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A Computational Model of Muscle Recruitment for Wrist Movements

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Fagg, Andrew H., Ashvin Shah, and Andrew G. Barto. A computational model of muscle recruitment for wrist movements. *J Neurophysiol* 88: 3348–3358, 2002. First published October 10, 2002; 10.1152/jn.00621.2002. To execute a movement, the CNS must appropriately select and activate the set of muscles that will produce the desired movement. This problem is particularly difficult because a variety of muscle subsets can usually be used to produce the same joint motion. The motor system is therefore faced with a motor redundancy problem that must be resolved to produce the movement. In this paper, we present a model of muscle recruitment in the wrist step-tracking task. Muscle activation levels for five muscles are selected so as to satisfy task constraints (moving to the designated target) while also minimizing a measure of the total effort in producing the movement. Imposing these constraints yields muscle activation patterns qualitatively similar to those observed experimentally. In particular, the model reproduces the observed cosine-like recruitment of muscles as a function of movement direction and also appropriately predicts that certain muscles will be recruited most strongly in movement directions that differ significantly from their direction of action. These results suggest that the observed recruitment behavior may not be an explicit strategy employed by the nervous system, but instead may result from a process of movement optimization.

INTRODUCTION

In performing many motor tasks, the CNS has the option of selecting from a range of joint motion patterns. While this redundancy offers tremendous flexibility, it also presents an ill-posed problem from the control perspective (Bernstein 1967). Nevertheless, stereotypical patterns are often observed in both the kinematic variables and the muscle activity patterns. These regularities are not only seen within an individual but are often observed across many individuals.

Hoffman and Strick (1999) investigated muscle activity involved in radial/ulnar deviation and flexion/extension of the primate wrist. Examining agonist EMG activation in a center-out, point-to-point movement task, they observed two particular regularities in the muscle recruitment pattern. First, the muscles were recruited in a smooth, cosine-like fashion as a function of movement direction (in the wrist joint coordinate system). Second, several muscles exhibited behavior in which the direction of maximal activation differed significantly from the muscle's pulling direction. Similar muscle recruitment behavior has been observed in a variety of experiments, including an isometric head stabilization task (Keshner et al. 1989) and isometric arm/wrist force production tasks (Buchanan et al. 1993; Flanders and Soechting 1990). In addition, Wickland et al. (1991) demonstrated differences between neck muscle pulling directions and their direction of maximal recruitment in a cat vestibulocollic reflex task.

Aside from constraints imposed by the task itself (moving the wrist to a specified position), what principles are employed so as to yield the observed stereotyped behavior? In the context of the generation of reaching movements, Flash and Hogan (1985) suggested a minimum jerk criterion and Uno et al. (1989) used a minimum torque change criterion to constrain the selection of joint-level motor commands. A variety of authors have suggested that some form of *effort minimization* might be employed to further constrain the choice of action. Within the equilibrium point domain, Mussa-Ivaldi et al. (1988) and Bizzi et al. (1991) chose muscle activation patterns that minimized the potential energy stored in opposing muscles. Lan and Crago (1994) and Lan (1997) also worked within the equilibrium point domain, but chose to minimize an objective function that included a term for the velocity of the joint equilibrium point. In studies using models of the lower limbs performing a walking task, Pedotti et al. (1978), and more recently, Collins (1995) compared several muscle optimization criteria (including total muscle force, total squared force, and muscle stress) and found that minimization of total squared muscle force produced muscle activation patterns that were most similar to EMG patterns exhibited by several limb muscles during movement. (In the case of Pedotti et al., total squared normalized force was preferred over total squared force.) In addition, Buchanan and Shreeve (1996) compared a number of optimization criteria (including squared force, squared normalized force, and squared and cubed stress) in isometric elbow and wrist tasks and found only slight differences in the predicted EMG activation patterns.

In this paper, we introduce a model of muscle recruitment in the Hoffman and Strick (1999) task. The model selects muscles based on their ability to produce the desired movement while minimizing the total effort (defined as the sum squared muscle activation) required to implement the movement. Taken together, these criteria lead to a cosine-like recruitment of muscles. Consistent with experiment, the model also predicts in

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some cases differences in a muscle's direction of action and its direction of maximal activation. However, under certain conditions, the criteria can lead to a recruitment pattern that deviates significantly from a cosine shape. This suggests that the cosine-like recruitment is not itself an intrinsic organizing principle, but instead results from a process of movement optimization.

MUSCLE RECRUITMENT FOR WRIST MOVEMENTS

Hoffman and Strick (1999) and Kakei et al. (1999) described a step-tracking task in which a human or monkey subject moved a manipulandum with its wrist to control cursor movement on a computer screen. The manipulandum allowed both wrist flexion/extension and radial/ulnar deviation. Prior to a block of trials, the wrist was fixed in a pronated, supinated, or midrange posture. Movements of the manipulandum resulted in *extrinsic* movements of the cursor: an extension of the pronated wrist produced an upward movement of the cursor, while a flexion of the supinated wrist produced the same cursor movement. In the experiment, a trial began with the cursor at the center of the screen. A target then appeared on the screen at one of several points (8 or 12, depending on the subject) falling on a circle around the starting location. The subject then moved the cursor to the displayed target.

During this task, Hoffman and Strick (1999) recorded the kinematics of movement and EMG activity from several muscles while the wrist was in the midrange wrist posture. In a subsequent study, Kakei et al. (1999) also recorded single neuron activity from the primary motor cortex (MI) while the wrist was in the pronated, midrange, and supinated postures. The muscles exhibited a typical two-phased behavior, with agonist muscle bursts initiating the movement; these were followed by antagonist braking bursts.

Hoffman and Strick (1999) defined the *best agonist direction* of a muscle as the extrinsic direction of wrist movement that elicited the largest agonist burst from that muscle. The time interval during which the muscle's agonist EMG was greater than 25% of its peak amplitude was defined as the *agonist burst interval*. Agonist activity of a muscle was determined by integrating the EMG activity of the muscle over the agonist burst interval. The agonist activity of a muscle was calculated for each direction of wrist movement (each target) while the wrist was in the midrange wrist posture of Hoffman and Strick (1999). Figure 1 shows the muscle activity patterns for extensor carpi ulnaris (ECU) and extensor carpi radialis brevis (ECRB) from a monkey subject. Also shown are the best-fit cosine functions for each case. The peak in the fitted cosine defines the muscle's *preferred direction* of activation. ECRB is shown to exhibit both positive and negative activation levels; these levels are relative to a baseline of activity that is present when the monkey was holding the cursor at the starting location.

The contribution to wrist movement by each muscle, referred to as the muscle's *pulling direction*, was determined by individually stimulating the muscles as the monkey held the manipulandum at the central position. Average pulling directions (in extrinsic space) for five muscles and three postures are shown in Fig. 2. As the wrist posture rotates 180° from pronation to supination, the pulling directions do not change by this degree, but rotate within the range of 74°–130°.

Of particular note is that some muscles were recruited most strongly for directions that differed significantly from their pulling directions. Figure 3 shows polar plots of normalized agonist muscle activity as a function of movement direction. In addition, measured pulling directions are indicated as open arrows; calculated preferred directions are given as closed arrows. The pulling and preferred directions of ECRB and ECU differ by as much as 45°, whereas the pulling and preferred directions of extensor carpi radialis longus (ECRL) and flexor carpi radialis (FCR) differ by at most a few degrees (Hoffman and Strick 1999).

