actually “worth” the added model complexity. Cross-validation provides a direct estimate, which we refer to as \( R^2_{cv} \), of how accurately a predictive model will perform with novel data (i.e., generalizability across subjects). This measure is obtained by fitting a model to only a subset of the full data set and calculating \( R^2_{cv} \) in the usual way from the residuals obtained when the model is used to predict the remaining, unfit data. Typically, a data set is broken into \( N \) folds, the model is fit to the data contained in \( N - 1 \) of the folds (training set), and \( R^2_{cv} \) is calculated from the one remaining fold (testing set). By calculating the average value of \( R^2_{cv} \) for all combinations of the \( N \) folds, the final measure of generalizability is obtained. Thus we employ \( R^2_{cv} \) directly as a selection criterion, because its value will actually decrease if unhelpful model terms are added.

Compared with cross-validation, other statistical techniques rely on numerous assumptions about the data. For example, standard stepwise regression uses \( F \) ratios for model term selection, which assumes an unreduced full model contains the actual underlying model as a reduced version (i.e., the actual model is nested within the full model). Alternatively, Akaikes or Bayesian information criteria assume the underlying data distribution is known so that the likelihood function for the parameters/data can be calculated. Cross-validation, however, can be used to find which model can better explain the data even if no version of the full model can account for the data. This is especially useful for a complex and noisy data set such as EMG data, which are unlikely to be fully captured by even a high-order model.

Analysis of static intervals. The general model form employed presently was a simple fourth-order (i.e., the total order of multiplicative terms) polynomial given by

\[
\text{EMG}_{\text{static}}(n) = G(d)\left\{a_0 + a_1 H(n) + a_2 V(n) + a_3 T(n) + a_4 T(n)^2 + a_5 H(n)V(n) + a_6 H(n)T(n) + a_7 V(n)^2 + a_8 V(n)T(n) + a_9 T(n)^2 + \ldots \right\} + B(d)
\]

where \( \text{EMG}_{\text{static}}(n) \) is neck EMG during the \( n \)th static interval and \( H, V, \) and \( T \) are 3-D head orientation components (horizontal, vertical, and torsional, respectively). Thus our model contained terms including all multiplicative combinations of 3-D kinematics variables, but only up to fourth order because of computational constraints. In addition, \( G(d) \) and \( B(d) \) are gain and bias parameters, respectively, that vary from day to day (\( d \)) to account for small fluctuations in EMG electrode characteristics (e.g., electrode impedance). In our data, the variability of these parameters relative to the mean was small across the days that their data were included in the analysis (M1, 5 days; M2, 9 days) for both animals and only accounted for a small amount of variance in the data. To quantify variability in gain and bias, since the measured voltages from different muscles were different, we divided the standard deviation of gain (bias) by the mean of gain (bias). These were first averaged across days for each muscle and then averaged across muscles for each animal. Mean \( \pm \text{SE} \) for these values across muscles were as follows: M1, gain \( (6.30 \pm 0.54\%) \) and bias \( (7.97 \pm 0.27\%) \); and M2, gain \( (6.80 \pm 0.30\%) \) and bias \( (7.63 \pm 0.44\%) \).
Data for each animal were randomly divided into 10 equal size subsets (folds). The folds included the data from all days (i.e., for 1,505 and 2,033 nonoverlapping intervals in animals M1 and M2, each fold consisted of ~150 and ~200 intervals, respectively). This process was similar for dynamic intervals (see below). During our regression procedure (see Fig. 1G), the following two steps were repeated alternately until the best model was determined: 1) addition of a new model term and 2) subtraction of included model terms. During the addition step, we added each of the available terms (terms that had not already been added to the current model) one at a time and determined the one term whose addition resulted in the largest increase in $R^2_r$. That term alone was then selected and added to the current model. If none of the available terms increased $R^2_r$, the regression was terminated and the current model was selected as the final, best model. After addition of every new model term, a subtraction step was performed by removing each of the current model terms one at a time to determine whether such elimination could improve $R^2_r$. The term whose removal increased $R^2_r$ the most was then eliminated from the current model and returned to the pool of available terms. The subtraction step was repeated until the removal of no more terms could improve $R^2_r$. At this point, we returned to the addition step. Addition and subtraction steps were repeated until the best model was determined for each muscle.

Each step in the above-described stepwise regression included calculating the $R^2_r$ for the current model. This was done over the 10 folds, but to further reduce variability in $R^2_r$, we created 10 unique, similarly sized sets of folds (partitionings). Thus each partitioning contained the same data but divided differently. After calculating the $R^2_r$ over the folds within each partition, we determined the final $R^2_r$ by averaging across the partitions. This procedure was repeated for all 12 muscles of each animal separately. Variability in $R^2_r$ across different partitionings of our data into folds would have led to variability in model form across these partitionings, had we produced separate models for each such partitioning. To examine whether these models (i.e., the specific sets of terms) would have varied much relative to the final models that we derived, the entire analysis for all 12 muscles of animal M2 for the static interval data was repeated three times. The model terms obtained for the three rounds were similar for each muscle (see Table 2).

Finally, to simplify the model determined via stepwise regression for each muscle and to determine the model terms that contributed most to the obtained model, we removed step by step the largest possible number of terms that collectively (together) contributed <0.05 to the total $R^2_r$ value of the model. The remaining terms of the simplified models are shown separately for each muscle in Table 1. We chose this cutoff (0.05) because it allowed us to significantly simplify each model without strongly affecting the final $R^2_r$. In general, the remaining terms signify the most important contribution of every muscle to the components of 3-D head kinematics.

