A Model of Wrist Movement Representation in Primary Motor Cortex (DRAFT - please do not distribute)

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Abstract

In executing a voluntary movement, we are faced with the problem of translating a specification of the movement in task space (e.g. a visual goal) into a muscle recruitment pattern. Among many brain regions, the primary motor cortex (MI) plays a prominent role in the specification of arm and hand movements. Early experiments suggested that individual MI cells contribute to movements in a visual-centered (or extrinsic) coordinate system. Subsequent experimental and theoretical work have argued for a muscle-centered encoding of movement by MI cells. However, in a recent two-dimensional wrist step tracking experiment, Kakei et al. (1999) observed both extrinsic-like and muscle-like task-related cells in MI. Thus result was interpreted as evidence for a cascade of transformations within MI from an extrinsic representation of movement to a muscle-like representation. This paper presents a model which examines the complexity of the transformation from the extrinsic visual space to the intrinsic muscle space that implements the wrist movements on which Kakei et al. (1999) focused. We demonstrate that, given a realistic extrinsic-like representation of movement, a simple linear network is capable of representing the transformation from the extrinsic-like cells to the necessary muscle activation pattern. This suggests that cells exhibiting extrinsic-like qualities can be involved in the direct recruitment of spinal motor neurons. These results call into question models that presume a serial cascade of transformations that terminates with MI pyramidal tract neurons (PTNs) that vary their activity exclusively with muscle activity.

1 Introduction

The primary motor cortex (MI) plays an important role in the control of voluntary movement. Early studies provided some evidence that single neuron activity recorded in MI was related to hand movements in a planar center-out reaching task (Georgopoulos et al., 1982) and a similar task in three-dimensions (Schwartz et al., 1988). The activity of neurons during these tasks was described as varying with the cosine between the neuron's *preferred direction* and the direction of movement in extrinsic space. Hand movement direction was approximated as the sum of the preferred directions of neurons weighted by their magnitudes of activities (Georgopoulos et al., 1982, 1986). This type of coding is referred to as *population coding*, and the overall direction of movement is the *population vector*. The authors of these studies suggested that a significant portion of MI neurons may encode movement in an *extrinsic* space, in which extrinsic movement rather than muscle activity levels or joint angle deviations are represented in MI.

In the center-out tasks used in the studies referred to above, the initial position of the hand did not change; one could not distinguish between direction of hand movement and the unique pattern of muscle activation or joint deviations required to make that movement. To study a broader range of movements, Caminiti et al. (1990, 1991) devised an experiment in which the primate performed a center-out task originating from different areas of extra-personal space. While the preferred directions of most individual cells in MI and the premotor cortex changed as the origin of movement in space changed, the population vector was still a reliable indicator of direction of hand movement. Furthermore, the shift in preferred directions of the cells as a whole roughly followed the shift in shoulder angle required to start the center-out task in a different area of space. Caminiti et al. (1990, 1991) proposed that both movement direction and position of the arm in space are represented in the activity of MI and premotor cortex cells. Under this representation, the visual information of the target, and hence the extrinsic direction of movement, is given in polar coordinate system centered at the shoulder.

Other parameters related to the kinematics of movement, such as velocity and acceleration, may also be represented in the activity of MI neurons. Moran and Schwartz (1999) and Schwartz and Moran (2000) showed that a model of MI neural activity as a function of speed as well as direction described MI neural activity in a center-out task well. Ashe and Georgopoulos (1994) proposed a multiple linear regression model including target direction, velocity, position, and acceleration in describing MI neural activity. It was found that all four parameters contributed to describing the activities of most of the MI neurons recorded in Georgopoulos et al. (1982), with target direction contributing the most, followed by velocity, position, and acceleration. These studies suggest that single neuron activity in MI may capture several parameters simultaneously.

To separate actual hand movement from what causes it – application of force – researchers have performed isometric force studies, in which a primate applies directional force to a stationary object with its hand. Georgopoulos et al. (1992) trained primates to apply directional force on an isometric object subjected to a bias force to produce a net force (applied force plus bias force) in a specified direction. MI neurons were found to be directionally tuned in the direction of the net force, not applied force. Sergio and Kalaska (1997) examined MI neural activity in the primate trained to exert directional isometric forces with its hand at different spatial locations. The activity (and preferred directions) of many MI neurons changed with the change in spatial location. This change in activity was similar to the change in activity of arm muscles during the task, suggesting that MI neuronal activity may include a representation of muscle activity. In comparing the activity of an MI neuron during isometric force output with its activity during actual movement, Sergio and Kalaska (1998) showed that while an MI neuron's activity between the two tasks was similar before the actual onset of force, it differed after force onset. Although the authors of these studies may provide conflicting interpretations, these studies support the idea that some MI neurons may represent movement-related parameters, such as force, other than kinematics.