METHODS

Through the modeling process, we hope to account for both the cosine-like muscle recruitment patterns and the observed deviations of the preferred direction from muscle pulling direction while introduc-

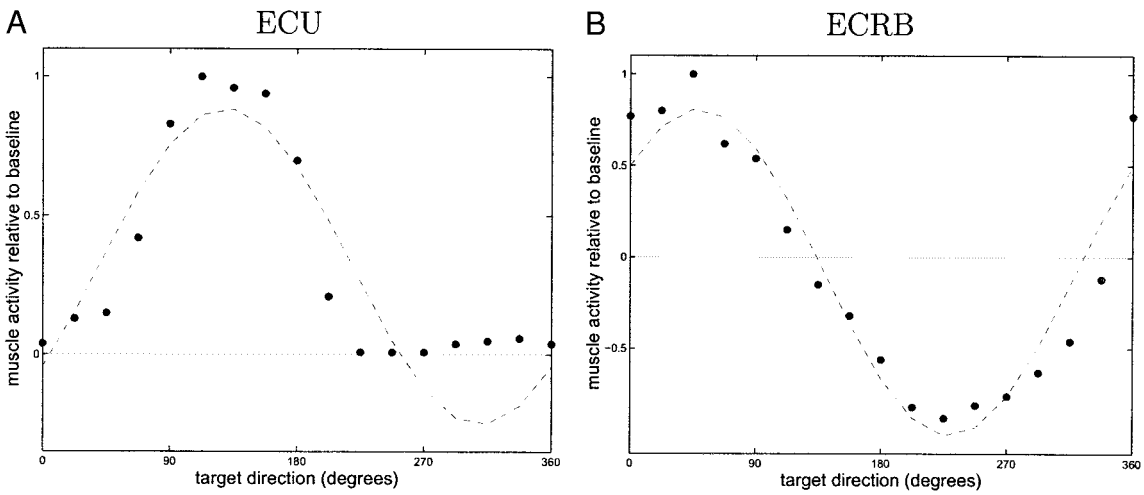

FIG. 1. Agonist muscle activity (normalized and relative to baseline) as a function of target direction for muscles extensor carpi ulnaris (ECU) (*A*) and extensor carpi radialis brevis (ECRB) (*B*) in the midrange wrist posture. Solid circles are muscle EMG recordings from a monkey subject performing the wrist step-tracking task. Dashed line shows the best fit cosine function. EMG data derived from Hoffman and Strick (1999) and D. L. Hoffman (personal communication). Ninety degrees corresponds to wrist extension; 180° corresponds to ulnar deviation.

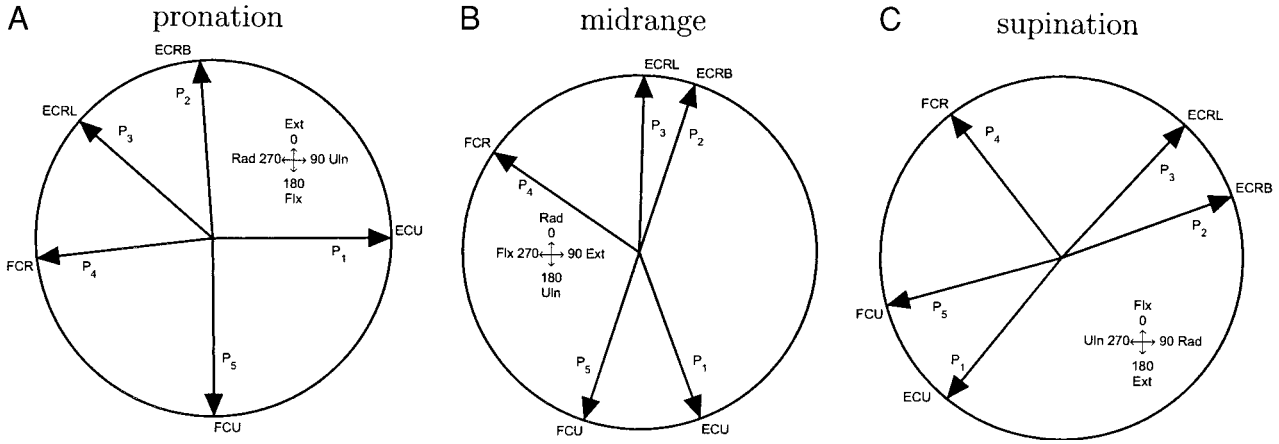

FIG. 2. Pulling directions of the 5 muscles primarily responsible for wrist actuation in the pronated, midrange, and supinated wrist postures (Hoffman and Strick 1999; D. L. Hoffman, personal communication). These vectors represent the average over 2 monkey subjects. Legend in each circle indicates extrinsic direction (in degrees) and joint movement (Rad, radial; Uln, ulnar; Flx, flexion; Ext, extension).

ing as few assumptions as possible about muscle dynamics. We have thus chosen a simple model of muscle action that focuses only on the total agonist muscle activation and ignores the time-course of EMG activity. Individual muscles are assumed to pull along straight lines in joint space, parameterized by wrist flexion/extension and radial/ulnar deviation. Figure 2 shows the muscle pulling directions for the five muscles that act as the primary movers of the wrist joint. In this analysis, we do not include the contributions of other muscles that cross the wrist joint. The extrinsic direction of action of each muscle (up/down and right/left) can be described as a two-element column vector, $\mathbf{P}_i^{\rho}$, where ρ is the wrist posture (pronated, midrange, supinated), and i is the muscle index.

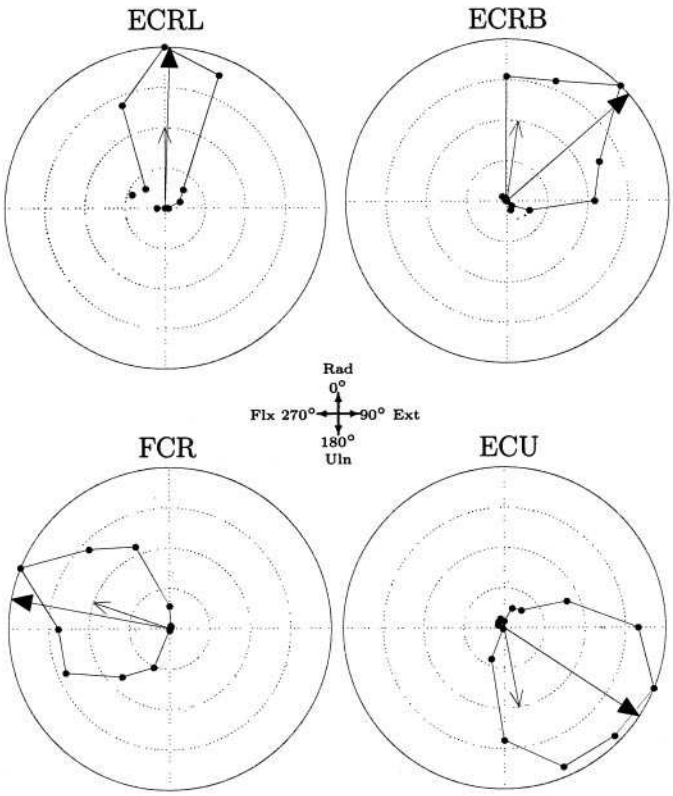

FIG. 3. Polar plot of normalized agonist muscle activity as a function of target direction from monkey muscles extensor carpi radialis longus (ECRL), ECRB, flexor carpi radialis (FCR), and ECU in the midrange wrist posture. Solid closed arrows represent calculated preferred directions; open arrows represent pulling directions. Legend in the middle of the figure denotes joint angle deviation and corresponding extrinsic direction of movement in degrees for the midrange wrist posture: Rad, radial; Uln, ulnar; Ext, extension; Flx, flexion. All data are derived from Hoffman and Strick 1999 and D. L. Hoffman (personal communication).

Muscles contribute to the endpoint of movement along their vector of action, where the length of the vector is proportional to the modeled muscle's activation level, a_i. This is analogous to the agonist activity of a muscle as defined by Hoffman and Strick (1999). We assume that the muscles contribute to the movement endpoint independently of one another. Thus for a given wrist configuration (ρ) and muscle activation vector (**a**), the endpoint of movement (**x**, a two element vector) can be described as follows

$$\mathbf{x} = \sum_{i \in A} \mathbf{P}_i^{\rho} a_i \qquad (1)$$

where A is the set of five muscles. This model of muscle action represents a simplification of that used by Penrod et al. (1974): relative muscle moment arms are not included. Furthermore, the model does not take into account differences in the muscles' force production ability. We revisit the implications of these simplifications in RESULTS.