### Analysis of dynamic intervals

We first took the simplified “static” model for each muscle (i.e., the orientation term coefficients obtained from the static intervals data) and added motion (3-D head velocity and acceleration) terms to it as described in the following equation:

$$ EMG_{\text{dynamic}}(n) = EMG_{\text{static}}(n) + G(d)\left\{ a_{\hat{H}}\hat{H}(n) + a_{\hat{\dot{H}}}\hat{\dot{H}}(n) + a_{\hat{\ddot{H}}}\hat{\ddot{H}}(n) + a_{\hat{V}}\hat{V}(n) + a_{\hat{\dot{V}}}\hat{\dot{V}}(n) + a_{\hat{\ddot{V}}}\hat{\ddot{V}}(n) \right\} $$

where $EMG_{\text{dynamic}}(n)$ is neck EMG during the nth dynamic interval and single- and double-dotted letters represent head velocity and acceleration, respectively. To avoid complexity in the model, we only tested multiplicative combinations of up to second-order terms. Whereas the orientation terms used for the movement analysis were fixed in each model (i.e., could not be added or subtracted during the fitting procedure), their coefficients could vary to account for any information about head orientation that might be included in dynamic interval data. We used the same stepwise regression procedure to determine which motion terms from Eq. 2 to include in our final models as we did for the static model in Eq. 1 and used the same 0.05 $R^2_r$ criterion to further simplify the derived models (see Table 3). We refer to the model with both orientation terms and motion terms (fit to the dynamic intervals) as the “complete model.”

We believe that for our purposes, this procedure provides a conservative, generalizable, and assumption-free method compared with other potential model fitting approaches. For example, a piecewise linear fit with a muscle recruitment threshold might provide a better fit in some restricted cases, but we opted not to do this for several reasons. First, adding such a threshold would add more assumption to the models, increase their complexity, and make them less generalizable. Second, different thresholds would be required for each dimension of the fit. Even then, there is no guarantee that a given muscle

### Table 1. Retained terms of simplified static models

<table>
<thead>
<tr>
<th>Left Neck Muscles</th>
<th>Right Neck Muscles</th>
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<tbody>
<tr>
<td><strong>Animal M1</strong></td>
<td></td>
</tr>
<tr>
<td>RCPmaj</td>
<td>H (0.39), V (0.16), H² (0.12)</td>
</tr>
<tr>
<td>OCI</td>
<td>H (0.48), H² (0.29)</td>
</tr>
<tr>
<td>COM</td>
<td>H (0.16), V (0.15)</td>
</tr>
<tr>
<td>BC</td>
<td>V (0.20), H² (0.18), H (0.12)</td>
</tr>
<tr>
<td>SP</td>
<td>H (0.24), HV (0.17), H² (0.10)</td>
</tr>
<tr>
<td>SCM</td>
<td>H (0.36), H² (0.12), V (0.10)</td>
</tr>
<tr>
<td></td>
<td>H (0.33), H² (0.21), V² (0.11)</td>
</tr>
<tr>
<td></td>
<td>H (0.44), H² (0.21)</td>
</tr>
<tr>
<td></td>
<td>V (0.19), H (0.15)</td>
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<tr>
<td></td>
<td>H (0.20), V (0.13)</td>
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<tr>
<td></td>
<td>H (0.33), H² (0.29)</td>
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<tr>
<td></td>
<td>V (0.18), H (0.16)</td>
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<tr>
<td><strong>Animal M2</strong></td>
<td></td>
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<tr>
<td>RCPmaj</td>
<td>H (0.51), H² (0.27)</td>
</tr>
<tr>
<td>OCI</td>
<td>H (0.33), H² (0.25)</td>
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<td>BC</td>
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<tr>
<td>SP</td>
<td>H² (0.32), H² (0.17)</td>
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<td>H (0.25)</td>
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<tr>
<td></td>
<td>H (0.21), H² (0.20), H² (0.12), V² (0.05)</td>
</tr>
<tr>
<td></td>
<td>H (0.37), H² (0.25), H² V² (0.10)</td>
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The retained orientation terms of the simplified static models collectively contributed more than 0.05 to the $R^2_r$, the model (see METHODS). The terms were derived from models with up to fourth-order terms. Different head orientation components are shown as H (horizontal) and V (vertical). Terms are shown in the order of their contribution to $R^2_r$. Numbers in brackets beside each term represent the variance accounted for by that term. RCPmaj, rectus capitis posterior major; OCI, occipital capitis inferior; BC, biventer cervicis; COM, complexus; SP, splenius capitis; SCM, sternocleidomastoid.

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RESULTS were exhaustively repeated for all of the above-mentioned references. Analysis of acceleration in space, head, and Fick coordinates. Therefore, this question was approached empirically, by transforming the kinematics data into the most reasonable coordinate system alternatives. Head orientation was originally recorded in a space-fixed coordinate system defined by three mutually orthogonal magnetic fields. The straight ahead, left-right, and up-down directions in the laboratory. Following methods described previously (Tweed et al., 1990), these were used to compute head orientation quaternion vectors relative to a center reference orientation but rescaled so that the components were angles (Fig. 2, A–C). Since the vertical Fick axis for head rotation typically tilts quite far backwards in monkeys (Crawford et al., 1999), we then transformed these data into Listing’s coordinates (Glenn and Vilis, 1992; Radau et al., 1994) such that the vertical and horizontal axes of rotation (at the reference orientation) were aligned with the horizontal-vertical plane (Fig. 2, E–G). Finally, these data were transformed into Fick angles (Fig. 2, I–K). Similarly, we calculated head movement parameters (velocity, acceleration) in every feasible combination of first and second time derivatives vs. angular velocity and acceleration in space, head, and Fick coordinates.

The cross-validated fits described for static and dynamic intervals in the RESULTS were exhaustively repeated for all of the above-described coordinate systems. Overall, we found a marginal superiority for fits that used head orientation and its derivatives in Fick coordinates. However, there was never any significant difference (across the 12 muscles we tested) between these fits and the fits made in other coordinate systems, either for static models that only included orientation terms fit to static data intervals (vs. space coordinates; M1/M2, \( P = 0.20/0.31 \)) or for complete models that also possessed motion terms fit to dynamic data intervals (vs. derivatives in space, \( P = 0.99/0.73 \); vs. angular velocities in space, \( P = 0.25/0.36 \); vs. angular velocities in head coordinates, \( P = 0.25/0.36 \), at least in the range of movements that we obtained (where the coordinate system-related differences were relatively small). This considerable effort was disappointing from the perspective of discriminating intrinsic coordinate systems but reassured us that we were not using the wrong coordinate system in our analysis. Since Fick coordinates usually provided as good or marginally better fits compared with the other alternatives, and since this coordinate frame fits best with the known behavior and physiology of the head control system (Crawford et al., 1999; Klier et al., 2007), we chose this as our default coordinate system, and henceforth we only present our findings for Fick angles.

Reference Frames and Coordinate Systems

Behaviorally, the head is known to follow a Fick-like strategy during static intervals (Crawford et al., 1999). Although premotor signals for head movement are consistent with the use of Fick coordinates (Klier et al., 2007) and resemble the physical structure of the neck vertebrae (Graf et al., 1995b; Vidal et al., 1986), it is not known whether these Fick coordinates persist at the mechanical level in the organization of muscles. Thus we could not assume that any one coordinate frame for head orientations and movements would provide the best fit for our EMG data. Therefore, this question was approached empirically, by transforming the kinematics data into the most reasonable coordinate system alternatives. Head orientation was originally recorded in a space-fixed coordinate system defined by three mutually orthogonal magnetic fields. The straight ahead, left-right, and up-down directions in the laboratory. Following methods described previously (Tweed et al., 1990), these were used to compute head orientation quaternion vectors relative to a center reference orientation but rescaled so that the components were angles (Fig. 2, A–C). Since the vertical Fick axis for head rotation typically tilts quite far backwards in monkeys (Crawford et al., 1999), we then transformed these data into Listing’s coordinates (Glenn and Vilis, 1992; Radau et al., 1994) such that the vertical and horizontal axes of rotation (at the reference orientation) were aligned with the horizontal-vertical plane (Fig. 2, E–G). Finally, these data were transformed into Fick angles (Fig. 2, I–K). Similarly, we calculated head movement parameters (velocity, acceleration) in every feasible combination of first and second time derivatives vs. angular velocity and acceleration in space, head, and Fick coordinates.

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RESULTS

Part I: Static Interval Analysis

We begin with a qualitative overview of the kinematics data used in our static interval analysis, also illustrating the steps involved in obtaining that data. Figure 2 shows vertical vs. horizontal (A, E, and I) and horizontal vs. torsional (B, F, and J) head orientations for the entire static interval data set used for the analysis in animal M2. Figure 2, C, G, and K, shows the 2-D surface fits made to data in B, F, and J using a method described previously (Glenn and Vilis, 1992; Radau et al., 1994; Tweed et al., 1990). Figure 2, D, H, and L, show axes of rotations for the corresponding coordinate system representations (see Fig. 2 legend for details). Data from animal M1 were very similar, and both resembled previously reported findings (Crawford et al., 1999).

Figure 2A shows head orientation in the original space-fixed coordinates. Note that horizontal head orientation range was...
larger [along the x-axis (left-right); 97°–105°] than the vertical range [y-axis (down-up); 28°–49°]. The torsional range [Fig. 2B, along the x-axis (counter clockwise-clockwise, CCW-CW); 37°–45°] was the smallest except for the downward vertical range in both animals. The analogous ranges in animal M1 were horizontal (92°–96°), vertical (30°–73°), and torsional (49°–44°). The surface fit (Fig. 2C) showed a twisted shape consistent with previous reports (Crawford et al. 1999; Glenn and Vilis 1992). Rotating these data into Listing’s coordinates (Fig. 2, E and F; see METHODS) did not alter the overall twisted shape of the 2-D surface fit (Fig. 2G), which still resembled the one in space coordinates (Fig. 2C). After the data were transformed into Fick coordinates (Fig. 2K), however, the twist disappeared, also resulting in a slight overall reduction of torsional thickness (standard deviation of the surface fit): 5.98 in Fig. 2K vs. 6.47 in Fig. 2G. Note again (as described in the METHODS) that only Fick coordinates are used in the data analysis below.

**Neck EMG activity as a function of head orientation.** We have provided examples of “raw” EMG activity selected from the static intervals in animal M2, plotted as a function of each of the three head orientation components, and show why a standard fitting method fails. Figure 3 shows a typical example where EMG activity for bilateral RCPmaj (left and right) of animal M2 are plotted as a function of horizontal (A and B), vertical (C and D), and torsional (E and F) head orientation (Fig. 3, A and B) and plotted the residuals as a functional of torsional head orientation (Fig. 3, G and H). Although some of the noise in the data disappeared, there was still a complex distribution and large variance in the normalized data set.

This simple example illustrates the fundamental problem with drawing conclusions based on simple fits to such data: the EMG data are highly noisy (not because of measurement error, but because EMG is fundamentally noisy) relative to the range of orientations (and below motion) that is observed in the head during natural gaze behavior. As a result, one can place little faith in the terms of a simple fit to such data. Therefore, we used a cross-validation-based approach as a conservative mean to extract the reliable terms of these relationships.

**Selection of static model terms.** We next turn to the cross-validation methodology described in the METHODS. Our first aim was to establish the level of model complexity (order of terms) required to obtain the best fit. Unfortunately, there is no way to know this without trying increasing orders of complexity until no further improvement is observed. (Note that cross-validation imposes a cost for adding more terms that cannot be validated, so these must be real improvements.)

Figure 4 plots $R_{cv}^2$ vs. maximum polynomial order. In most muscles, a model with terms up to second-order improved $R_{cv}^2$ relative to the results from a model with only first-order linear terms [change in $R_{cv}^2$: M1, minimum (0.01), maximum (0.18), mean (0.07); M2, minimum (0.01), maximum (0.28), mean (0.15)]. From second- to third-order models, the increase in $R_{cv}^2$ was smaller than 0.05 in all except left (L)-SP, right (R)-SP, and R-SCM in M2 [M1, minimum (−0.01), maximum (0.06), mean (0.02); M2, minimum (−0.02), maximum (0.18), mean (0.04)]. A fourth-order model provided only a very small increase in $R_{cv}^2$ for some muscles, except in muscles L-BC, L-SCM, and R-OCI in animal M1 and L-SP and R-SP in M2 in which the performance was lower. Thus fourth-order static models provided the highest $R_{cv}^2$ values, meaning that these were the most generalizable models. Therefore, we will henceforth use these fourth-order models to describe EMG-head
orientation relationships, although after model simplification, the model retained a fourth-order term only for L-SP in animal M2 (Tables 1 and 2).