With five muscles, a control system has a total of three redundant degrees of freedom from which to select a solution. How does the CNS resolve these redundancies such that the muscle activation patterns observed by Hoffman and Strick (1999) are achieved? Many different kinematic and dynamic constraints have been suggested for resolving redundancy in a variety of tasks (e.g., Buchanan and Shreeve 1996; Pedotti et al. 1978; van Bolhuis and Gielen 1999; Yamaguchi et al. 1995). One constraint that is particularly relevant to this task is that of minimization of total effort. In other words, we would like the control system to select muscle activation vectors such that both the desired endpoint position is achieved and the muscles expend as little effort as possible in pulling against one another. Note that any movement to a target that does not fall along the line of action of a single muscle requires that two or more muscles pull against one another to some degree.

The results of Penrod et al. (1974) and Pedotti et al. (1978) argue against the minimization of the sum of muscle activation. In contrast, Pedotti et al. (1978) and Collins (1995) argue for a form of squared muscle activation (normalized or absolute activation, respectively). Furthermore, Buchanan and Shreeve (1996) suggest little difference in predicted EMG between these two options. Due to these results and to mathematical parsimony, we choose here to employ a minimum squared muscle activation criterion. The following error function

represents one way to capture the two criteria (endpoint error and muscle activation)

$$E = \frac{1}{2}\left\|\mathbf{x}_{\mathbf{targ}} - \sum_{i\in A}\mathbf{P}_i^o a_i\right\|^2 + \frac{\lambda}{2}\|\mathbf{a}\|^2 \quad (2)$$

subject to: $a_i \geq 0$ for all $i \epsilon A$, where $\mathbf{x}_{\mathbf{targ}}$ is a vector representing the target location, λ is a regularization parameter set to 0.02, $\mathbf{a}$ is the muscle activation vector, and $\|\cdot\|$ denotes the magnitude (Euclidean norm) of a vector. The regularization parameter represents a trade-off between target error and muscle activation. Since all movements are of magnitude 1, and $\|\mathbf{a}\|^2$ is also on the order of 1 for most movements, $\lambda = 0.02$ represents allowable errors on the order of 2% of movement magnitude. The requirement that $a_i \geq 0$ for all muscles captures the constraint that muscles pull without pushing.

Note that a possible alternative formulation is one that only considers muscle activation vectors that exactly reach the target (i.e., $\Sigma_{i\epsilon A}\mathbf{P}_i^o a_i = \mathbf{x}_{\mathbf{targ}}$), and minimize $\|\mathbf{a}\|^2$ within that subspace. However, such a formulation does not allow one to trade movement accuracy with the amount of required effort. In particular (depending on the task), arbitrarily large muscle activation levels may be selected.

For a given target, $\mathbf{x}_{\mathbf{targ}}$, a solution is found by first randomly selecting $\mathbf{a}(t = 0)$ (each element, a_j is drawn from a uniform distribution over [0,1]) and then employing a gradient descent method, where the error gradient with respect to muscle activation a_j is as follows

$$e_j(t) \equiv \frac{\partial E}{\partial a_j} = -\left(\mathbf{x}_{\mathbf{targ}} - \sum_{i\in A}\mathbf{P}_i^o a_i(t)\right)^T \mathbf{P}_j^o + \lambda a_j(t) \quad (3)$$

The muscle activation levels are updated according to

$$a_j(t+1) = \begin{cases} a_j(t) - \alpha e_j(t) & \text{if } a_j(t) - \alpha e_j(t) > 0 \\ 0 & \text{otherwise} \end{cases} \quad (4)$$

where $\alpha = 0.02$ is a step-size parameter. This equation updates the muscle activation vector according to the error gradient as long as the individual muscle activation levels remain nonnegative. Note that this is not intended as a biologically plausible learning procedure, but simply a mathematical technique for finding a solution to the optimization problem.

For the results that follow, the gradient method was applied independently for each of three wrist postures and 12 targets equally spaced along a unit circle surrounding the starting position—yielding a total of 36 distinct tasks. The optimization procedure was performed iteratively on each of the 36 tasks until convergence was reached (this defines a single experimental run). Convergence was defined as the activation of no muscle changing more than 10^{-7} on a single optimization step. Thirty independent optimization runs were executed, each with a unique starting position for each muscle and task. The optimization procedure converged to a solution of 19,705 ± 420 (SD) steps. For the individual tasks, the muscle activation level at convergence deviated from the average over all runs by $5.22 \times 10^{-5} \pm 6.57 \times 10^{-5}$, regardless of the initial conditions. This result indicates that a unique solution exists for each of the 36 tasks. The average target error was 0.034 ± 0.031 and the average total muscle activation ($\|\mathbf{a}\|$) was 1.10 ± 0.43.

As in Hoffman and Strick (1999), muscle activation values for the set of targets (and a single wrist posture) were fit to a cosine-shaped function of the form $B\cos(\theta - C) + D$. Low muscle activation levels (in our case, less than 0.05) were given a zero weight in the fitting process. The muscle preferred direction for a given wrist posture is defined as the value of parameter C.

RESULTS

The model-computed muscle activation pattern and cosine fit for ECU and ECRB in the midrange wrist posture are shown in Fig. 4. Note the qualitative similarities with the monkey activation patterns for the corresponding muscles in Fig. 1. Both muscles exhibit a truncated, cosine-like recruitment pattern in which the activation level is cutoff at a minimal level of activation (zero in these cases). The preferred directions for both modeled muscles occur at approximately the same orientation as in the monkey subject. In addition, the range of the positive muscle activation (relative to baseline) is similar across experiment and model: ECRB is active above baseline over a 197° range (compared with 169° exhibited by the monkey), and ECU is active for 239° (compared with 248°).

Another important result from this model is that for any given wrist posture, muscles are activated in a cosine-like manner. This activation pattern is not explicitly included in the model, but results from the criterion of minimizing total effort. Without this criterion, many different activation patterns satisfy the remaining criterion (movement accuracy), and hence no clear pattern would necessarily arise for a single muscle. The key reason for the cosine-like recruitment is the fact that,

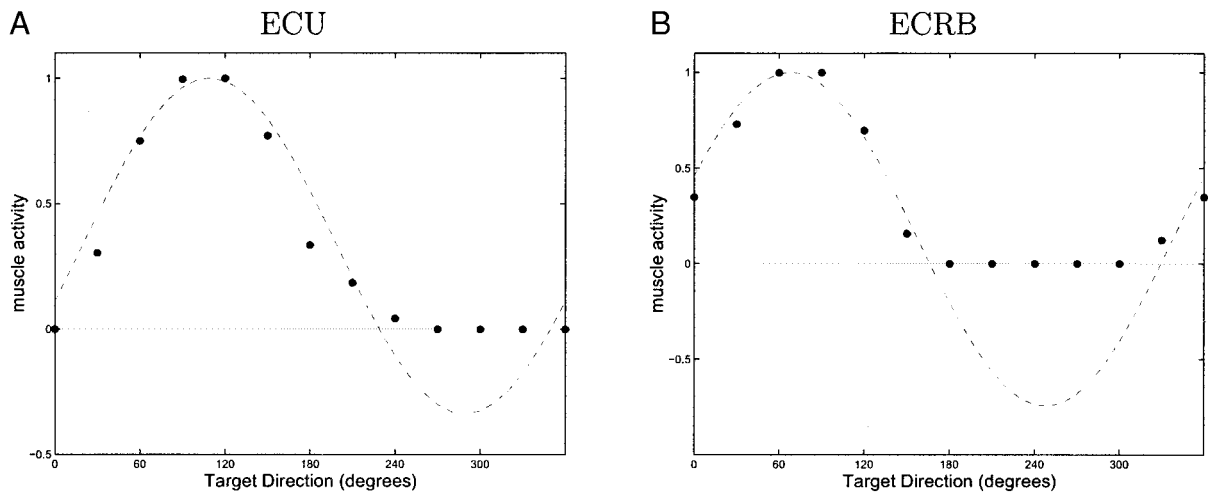

FIG. 4. Normalized muscle activity as a function of target direction as produced by the model for muscles ECU (*A*) and ECRB (*B*) in the midrange wrist posture. Solid circles represent muscle activation; dashed line represents a cosine fit. Compare with monkey data of Fig. 1.