We next describe the actual terms that arose from these fits. The terms of the simplified static models (which only included terms that contributed more than 0.05 to $R_{cv}^2$, see METHODS) are summarized in Table 1. To summarize, 1) horizontal terms were the most consistent, 2) first- and second-order terms dominated in both the horizontal and vertical dimensions in most models, and 3) no torsional terms were retained. These key findings are discussed below. Note that some observed head orientation dependencies [e.g., horizontal component dependency for neck extensors (COM and BC); see Table 1] were different from what would be expected from the anatomy of neck musculoskeletal architecture (see Discussion).

Static model fits and coefficients. Horizontal head orientation. Figure 5 plots the simplified cross-validated models for predicted EMG vs. horizontal head orientation for animal M1 (black traces) and M2 (red traces). For the muscles that also had vertical terms in their simplified model (L-RCPmaj, R-RCPmaj, L-COM, R-COM, L-BC, R-BC, L-SP, L-SCM, and R-SCM in animal M1; L-COM, R-SP, L-SCM, and R-SCM in animal M2; see Vertical head orientation), we did not plot the zero intercept of the model, because this did not necessarily represent the actual data range. Instead, we plotted the predicted EMG value for the average vertical head orientation associated with each horizontal head orientation was used to plot these models (see METHODS). The y-axis in each panel is normalized relative to the $R_{cv}^2$ value of the model for each muscle. More specifically, the overall height of each curve was first scaled to range from 0 to 1 and then multiplied by the $R_{cv}^2$. Thus the height of each curve indicates the performance of the model. Plotted models are second-order except for left SP, right SP, and right SCM in animal M2 in which the models are up to fourth order. Vertical scale bars denote 10 μV.
to fourth-order terms. The y-axis in each panel is scaled relative to the $R_{cv}^2$ value for each muscle.

L-RCPmaj and L-OCI muscles (Fig. 5, A and C, respectively) showed a very similar pattern in both animals. The EMG activity of both muscles increased with more eccentric ipsilateral horizontal head orientations and reached its maximum for the leftmost head orientation. A similar but symmetric model was observed for R-RCPmaj in both animals (Fig. 5, B and D, respectively). Activity of R-RCPmaj in animal M1 also increased similarly to the same muscle in animal M2, but the slope of the model was different. Plots for bilateral COM in animal M1 (Fig. 5, E and F, black traces) were linear (i.e., with only first-order terms), and neck EMG was higher for more eccentric contralateral head orientations. In animal M2, although the models for bilateral COM were second-order, a similar trend was observed.

The models for L-BC and R-BC muscles in animal M1 showed a symmetric shape (Fig. 5, G and H, black traces) with a higher EMG activity for more eccentric ipsilateral head orientations. In animal M2, however, bilateral BC, did not show a clear directional pattern (Fig. 5, G and H, red traces). Note that the $R_{cv}^2$ values for these two muscles in animal M2 were noticeably lower compared with other muscles in both subjects (L-BC, 0.17; R-BC, 0.17). Bilateral SP in both animals (Fig. 5, I and J), similar to horizontal head turners (RCPmaj and OCI), showed a symmetric pattern that was overall comparable between the two animals. Bilateral SCM (Fig. 5, K and L) in both animals, however, showed a directional pattern similar to that of COM muscles. Overall, during static intervals, most neck muscles showed a clear directional activation for horizontal head orientation. The activity was higher for ipsilateral head orientations in RCPmaj, OCI, BC, and SP muscles, whereas it was higher for contralateral orientations in COM and SCM muscles.

**Vertical head orientation.** Vertical terms were only retained in the simplified models of a few muscles (see Table 1) and never made the highest contribution to $R_{cv}^2$ except for muscles (with the associated terms in parentheses) L-BC (V), R-COM (V), and R-SCM (V) in animal M1. In animal M2, fewer muscles had a vertical term in their model including L-COM (V), R-SP (V²), L-SCM (V), and R-SCM (H²V, H²V²), but in none did the vertical terms make the highest contribution to $R_{cv}^2$. Figure 6 shows the model fits for the only bilateral muscle pair (L-SCM and R-SCM) that retained at least one vertical term in both animals. Figure 6 plots predicted EMG activity on the z-axis (height) as a function of horizontal and vertical head orientation (base). The z-axis in each panel is scaled relative to the $R_{cv}^2$ value of the model for each muscle. Predicted EMG activity increased with upward head orientation for both L-SCM and R-SCM (Fig. 6, A and B, respectively) in animal M1. Although the SCM contributes dynamically to downward head movements, during upward head tilts, the center of mass of the head translates to behind the spinal column, and therefore SCM (and potentially other neck flexors) could contribute to counteracting the gravitational pull of the head. Animal M2 showed a similar directional selectivity for L-SCM (Fig. 6C), but its R-SCM (Fig. 6D) showed a more complex pattern with predicted EMG peaking at an intermediate vertical orientation (50° down to 30° down) and dropping off in both directions (80° down to 40° down; 40° down to 10° up). For L-SCM in both animals (Fig. 6, A and C) and R-SCM in animal M1 (Fig. 6B), first-order vertical terms (V) were retained, whereas for R-SCM in animal M2 (Fig. 6D), higher order orientation interaction terms ($H^2V, H^2V^2$) were retained.

Figure 7 similarly illustrates the model prediction for L-COM, a muscle that showed consistent vertical terms in both animals (but only on the left side). For L-COM in both animals, only first-order vertical terms (V) were retained, and similar to L-SCM, the EMG activity was higher for more upward compared with downward head orientations in both animals. The overall shape of the model planes for both animals were similar to the ones for L-SCM of the same animal. Overall, in most muscles we tested, the relationship between EMG and vertical component was small and inconsistent among most muscles.

**Torsional head orientation.** In our static interval data set (where the only torsional orientation components were random variations about the average 2-D Fick range), the relationship...
between neck EMG and torsional head orientation was negligible or nonexistent.

**Part II: Dynamic Interval Analysis and Motion Terms**

Figure 8 illustrates the type and range of motion data of our dynamic intervals. Figure 8A shows horizontal vs. vertical components, and Fig. 8B shows horizontal vs. torsional components, of first time derivatives of head orientation in Fick coordinates for head movements recorded over a 100-s interval in animal M2. Note the small empty area around center head orientation in Fig. 8A that indicates our criterion for selecting head movement intervals (i.e., head speed >10°/s).

The probability distribution of first (Fig. 8C) and second (Fig. 8D) time derivatives of 3-D head orientation components are shown for the entire dynamic interval data set for animals M1 (solid) and M2 (shaded). The effect of our data selection criterion can again be seen as the empty bins in the center of histograms of first time-derivative panels (Fig. 8C). Overall, despite minor differences, the distribution patterns of both time derivatives were similar between the corresponding components of the two animals. As noted in METHODS, a comparison of fits between different coordinate representations failed to reveal significant differences, so we only show the results for Fick coordinates.

**Adding motion terms to the model.** We first established how much variance in the dynamic interval dataset could be explained by our simplified models derived from the static interval data. We did this by performing our stepwise regression (using only the terms retained in the simplified static models) separately for each muscle and then averaging the $R^2_{cv}$ values across all muscles of each animal. The results for the dynamic interval data set (including both acceleration and deceleration phases) are shown as open bars in Fig. 9A (the $R^2_{cv}$ values for individual neck muscles are shown in Supporting Table 1, http://www.yorku.ca/jdc/documents/Farshadmanesh_etal_2011_Supporting_Material_JNP.pdf). The terms derived from the static interval data still accounted for a considerable amount of variance in the dynamic interval data ($R^2_{cv}$: M1, 0.18; M2, 0.21).

Next, we added motion terms to the model to examine their contribution. To limit model complexity (see METHODS), these only included up to second-order motion terms (i.e., first and second time derivatives of head orientation components and their multiplicative combinations). The stepwise regression results are shown as solid bars in Fig. 9A. Adding motion terms in both animals improved the model performance ($R^2_{cv}$: M1, 0.25; M2, 0.36).

Next, we tested the retained terms of the simplified complete models on the full dataset (including both static and dynamic intervals). The $R^2_{cv}$ values, averaged across muscles, are shown in Fig. 9B. Although the performance of both the static model (shown as vertical dashed lines for comparison) and the complete model tested on the full data set were better compared with those fitted to dynamic intervals, orientation terms (open bars) still showed a significant contribution to explaining the variance, with addition of the motion terms (solid bars) improving the $R^2_{cv}$. In both animals, however, the $R^2_{cv}$ of the complete model tested on the full data set was still lower compared with that of the static model fitted to static interval data (vertical dashed lines; M1, full = 0.41, static = 0.52; M2, full = 0.50, static = 0.61).

Thus, overall, despite the addition of motion terms, orientation terms continued to dominate and there was less variance accounted for when data from the dynamic intervals were included.

**Acceleration vs. deceleration.** Our dynamic interval data set included both acceleration and deceleration phases, and there is no guarantee that the muscular control of head acceleration and deceleration is the same. Therefore, we analyzed these two phases of head movement separately to see whether neck muscle activation patterns were indeed different. The retained motion terms of the simplified complete models, shown separately for acceleration and deceleration phases of the dynamic interval data, are summarized in Table 3.

Recall that the time lag between neck EMG and observed head movement was a free variable in these fits and was not constrained to physiological ranges (see METHODS). Our obtained lags were shorter than other estimations (Botterman et al. 1986) and similar between the two animals but were longer for acceleration phase [M1, 14.46 ± 2.84 ms (mean ± SD); M2, 16.46 ± 3.07 ms] vs. deceleration phase (M1, 2.15 ± 1.30 ms; M2, 4.07 ± 2.59 ms). This is consistent with known muscle physiology, because 1) acceleration is produced by the rate of agonist shortening, whereas deceleration is controlled by the rate of antagonist lengthening; and 2) muscles develop forces faster during active lengthening than during active contractions (Brown and Loeb 2000).

Moreover, the retained model terms were not always the same for the acceleration and deceleration phases. For example, in both animals (see Table 3), the retained terms for bilateral COM, BC, and SP muscles were similar for both phases, but the terms for the RCPmaj, OCI, and SCM muscles, or the order of their importance, were different between acceleration and deceleration phases. Both velocity and acceleration terms were observed, but velocity terms made a larger contribution to the $R^2_{cv}$ in most muscles for both animals. The exception to this was R-COM in animal M2 (where the retained term was $H^2H^2$). The two animals did not show identical results: overall, in animal M2, fewer muscles had a velocity term (4 of 12) compared with animal M1 (9 of 12). Perhaps most importantly, and in contrast to static models, the models for several muscles in both animals retained torsional terms for velocity, acceleration, or their multiplicatives. These findings are illustrated below.

**Visualizing the EMG vs. 3-D head motion relationship.** To visualize and conceptualize the complex quantitative relationships between neck muscle EMG and head motion shown in Table 3, we treated the coefficients of the horizontal, vertical, and torsional terms of our fits as 3-D vectors. Figure 10 plots these vectors as they would be viewed from behind and from the side (left and right sides of each panel, respectively) for left (black) and right muscles (red). Thin, solid arrows denote the coefficients for animal M1, whereas thick, semitransparent arrows represent coefficients for animal M2. According to the right-hand rule (i.e., holding the thumb of the right hand aligned with the axis of rotation, the fingers will curl toward the direction of rotation), the direction of each arrow (i.e., the sign of the plotted coefficient) indicates that the activity of a given muscle increased when the head moved in that direction. For example, for a coefficient with a positive sign, a head rotation in left/up/CW direction increased its value, whereas a right/down/CCW head rotation decreased it. Only the coeffi-
cients for velocity terms are shown in Fig. 10 because they were generally more consistent between the animals. Empty panels indicate that there was no velocity term in the simplified model for that muscle for any of the animals.