in this system, a muscle's mechanical contribution to a movement is proportional to the cosine of the angle between the movement direction and the muscle's line of action. As this angle increases, the same level of activation contributes less to the desired movement. Furthermore, this situation requires the recruitment of other muscles to counteract movements orthogonal to the desired movement direction (increasing the cost in terms of total effort). As a result of the minimum effort criterion, it thus becomes advantageous to respond to these large angles between pulling and desired direction by reducing the muscle's activation level in favor of increasing the activation level of other muscles that have a better mechanical advantage in the direction of the desired movement. Furthermore, the specific choice of the *total squared muscle activation* criterion ensures that the responsibility for a movement is distributed across as many muscles as possible (subject to the muscles' mechanical advantage). To see this intuitively, suppose that two muscles happen to pull in very similar directions as the desired movement direction. Under the total squared muscle activation criterion, both muscles would be activated to equal levels, rather than activating one and not the other. This happens because: $0.5^2 + 0.5^2 < 0^2 + 1^2$. We will address this point further in the DISCUSSION.

Polar plots of muscle activation for four muscles (ECRL, ECRB, FCR, and ECU) in the midrange posture as calculated by the model are shown in Fig. 5. The plots also show muscle pulling (open arrow) and preferred (filled arrow) directions. On a qualitative level, the model behavior provides a reasonable match to the corresponding monkey data (Fig. 3), especially in regard to the magnitude of deviation of the muscle preferred and pulling directions for ECRB and ECU.[1]

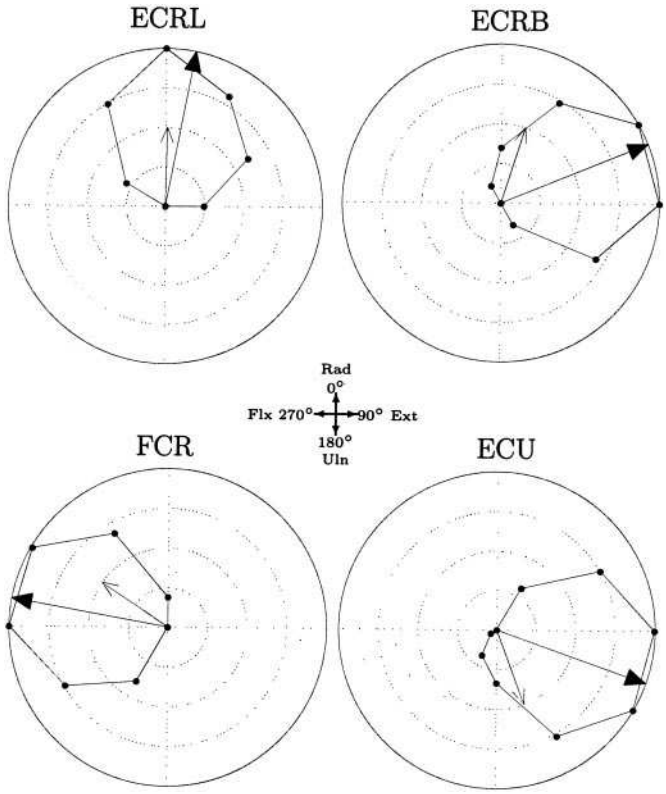

FIG. 5. Polar plot of normalized muscle activity as a function of target direction as produced by the model for muscles ECRL, ECRB, FCR, and ECU in the midrange wrist posture. Closed arrows indicate muscle preferred direction; open arrows represent pulling direction. Compare with monkey data of Fig. 3.

Figure 6 summarizes the preferred directions observed for the same four muscles (again in the midrange posture) for the model (solid line), and the range of preferred directions observed over several monkey (open triangle) and human (hashed triangle) subjects. Human and monkey data are from Hoffman and Strick (1999). Although the model-preferred directions and those recorded from monkey and human subjects do not match exactly, there is reasonable agreement between experiment and model.

What is the origin of the difference between muscle pulling and preferred direction? This difference arises from a combination of the distribution of muscle pulling directions and the minimum effort criterion. Returning to Fig. 2*B*, consider two targets that fall on the unit circle: one that is aligned with ECRB and another that falls at the midpoint between ECRB and ECU. To implement a movement to the first target, one possible solution is simply to recruit ECRB at an activation level of one. However, the second target requires that at least two muscles are recruited. Without loss of generality, assume that only ECRB and ECU are recruited. Because these muscles largely pull against one another, it is necessary to activate both muscles at a level that is far greater than one. This results in a significant difference between ECRB's pulling and preferred directions, with its preferred direction tending toward the pulling direction of ECU. Furthermore, the magnitude of the deviation is greater with a larger difference in the pulling directions.

As the wrist is rotated from the pronated to supinated configuration, the distribution of muscle pulling directions changes in a nonuniform manner (recall Fig. 2). This potentially leads to changes in the relationship between pulling and preferred directions as a function of wrist configuration. Figure 7 shows the activation pattern of muscle flexor carpi ulnaris (FCU) in the three postures. As the wrist rotates a full 180°, FCU's pulling direction changes less than 90°.[2] The preferred direction follows a similar pattern but deviates significantly from the pulling direction in only the midrange posture (by 27°).

A similar pattern is exhibited by all of the modeled muscles. Figure 8 shows a scatter plot that summarizes, for all experimental conditions, the deviation of preferred direction from pulling direction as a function of pulling direction. (We use *preferred direction deviation* to refer to the difference in preferred and pulling directions.) Each set of three connected points corresponds to a single muscle over the three wrist postures. Open circles represent the preferred direction deviation with the pronated wrist; solid dots correspond to the midrange posture; and squares correspond to the supinated wrist.

Focusing on the distribution of muscle pulling directions (Fig. 2*B*), note that the largest rotational gaps between muscle pairs occur between ECRB/ECU and FCU/FCR. As discussed above, the preferred direction of a muscle bordering a large gap

[1] The difference in pulling direction for muscle FCR (and other muscles) in the two figures is due to the fact that one (Fig. 1) corresponds to a single subject, whereas the pulling direction used by the model is the average pulling direction over two monkey subjects.

[2] Hoffman and Strick (1999) do not report the recruitment pattern for muscle FCU.

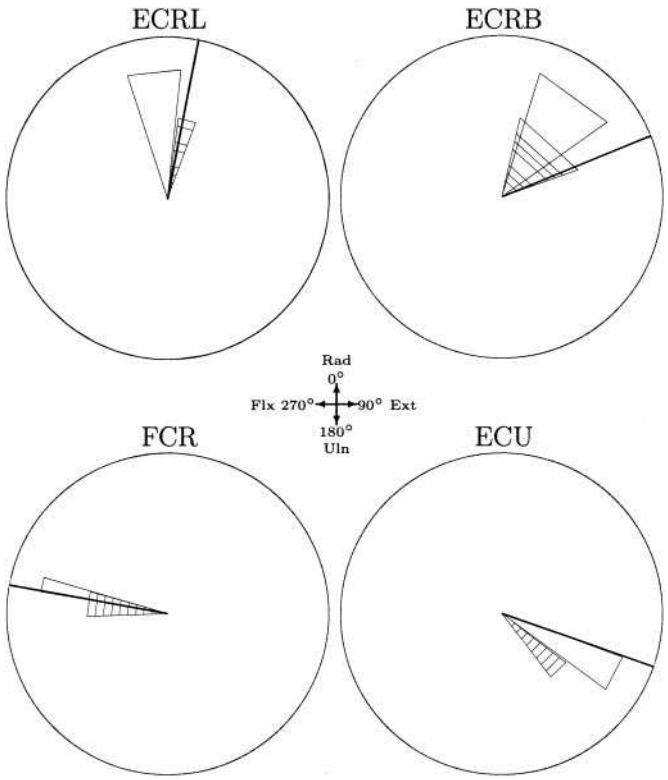

FIG. 6. Preferred directions of human, monkey, and model muscles ECRL, ECRB, ECU, and FCR in the midrange wrist posture. Long solid lines indicate preferred direction produced by the model. Open triangles represent the preferred direction, including inter-subject variation, observed in monkey EMG recordings. Hashed triangles represent the range of preferred directions measured in human EMG recordings. Monkey and human data from Hoffman and Strick (1999).

will be skewed toward the gap. This is illustrated in Fig. 8 by the filled circles, which show a clockwise deviation by ECRB and FCU, and a counter-clockwise deviation by ECU and FCR. Note also that the largest deviations correspond to those muscles bordering the largest gap (ECRB/ECU). In contrast, muscle ECRL exhibits a slight clockwise deviation (toward ECRB), despite its proximity to its two neighbors (ECRL has a pulling direction that differs by less than 50° from ECRB and FCR in the midrange wrist configuration). Under these conditions, the influence of the immediate neighbors may be outweighed by that of the remaining muscles. This latter effect is due to the use of the *squared* muscle activation criterion in the optimization process (*Eq. 2*). Although this effect does not occur for the total muscle activation case (i.e., $\Sigma_{i\epsilon A} a_i$; where a_i is raised to an exponent of 1), it would occur to varying degrees for any exponent greater than one.

REVISITING "COSINE" TUNING

Is the truncated, cosine-like recruitment pattern the only possible behavior for a muscle satisfying both accuracy and effort-based constraints? As described above, the deviation of preferred from pulling direction results from the fact that under certain conditions, muscles must expend a large portion of their effort pulling against one another to implement movements that fall between their respective pulling directions. As the target shifts away from the pulling direction of certain individual muscles, these muscles must be recruited to an even higher degree. This results in the shift of the muscle's activation peak (and in turn, of the preferred direction). Under what conditions does this increase in activation occur?

Figure 9*A* shows a simplified model of recruitment involving only two muscles. $\bar{\mathbf{P}}_1$ and $\bar{\mathbf{P}}_2$ are unit vectors describing the pulling directions of the two muscles; their (fixed) relative orientation is ψ. If we assume that the two muscles are recruited with activation levels a_1 and a_2, we have the following relationship

$$\mathbf{X} = a_1\bar{\mathbf{P}}_1 + a_2\bar{\mathbf{P}}_2 \tag{5}$$

Substituting for angles θ and ψ

$$\begin{bmatrix} \cos(\theta) \\ \sin(\theta) \end{bmatrix} = a_1\begin{bmatrix} 1 \\ 0 \end{bmatrix} + a_2\begin{bmatrix} \cos(\psi) \\ \sin(\psi) \end{bmatrix} \tag{6}$$

Given a desired target direction (specified by θ), and assuming that $\psi \neq k\pi$ for any integer k, a unique muscle recruitment vector exists (due to the fact that two muscles are being used to produce a two-dimensional movement between the two muscle pulling directions). This vector is described as follows

$$a_2 = \frac{\sin(\theta)}{\sin(\psi)} \tag{7}$$

$$a_1 = \cos(\theta) - \cos(\psi)\frac{\sin(\theta)}{\sin(\psi)} \tag{8}$$

This solution yields two characteristic muscle activation behaviors that are illustrated in Fig. 9*B*. In both of these cases, when $\theta = 0$, the required muscle activation vector is: $a_1 = 1$ and $a_2 = 0$. When $\theta = \psi$, the required activation vector is the opposite: $a_1 = 0$ and $a_2 = 1$. The two cases differ in the muscle activation vector between these two extremes. In only one case (shown as the bold curve of Fig. 9*B*), the muscle activation exceeds a level of one and exhibits a maxima between 0 and ψ (excluding the 2 extremes). Whether this case occurs or not depends on the relative pulling directions of the two muscles (ψ). The transition between these two cases occurs under the following condition

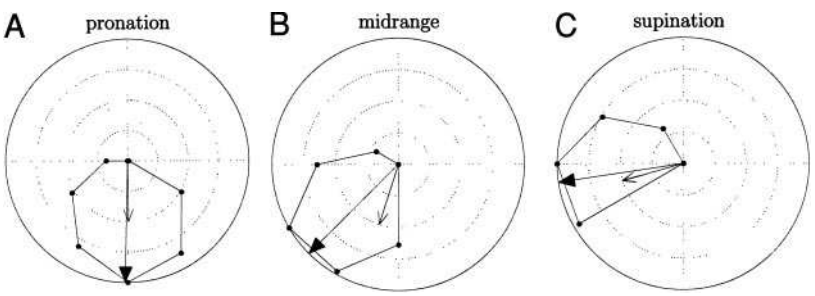

FIG. 7. Polar plot of normalized muscle activity as a function of target direction for the modeled FCU in the pronated (*A*), midrange (*B*), and supinated (*C*) postures. The notation is the same as in Fig. 5. Note the alignment of the pulling (open arrow) and preferred (closed arrow) direction in the extreme postures.

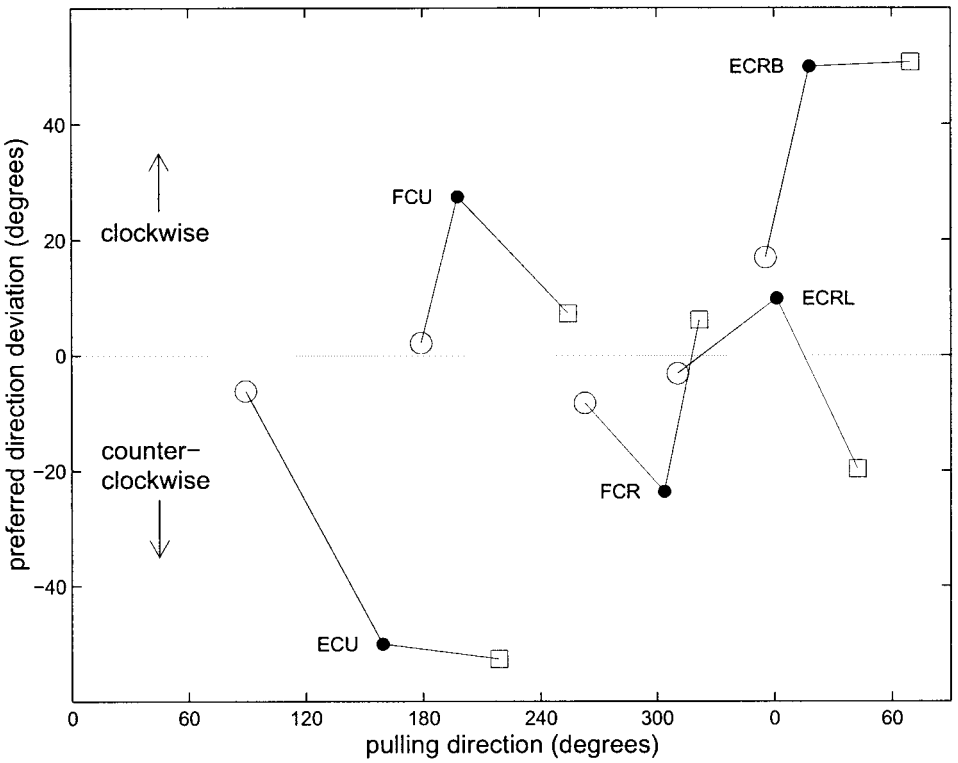

FIG. 8. Scatter plot showing the deviation of muscle preferred direction from pulling direction as a function of pulling direction for each muscle in each wrist posture: pronation (○), midrange (●), and supination (□). Each connected set of 3 points corresponds to 1 muscle.

$$0 = \frac{da_1}{d\theta}(\theta = 0) = -\sin(\theta = 0) - \cos(\psi)\frac{\cos(\theta = 0)}{\sin(\psi)} = -\frac{\cos(\psi)}{\sin(\psi)} \quad (9)$$

which holds only when $\psi = 90°$.[3] When $\psi > 90°$, we have the case in which the activation of muscle 1 exceeds a value of one for some $\theta > 0$. In turn, we observe a shift of the muscle peak activation away from its pulling direction. Furthermore, if we imagine a situation in which a muscle's pulling direction differs from its neighbor muscles[4] by greater than 90° in *both* the clockwise and counter-clockwise directions, this simple model predicts *two* peaks in the activation of muscle 1.