During the acceleration phase (Fig. 10A), bilateral RCPmaj in animal M1 and R-RCPmaj in animal M2 showed higher activity for both horizontal and torsional head rotations: left (right) muscles were more active for leftward/CW (rightward/CCW) directions. L-RCPmaj in animal M2, however, showed directionality only for CW head rotations. Similarly, L-OCI in both animals was more active for leftward/CW directions, whereas R-OCI in animals M1 and M2 showed directionality only for CCW and rightward head rotations, respectively. Bilateral COM in animal M1 and bilateral BC in both animals were more active for upward head movements. Bilateral SP in animal M1 and R-SP in animal M2 showed selective activation for contralateral torsional head rotations. Whereas R-SCM in animal M1 was more active during leftward, downward, and CW head rotations, L-SCM only showed CCW directionality. Bilateral SCM in animal M2 only showed selective activation for downward head movements.

During the deceleration phase (Fig. 10B), bilateral BC and SP in both animals and bilateral COM and L-SCM in animal M1 all showed a directional selectivity similar to the acceleration phase results. R-SCM in animal M1, however, showed directionality only for leftward and CW head rotations (compared with leftward, downward, and CW during the acceleration phase). Moreover, during deceleration, the horizontal directionality of bilateral RCPmaj and OCI disappeared in both animals, instead showing a symmetric activation for torsional head rotations: left/right muscles were more active for CW/CCW directions. Overall, during head movements, most neck muscles had retained velocity terms in their models during both acceleration and deceleration phases, with different terms being retained during the two phases for RCPmaj, OCI, and SCM muscles. For other muscles, the contributions of the terms were similar across acceleration and deceleration phases.

DISCUSSION

This is the first study to use a cross-validation-based stepwise regression procedure to examine neck EMG and 3-D head kinematics relationships for the diversity of neck muscles that we implanted. It is important to differentiate that we did not simply correlate the EMG for each muscle against head orientation and movement parameters (which might sometimes reflect meaningless cross-correlations in a multidimensional, redundant system). Our cross-validation-based algorithm allowed us to systematically test the kinematic parameters encoded by the EMG signal for each muscle and to calculate most contributing coefficients of those relationships. However, it is also important to note that 1) we targeted to record EMG from only 12 neck muscles (primarily those associated with rotations about the upper cervical vertebrae); 2) we only recorded this activity during gaze shifts; and 3) we only recorded head orientations and rotations, because these contribute to gaze direction for all but the closest targets. Thus we cannot discuss translational motion of the head, and we cannot know if our results generalize to other neck muscles or head-neck behav-

![Fig. 6. Predicted EMG activity (z-axis) vs. horizontal and vertical head orientation (base) as obtained from our cross-validation-based stepwise regression. Models for left and right SCM muscles are shown for animals M1 (A and B) and M2 (C and D). The z-axis in each panel is normalized relative to the $R^2_{cv}$ value of the model for each muscle (see Fig. 5 legend). Vertical scale bars denote 10 $\mu$V.](image-url)
The variance during head movement, although the addition of holding intervals could still account for most of the EMG over, the same orientation terms (derived from static head-orientation as the only independent variable, could generalize cases, a fourth-order polynomial model, with horizontal head regression procedure suggested that a second (and in some sional head orientation observed during gaze holding. Our EMG showed no relationship to the small variations in tor-sional head orientation are not the product of systematic or putative eye-only saccades (Oommen and Stahl 2005).

**Neck EMG vs. Head Orientation During Static Intervals**

Our postural results during static intervals (approximately corresponding to gaze fixations) were reasonably similar to results from previous studies of neck EMG and head posture in monkeys (Corneil et al. 2001; Lestienne et al. 1995) and humans (Keshner et al. 1989). For example, Corneil et al. (2001) showed symmetric EMG activation related to the eccentricity of horizontal head orientation for RCPmaj, OCI, SP, and SCM in the monkey. Similarly, we observed an overall consistent and symmetric horizontal head orientation dependency for most neck muscles. Of the muscles tested by Corneil et al. (2001), only COM showed EMG activity consistently increased as a function of head eccentricity, whereas we were able to detect a consistent vertical correlation in SCM and COM muscles. Corneil et al. (2001) also observed increased but inconsistent EMG activity in several horizontal head turner muscles (RCPmaj, OCI, and SP) for extreme upward (but not downward) head orientations, beyond those tested in this study.

A higher demand for EMG signals related to horizontal (as opposed to vertical) head orientation in head posture control in the muscles we recorded is likely related to mechanical factors. As in humans (Glenn and Vilis 1992), monkeys use a proportionately larger head contribution to horizontal gaze compared with vertical gaze (Crawford et al. 1999). This range of head motion likely corresponds to the range of motion about the upper cervical vertebrae in primates (spanned by most of the muscles we recorded from), whereas large vertical head movements are provided by the cervicothoracic junction (Graf et al. 1995a). The passively borne center of mass of the head on the vertebral column is different for horizontal and vertical head movements (Graf et al. 1995a, 1995b), but significant gravitational forces likely only come into play during larger vertical head rotations (not observed in our data). In contrast, it appears that the dominant force that muscles must counteract during the head-holding phase of most gaze shifts is the elastic restoring force in the horizontal dimension, presumably arising from the vertebral column and surrounding tissues, including muscles (Peterson and Richmond 1988).

The lack of a reliable relationship between neck EMG and head torsion in our data suggests that small normal variations in torsional head orientation are not the product of systematic

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**Fig. 7.** Predicted EMG activity (z-axis) vs. horizontal and vertical head orientation (base) as obtained from our cross-validation-based stepwise regression. Models for left COM muscles are shown for animals M1 (A) and M2 (B). The z-axis in each panel is normalized relative to the $R^2$ value of the model for each muscle (see Fig. 5 legend). Vertical scale bars denote 10 $\mu$V.