Does this same double-peaked behavior hold in the original model in which redundancies are resolved using a minimum effort criterion? With all five muscles involved in the task, it is not possible to ask this question since all muscles always have a neighbor whose pulling direction is within 90° of its own.[5] However, if one imagines the removal of muscle FCU from the available set of muscles, muscle ECU is left with neighbors whose pulling directions are as much as 120° from its own when the wrist is positioned in the midrange posture. For both the supinated and pronated wrist postures, the nearest neighbor to ECU is at approximately 90°.

Figure 10 illustrates the modeled behavior of ECU that results from applying the optimization process to the impoverished, four-muscle system for the three wrist postures. The muscle pulling directions are indicated by vertical lines. In the midrange posture, ECU exhibits a double-peaked behavior with a minimum near its pulling direction. This behavior deviates significantly from the cosine-like recruitment pattern that has been typically observed. For the extreme postures, ECU demonstrates only a single peak. Note that the peak occurs on different sides of the muscle's pulling direction. This effect is due to the radical change that occurs in ECU's pulling direction throughout the range of motion relative to ECRB and FCR.

In short, the use of the minimization of effort criterion to resolve redundancies in selecting muscle activation levels yields similar patterns to those that are observed experimentally, but predicts a deviation from this recruitment behavior under certain modified experimental conditions (specifically, removal of a specific muscle). Because the model yields both the cosine-like and double-peaked behaviors in the recruitment pattern with the same set of available muscles, we expect that this prediction is testable with a monkey subject.

SENSITIVITY ANALYSIS

One critical simplifying assumption made in the design of the model is that for a given activation level, every muscle contributes equally to the generated movement (the only difference being in the direction of movement). This fails to capture differences in both muscle moment arm and muscle force production ability. Because measurements of these quantities can vary quite dramatically (Buchanan and Shreeve 1996), we chose to make the assumption of least commitment. Although this choice limits our ability to make precise comparisons to the Hoffman and Strick (1999) experimental results, it still allows us to explore the general principles involved in movement selection. However, the question still remains as to the significance of making such an assumption.

[3] Note that to properly evaluate the derivative at $\theta = 0$, we must take a right-handed derivative since the equation for a_1 is only defined over the range $0 \leq \theta \leq \psi$.

[4] We use the term neighbor muscle to describe the muscle whose pulling direction is most similar to the first.

[5] Note that in the five-muscle model, the transition between characteristic behaviors illustrated in Fig. 9*B* does not necessarily occur precisely at $\psi = 90°$. This is due to the fact that the squared muscle activation optimization criterion tends to recruit more than two muscles for any particular movement direction.

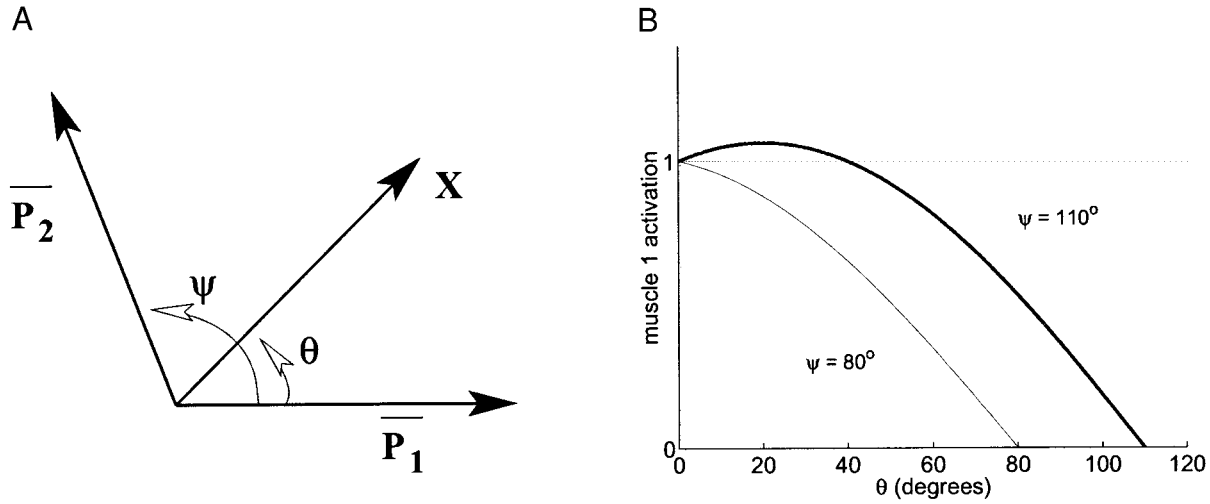

FIG. 9. A simplified muscle recruitment model (*A*), and the schematic recruitment of muscle 1 as a function of target direction (*B*). Depending on the rotational distance between the 2 muscles (ψ), muscle 1 will be recruited in 1 of 2 distinct patterns, as shown in *B*. In the 1st pattern, muscle 1 only obtains a maximum activation level of 1 when $\theta = 0$ (light curve); in the 2nd pattern, muscle 1 achieves a level of activation above 1 (bold curve) at a target between 0 and 4.

One way to ask this question is to alter the pulling strength of an individual muscle and examine the resulting changes in preferred direction of the entire set of muscles. In the model, this is implemented by changing the length, but not the direction, of the corresponding muscle pulling direction vector ($\mathbf{P}_i^o$; see Fig. 2 and *Eq. 2*).

Figure 11*A* demonstrates the changes that result from increasing (solid lines) or decreasing (dashed lines) the pulling strength of ECRL by 50%. The two muscles that are most affected by the change, FCR and ECRB, are the two immediate neighbors to ECRL and are drawn in black. In the case of the reduced pulling strength, one possible solution to the muscle recruitment problem is to simply increase the magnitude of activation of ECRL. However, this is not the optimal solution from the perspective of minimizing effort. Instead, the responsibility for the loss in strength is distributed across the neighboring muscles. This results in an increase in activation of the neighboring muscles for movements in the general direction of ECRL's pulling direction. In turn, this causes a shift in the preferred direction of FCR and ECRB toward the pulling direction of ECRL. In Fig. 11*A*, this effect is shown in the clockwise change in preferred direction deviation by FCR in all three wrist postures (solid lines to dashed lines represent a relative reduction in pulling strength). Furthermore, ECRB undergoes a counter-clockwise change of preferred direction deviation. Also note that ECRB exhibits the largest changes in preferred direction deviation (relative to FCR). This is due to the fact that the pulling direction of ECRB is closer to ECRL than is FCR. As a result, ECRB is able to bear a larger degree of the responsibility for the movement.

The most extreme changes in preferred direction deviation are observed when the pulling strength of FCR is altered (Fig. 11*B*). As in the previous case, we observe a change in the opposite direction by the two neighboring muscles with a reduction in pulling strength: FCU exhibits a clockwise change in preferred direction deviation and ECRL shows a counter-clockwise change. Note that the magnitude of change between the two cases is often large enough to force a change in the sign of the preferred direction deviation for both muscles as the wrist is rotated from pronation to supination.

For most muscles, the qualitative pattern of preferred direction deviation as the wrist rotates through its full range does not change substantially with significant changes in the torque-generation ability of individual muscles. These results suggest that this is a viable model for making qualitative predictions of wrist muscle activation as a function of task, but also demonstrates the limits of the model in making precise quantitative predictions.