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<table>
<thead>
<tr>
<th>Muscle</th>
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*Note: Values are normalized $R^2$.*
muscle synergies, but are simply due to “noise” in an over-redundant system. This is likely because the system is simply trying to minimize torsion in Fick coordinates during gaze control (Crawford et al. 1999; Glenn and Vilis 1992) and because these small errors would have miniscule contributions to gaze direction with eye orientation within a normal range. This does not mean that these muscles are not involved in the holding of larger systematic torsional tilts. Although the range of lateral flexion is restricted in both monkeys and humans (Graf et al. 1995a), it can be controlled both reflexively and voluntarily. To determine the muscle synergies that produce systematic torsion, one would have to record neck EMG during more extreme torsional ranges, during either natural behavior or invasively evoked conditions (e.g., stimulation of the INC that results in large torsional head tilts; see Klier et al. (2002)).

Neck EMG vs. Head Kinematics During Active Head Rotation (Dynamic Intervals)

In our analysis of the head movements, we found a directionally specific activation for all of the tested neck muscles, similar to previous observations (Corneil et al. 2001; Lestienne et al. 2000). In particular, RCPmaj and OCI in both animals showed ipsilateral activation for horizontal head movements, whereas R-SCM in animal M1 was more active for contralateral horizontal movements. The lack of a clear consistent contralateral activation for SCM, which is a very strong muscle and presumably is recruited mostly during brisk head turns, could be partially explained by our paradigm and data selection criteria that excluded quick head movements (see METHODS). COM and BC muscles were active for upward head movements, whereas SCM in both animals was active during downward head movements. For torsional movements, RCPmaj, OCI, SP, and SCM showed a directional activation, similar to recruitment of neck turners observed by Corneil et al. (2001) during oblique inclining head movements in monkeys. Furthermore, we found different directionality for acceleration and deceleration phases of movement in RCPmaj, OCI, and R-SCM muscles. This difference could presumably be due to different muscle synergies employed by the central nervous system during different phases of the movement interval as shown for joint elbow movements (Gottlieb 1998) to match demands of the movement (e.g., movement initialization or braking).

In contrast to some studies (Corneil et al. 2001), our results suggest a nonlinear relationship between neck EMG and head kinematics, which is not surprising given the more extensive sampling of head postures and movements in our data set. This is also shown in humans, during isometric stabilization tasks,
Subjects (M1 and M2). For dynamic data (M1, bars), the models (open bars) and orientation + motion terms (complete models; solid bars). The $R^2$ values for all muscles were pooled and averaged within each animal. For comparison, vertical dashed lines in B show the results of static models fitted to static interval data. Error bars denote SE. Full data: M1, $n = 6,105$; M2, $n = 4,653$. To obtain head movement parameters (velocity, acceleration), we first separately calculated both angular velocity (angular rotation about a finite axis) and the first time derivative of head orientation (Tweed and Vilis 1987). Second, in addition to the coordinates mentioned above, we considered a head-fixed coordinate frame as observed in the vestibular system (Angelaki and Cullen 2008; Green and Angelaki 2003) and in some cortical gaze control sites (Martinez-Trujillo et al. 2004). Leaving out self-contradictory possibilities, the following combinations (as presented in this figure) were explored: the first time derivatives of the laboratory-fixed Listing’s frame angle vector (space-D), the first time derivative of the Fick angles (Fick-D; shown), and the physical angular velocity (°/s) referred to either laboratory-fixed axes (space-A) or head-fixed axes (head-A). Similar definitions hold for acceleration. The selection of head movement intervals for each representation was performed using the corresponding calculated head speed (space-A, head-A) or magnitude of the first-order time derivative of head orientation (space-D, Fick-D). Note that (as described in the text) only results using Fick coordinates are shown.

Muscle Anatomy vs. Functional Activation

It is difficult to assume functional use from anatomy in a highly redundant system where different animals could develop and learn very different combinations of muscle activation patterns to produce the same behavior. Indeed, our findings did not completely agree with the expected pulling directions of the examined neck muscles. For static head posture, we found a clear nonlinear horizontal head orientation dependency not only for horizontal head turners but also for neck extensors (BC and COM) together with a lack of clear relationship for vertical/torsional orientations. For head movements, we observed more consistency with the anatomy of examined muscles. Most horizontal head turners (RCPmaj and OCI in both animals and R-SCM in M1, but not SP) showed preferred activation for horizontal head movements with vertical head movement dependency seen in BC, COM, and SCM (albeit only during deceleration phase for the latter muscle). Torsional component dependency in RCPmaj, OCI, and SCM was similar to that in previous studies in monkeys (Farshadmanesh et al. 2008) and humans (Conley et al. 1995).

This is not always the case for all muscles. Activation directions in the upper limb of humans have been shown to be closely aligned with pulling directions of the muscles (Buchanan et al. 1986). Moreover, well defined directions of maximal activation for neck muscles have been observed in cats (Baker et al. 1985) and humans (Keshner et al. 1989; Zangemeister et al. 1982). Some studies in humans, however, suggest that preferred activation in neck muscles do not always align (Keshner et al. 1989) or only partially agree (Conley et al. 1995) with their anatomically implied pulling directions (Baker and Wickland 1988; Lockhart et al. 1972). For example, Siegmund et al. (2007) found that SCM and posterolateral neck muscles exhibited directional preference consistent with anatomy but that SP did not. Moreover, it has also been shown that in at least some neck muscles there is a dual directional preference (i.e., preferred activation of a given muscle for 2 different directions in the same subject). This has been observed in SP in humans (Keshner et al. 1989) and RCPmaj during axial rotations of the head in cats (Peterson et al. 2001). This is especially true for 3-D moments due to the strong influence of axial rotation (Vasavada et al. 2002).

Finally, it is known that during tasks with multiple requirements (e.g., performing a horizontal head rotation while maintaining a stable vertical head posture), multiple muscle recruitment strategies appear, with each being optimized for the demands of the task (Peterson et al. 2001). Therefore, it is quite possible that the group of muscles tested in the present study were recruited by different synergies according to the task and not exclusively based on their expected anatomical configurations. If so, one might expect different rounds of the cross-validation procedure to yield different results, even for the same muscles tested, under different behavioral conditions.