DISCUSSION

The production of wrist movements involves the differential recruitment of many more muscles than skeletal degrees of freedom. In this paper, we present a model of wrist muscle recruitment in the Hoffman and Strick (1999) task. This model produces wrist flexion/extension and radial/ulnar deviation movements using a total of five muscles. Redundant muscle recruitment vectors that produce the specified wrist movement are resolved through the use of a minimum effort criterion. The introduction of this criterion forces a muscle to "hand off" responsibility for a movement when another muscle has a better mechanical advantage with respect to the specified movement. However, the fact that we are minimizing the sum of squared muscle activation implies that a certain degree of sharing will occur between muscles that pull in similar directions. Hence, the model predicts a "cosine-like" recruitment of the muscles as a function of movement direction, and that muscle activation will occur for about half of the movement range.

While minimizing the sum of muscle activity (not squared) yields a cosine-like activation pattern, this criterion will only activate two muscles for any particular movement direction (Buchanan Shreeve 1996; Penrod et al. 1974). This results in muscle activation patterns that are significantly narrower than with the squared-force criterion—a result that is not observed experimentally.

The cosine tuning properties exhibited by muscles are also found on a neural level. Georgopoulos et al. (1982) showed

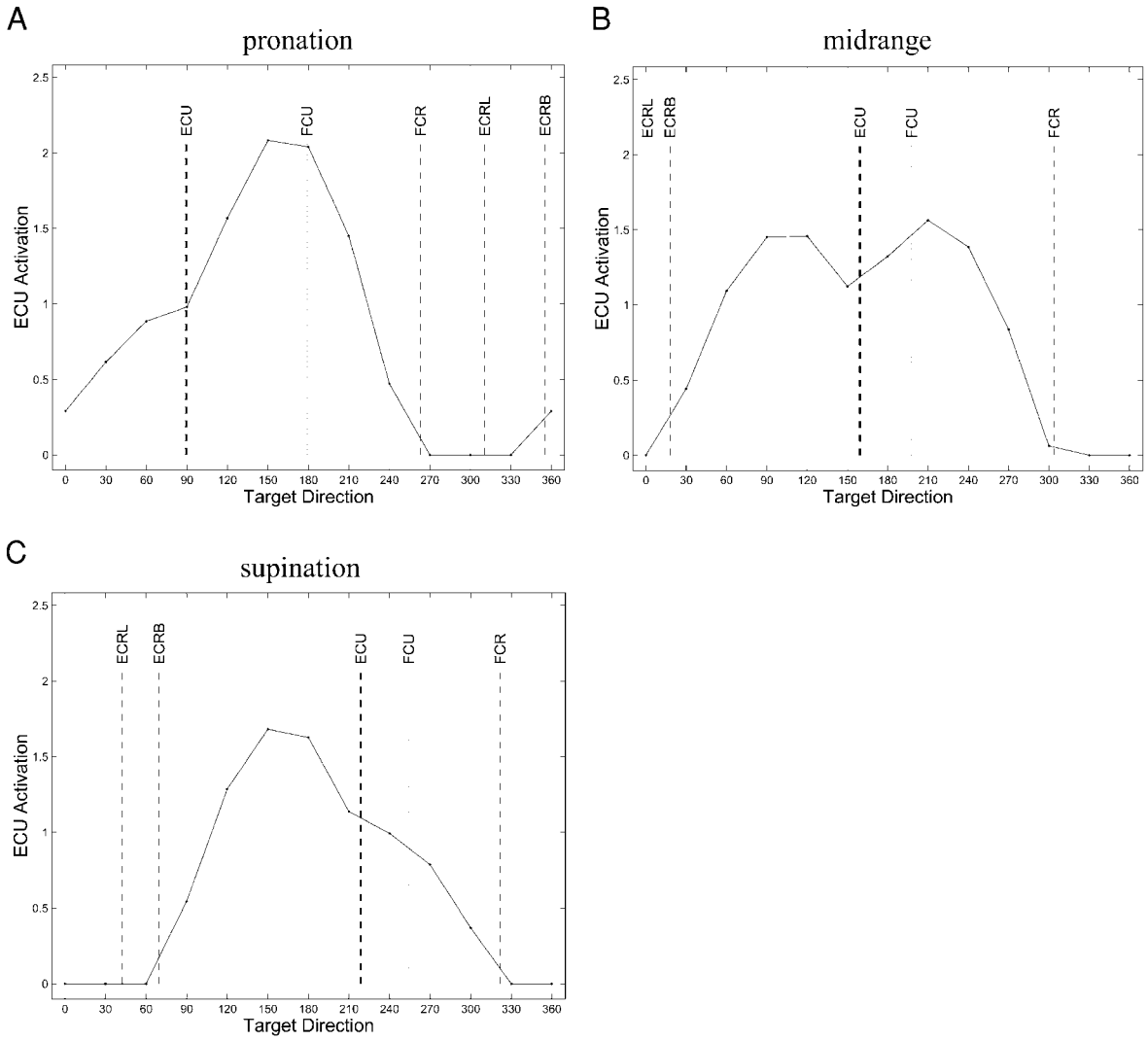

FIG. 10. Activation of muscle ECU as a function of target direction for the pronated (*A*), midrange (*B*), and supinated (*C*) wrist postures. Dashed vertical lines indicate the pulling direction of each muscle. Muscle FCU was deactivated prior to application of the optimization process; its pulling direction is shown as a light, dotted line. Only in the midrange posture is ECU separated from both its nearest neighbors (ECRB and FCR) by a rotational distance of >90°. Hence, the double-peaked activation function is observed in this posture.

how the activity of primate MI neurons varied as the cosine of the angle between the neuron's preferred direction and the direction of planar arm movements. Later work extended similar results to three-dimensional movements (Georgopoulos et al. 1986; Schwartz et al. 1988). Georgopoulos (1988) and Hoffman and Strick (1999) have suggested that the cosine-like recruitment of some muscles is a reflection of similar behavior in neuronal populations in the brain. Although this provides an immediate causal explanation of the observed recruitment patterns, our results demonstrate that this may in fact be the result of an optimization process that includes minimization of muscle activation.

Others, including Mussa-Ivaldi (1988) and Zhang and Sejnowski (1999), have also argued that cosine-like activation could result from effort-related or computational constraints. More recently, Todorov (2002) examined the effects of noise on the optimal selection of muscle activation patterns in an isometric force production task in humans. In his corresponding model, he assumed signal-dependent noise in which the magnitude of muscle noise increased with the magnitude of the motor command (Berthier 1994; Harris and Wolpert 1998). The optimal muscle activation vector for redundant muscles distributed the responsibility of actuation across the available muscles. Furthermore, he demonstrated that his optimal control formulation combined with the noise model reduced to a minimum squared force error criterion, and that this criterion in turn yielded a cosine-like recruitment of muscles.

Our model predicts under certain circumstances a nontrivial deviation from the truncated cosine muscle activation pattern. When a muscle's pulling direction differs from both of its neighbors by an orientation greater than 90°, the model predicts a double-peaked activation pattern in which the valley between the peaks corresponds to the muscle's pulling direction. Experimental verification of this prediction would lend further support to the idea that cosine-like recruitment of muscles (and quite possibly cortical cells) is not necessarily an intrinsic mode of behavior, but instead results from constraints placed on the generation of movement.

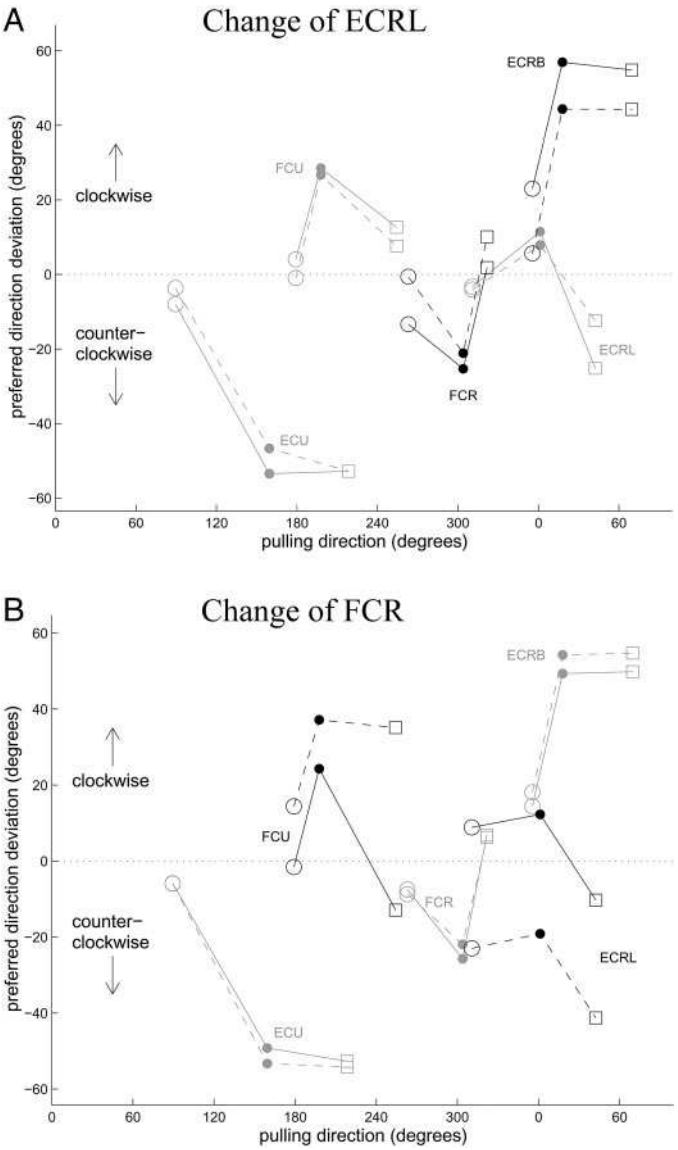

FIG. 11. Changes in preferred direction deviation due to alterations in the pulling strength of ECRL (*A*) and FCR (*B*). Muscle and posture notation is the same as in Fig. 8. Solid lines correspond to the case in which muscle strength has been increased by a factor of 50%; dashed lines represent the case of reducing muscle strength by 50%. Immediate neighbors of the affected muscle are drawn in black; remaining muscles are drawn in gray.

The model presented in this paper also predicts systematic deviations between a muscle's direction of action (the pulling direction) and the movement direction at which the muscle is maximally activated (the preferred direction). Furthermore, the model predicts that the relationship between preferred and pulling direction will change for many muscles as the wrist configuration is altered from pronation to supination. We explain this effect as an interaction of the minimum effort criterion with the fact that muscle pulling directions are not evenly distributed, and that this distribution changes with wrist configuration. This is consistent with the Flanders and Soechting (1990) notion that muscles in some cases must be recruited in directions different from their pulling direction to balance the action of other muscles.

While our model offers a possible explanation as to the strategies the brain might use in recruiting muscles, the model is rather abstract. In particular, we focused on a static version of the task in which the model is responsible for producing a quantity that is only cursorily related to the total agonist activation. Furthermore, we assumed that individual muscles produce straight-line movements in wrist joint space and that their action is independent of one another. Hoffman and Strick (1999) detailed the temporal recruitment of muscles during both the agonist and antagonist phases of movement. In particular, they observed not only a modulation of EMG magnitude with the direction of wrist movement, but in some cases also observed changes in the timing of the peak activation of the agonist EMG burst. In continuing modeling work, we plan to address these temporal and dynamic issues. In particular, we see the stretch reflex as playing a critical role in specifying the timing and magnitude of the antagonist muscle burst (Houk et al. 1999).

Flanders and Soechting (1990) examined the recruitment of a variety of shoulder and elbow muscles in an isometric force production task in free space. The activation of most muscles as a function of force direction in a plane was best described by a sum of two (and in a few cases, three) truncated, offset cosine functions. In many cases, the pair of cosines were offset by approximately 180°, indicating a co-contraction of opposing muscles that may serve to balance the action of other muscles or to stabilize the joint. They argued that the use of a minimization of effort approach to resolving muscle recruitment redundancies does not properly account for this observed co-contraction. While our model does not exhibit this co-contractive behavior, the use of such an effort-based criterion does recruit muscles so as to properly balance the forces produced by the other muscles. Furthermore, one could imagine in the future including other optimization terms that introduce other task constraints, such as postural stability.

As shown by the sensitivity analysis, altering the mechanical advantage of a muscle can affect the behavior of the preferred directions of muscles with neighboring pulling directions. In its current form, the model assumes that all muscles pull with equal strength. The similarities between the model muscle activation patterns and those described in Hoffman and Strick (1999) suggest that this was a reasonable assumption. However, there are differences that can be partially accounted for by calibrating the pulling strengths of the model muscles to better fit the strength and mechanical advantage of the muscles. Even though such a calibration might produce a better fit to the data (e.g., a calibration procedure similar to that of Buchanan et al. 1993), our sensitivity analysis indicates that the qualitative behavior of the preferred directions will not change dramatically. This is the case because the relative muscle pulling directions (and not their strengths) dominate the selection of the preferred directions.

Buchanan and Shreeve (1996) presented a model of muscle recruitment in isometric force production tasks involving either the wrist or the elbow. The model included a more detailed account of the path taken by each muscle and thus better accounted for moment arm differences. In addition, the model also took into consideration the differences in the muscles' ability to produce forces. With this model, Buchanan and Shreeve (1996) compared the use of a variety of likely cost functions in the selection of muscle activation levels (including sum squared force and sum squared stress). They observed that recruitment patterns generally followed a cosine-like behavior.

Most importantly, they demonstrated that the choice of cost function did not significantly alter the muscle preferred directions. However, the authors did not examine the issue of shifting pulling directions with changes in wrist configuration.

Citing concerns about the difficulty of identifying an optimality criterion, the uniqueness of this criterion, and the failure of certain criteria to predict muscle activation patterns (specifically, total force and total fatigue), Theeuwen et al. (1996) alternatively chose to directly estimate the relative contribution of individual motor units to torques applied by the arm. In this approach, paired observations are first made between motor unit activity and the resulting isometric torques. Taking into account the mechanics of muscle action across the joints, a singular value decomposition algorithm was then employed to estimate the contribution made by each motor unit to the net measured torque. We view this work as quite compatible with ours—the technique of Theeuwen et al. (1996) allows one to construct a high-quality model of the transfer function from motor unit activation to joint action. With such information, it becomes possible to ask more precise questions about what quantities might be optimized and to make stronger predictions about muscle activation patterns that might result under novel situations.

In this paper, we drew on the results of Buchanan and Shreeve (1996), Pedotti et al. (1978), and Collins (1995) in selecting the total squared muscle activation criterion. However, we do not wish to argue for the brain's use of a particular minimization criterion in resolving redundancies. Engelbrecht (1999) reminds us that optimality criteria can have *descriptive power* without necessarily providing a direct explanation of a phenomenon. We believe that our results suggest (in a testable manner) that the total squared activation criterion does show utility in describing muscle recruitment patterns.

In continuing work, we are examining the role of primary motor cortex in the recruitment of wrist muscles during this task. Kakei et al. (1999) have recorded from MI as wrist movements are made and have observed that a reasonable proportion of cells are recruited in a muscle-centered coordinate system. However, approximately one-half of the task-related MI neurons reflected a visual (or extrinsic-like) coordinate system. Although it has been argued that this is indicative of a serial coordinate transformation process that takes place within MI (possibly with the assistance of other brain regions), our ongoing modeling work indicates that extrinsic cells can be directly involved in the recruitment of muscles (Shah et al. 2002). This has important implications for how quantities (state variables) are represented and utilized in the brain.

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