Implications for Neural Control

Motor neurons that drive the neck muscles are thought to receive input from several brain stem structures (Ito and Sasaki...
Table 3. Retained terms of simplified complete models

<table>
<thead>
<tr>
<th>Left Neck Muscles</th>
<th>Right Neck Muscles</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Animal M1, acceleration</strong></td>
<td><strong>Animal M1, deceleration</strong></td>
</tr>
<tr>
<td>RCPmaj</td>
<td>$T (0.10), \dot{V}V (0.07), \ddot{T} (0.02), \dddot{T}^2 (0.01)$</td>
</tr>
<tr>
<td>OCI</td>
<td>$T (0.10), \dot{T} (0.05), H (0.04), \dddot{T}^2 (0.02)$</td>
</tr>
<tr>
<td>COM</td>
<td>$V (0.06)$</td>
</tr>
<tr>
<td>BC</td>
<td>$V (0.05), \dddot{T}^2 (0.01)$</td>
</tr>
<tr>
<td>SP</td>
<td>$T (0.04), H (0.01)$</td>
</tr>
<tr>
<td>SCM</td>
<td>$T (0.04)$</td>
</tr>
<tr>
<td><strong>Animal M2, acceleration</strong></td>
<td><strong>Animal M2, deceleration</strong></td>
</tr>
<tr>
<td>RCPmaj</td>
<td>$T (0.13)$</td>
</tr>
<tr>
<td>OCI</td>
<td>$H (0.16), \dot{T} (0.10)$</td>
</tr>
<tr>
<td>COM</td>
<td>$VV (0.09), \dddot{T}^2 (0.05), \dot{V}V (0.01)$</td>
</tr>
<tr>
<td>BC</td>
<td>$V (0.08)$</td>
</tr>
<tr>
<td>SP</td>
<td>$HH (0.19), \ddot{T} (0.13)$</td>
</tr>
<tr>
<td>SCM</td>
<td>$V (0.07)$</td>
</tr>
</tbody>
</table>

Data are the retained motion terms of the simplified complete models for acceleration and deceleration phases of head movement for animals M1 and M2. These terms collectively contributed more than 0.05 to the accounted for by that term. However, perhaps not surprisingly, when these deficits are examined in more detail, this simple model does not capture its full complexity (Farshadmanesh et al. 2007).

Our data seem to support these observations. First, we observed a clear qualitative division of EMG coefficients between horizontal and vertical/torsional kinematic components. Second, this division predicts specific signals in the horizontal and vertical/torsional neural control systems.

Despite their fundamental differences, the oculomotor system and head control system appear to share some common features. First, as in the oculomotor system, the brain stem structures downstream of the SC show a division of control for horizontal and vertical head movements in both cats (Grantyn and Berthoz 1987; Isa and Naito 1995; Sasaki et al. 1999) and monkeys (Cowie and Robinson 1994; Klier et al. 2002; Quessy and Freedman 2004). For example, electrical stimulation of the nucleus reticularis gigantocellularis (Quessy and Freedman 2004) and paramedian pontine reticular formation (Gandhi et al. 2002), but little is known about these control signals and their relationship to head kinematics (Corneil et al. 2002; Zajac and Gordon 1989). Efforts have been made to approximate the underlying neural mechanisms that control neck muscles based on the properties of EMG signal (Agarwal and Gottlieb 1975; Bouisset and Goubel 1971; Zangemeister et al. 1982), but the accuracy of such estimates have been difficult to establish except in isometric experimental conditions (Hannaford et al. 1986). One contribution of the current study is that by establishing reliable quantitative links (coefficients) between neck EMG and multidimensional head kinematic parameters (see Tables 1 and 3, Figs. 5, 6, 7, and 10), one might develop new and more rigorous predictions about the nature of neural head control signals.
One of the original goals of this study was to test whether EMG could be used to establish the contribution of neck muscles to the Fick strategy used for head movements during gaze shifts (Crawford et al. 1999; Klier et al. 2007), similar to the role played by eye muscles in maintaining Listing’s law (Demer et al. 1995; Klier et al. 2006; Meng et al. 2005). There is ample evidence that both neck anatomy (i.e., configuration of the first and second cervical vertebrae, respectively; Richmond and Vidal 1998) and brain stem control signals (Klier et al. 2007) are aligned with such a coordinate system. Unfortunately, we were not able to establish in this study whether neck muscle EMG similarly aligns best with parameters in Fick vs. any other coordinate system or to encode motion variables such as angular velocity vs. orientation derivatives. In retrospect, this limitation was simply because differences between these models were small (in the range of head orientation/movement that we attained in our gaze paradigm) compared with the amount of background EMG noise. However, this does not mean that such an analysis could not succeed under different experimental conditions, for example, during gaze shifts to extreme target ranges, head torsion during INC stimulation (Klier et al. 2007), or trained head movements (Walton et al. 2008, 2007), although the latter options may lead to violations of the normal Fick strategy observed during normal gaze shifts (Ceylan et al. 2000).

In summary, our results demonstrate that 1) 3-D kinematics variables for head orientation can be reliably decoded from neck EMG, and 2) these variables could not have been predicted from knowledge of musculoskeletal anatomy. These data may provide important new clues for identifying the signals that one should expect to see in the brain stem control signals and predict very different multidimensional control signals for head orientation and movement during gaze shifts. Moreover, the cross-validation-based analysis developed might work equally well to directly establish reliable relationships between neural signals, neck EMG, and head kinematics.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: F.F., B.D.C., and J.D.C. conception and design of research; F.F. and H.W. performed experiments; F.F., P.A.B., and G.P.K. analyzed data; F.F., P.A.B., B.D.C., and J.D.C. interpreted results of experiments; F.F. prepared figures; F.F. drafted manuscript; F.F., B.D.C., and J.D.C. edited and revised manuscript; F.F., B.D.C., and J.D.C. approved final version of manuscript.

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NECK MUSCLE ELECTROMYOGRAPHY AND HEAD KINEMATICS