While an extrinsic representation of movement in MI seems to follow from the results of many of the studies outlined above, representations of movement in *intrinsic space*, such as muscle activity or joint angle deviation, should not be excluded. For example, Mussa-Ivaldi (1988) developed a model in which neural activity was dependent on muscle shortening velocity rather than movement direction. In this framework, muscle shortening velocity, muscle moment arms, joint angles, and hand movement were all linearly related. A cell's preferred direction was related to the joint configuration and muscle moment arms. Because different movement directions in Georgopoulos et al. (1982) originated from the same starting location, cellular activity as a function of muscle shortening rates was mathematically equivalent to activity as a function of movement direction for the task described in Georgopoulos et al. (1982). Mussa-Ivaldi (1988) showed how a *muscle space* representation of movement can describe the MI neural activity from Georgopoulos et al. (1982), which was used by Georgopoulos et al. (1982) to argue that MI represented movements in an *extrinsic space*.

Several other studies suggested that neurons in MI encode movement in intrinsic space. In comparing onset time and activity of MI neurons with onset time and electromyographic activity (EMG) of elbow and shoulder muscles during movement, Scott (1997) showed that MI cell activity correlated with muscle EMG activity. In studies by Scott and Kalaska (1995, 1997), a primate varied its arm configuration but performed the same hand trajectory. During this task, the activity and preferred directions of many MI cells differed as arm configuration changed. A model of cellular activity based on hand movement direction could not account for these changes while models based on joint kinematics or joint torques could (Scott and Kalaska, 1997). However, the authors were careful to point out that these results do not conclusively show that MI encodes movement in a specific space; they do show that representation of hand movement in MI may be more complicated than previously thought. In another study, Ajemian et al. (2000) showed how describing MI neural activity with joint angle-based preferred directions fit the data of Hocherman and Wise (1991) better than if the PDs were based in extrinsic spaces. Because MI sends projections directly to the spinal cord, among other areas, the idea that MI represents movement in an intrinsic space (that the neural activity covaries with what it controls) is an attractive one.

Most of the studies outlined above support the notion that MI encodes movement in a certain space, be it extrinsic or intrinsic. However, a recent study (Kakei et al., 1999) provided surprising evidence clearly showing the existence of both extrinsic-like *and* muscle-like MI neurons during a simple wrist movement task. The existence of both types of neurons may support the theory that a serial processing scheme takes place within MI. Under this type of processing, MI transforms an abstract, extrinsic representation of movement (through a population of extrinsic MI neurons) into an intrinsic space (through a population of intrinsic MI neurons) (Kakei et al., 1999). This process may take multiple steps, but eventually ends in a muscle space representation of movement which send projections through the pyramidal tracts to command muscles.

This serial processing scheme may be supported by studies that investigate the timing of MI neural activity relative to movement (for further review, see Caminiti and Johnson 1992). In a study by Fu et al. (1995) involving a center-out reaching task with varying distances, some MI neurons were shown to be modulated by target direction, some by target position, some by distance of movement, and some by more than one of these parameters. Fu et al. (1995) showed that highest modulation of a neuron by target direction occurred slightly before movement onset, while highest modulation by target position occurred after movement onset; highest modulation by target distance occurred last. These results imply that neural activity in MI may sequentially represent different aspects of movement, though direct evidence for a coordinate transformation is not seen.

A serial processing scheme is appealing because it is straightforward and offers a single mechanism for controlling movements. It also implies that the only projections MI sends to the spinal cord to control muscles arise from neurons that explicitly encode movement in muscle space. However, the complex architecture and neural behavior of the brain allows for the possibility of non-serial processing schemes (Kalaska and Crammond, 1992). Is it necessary for neurons that command muscles to show activation patterns very similar to that of the muscles they command? Is it possible for populations of MI neurons that represent movement in different spaces, such as extrinsic space, to each *directly* activate muscles for a given movement? We suggest that rather than requiring the progression of several stages of a serial coordinate transformation, the activity of a population (or populations) of MI neurons recruited for a certain task is associated with the appropriate muscle activations for that task. Figure 1 illustrates a serial processing scheme (left) versus a more flexible processing scheme (right). For simple or well learned tasks that are best planned in an extrinsic space, a population of extrinsic MI neurons may be able to directly activate the muscles appropriately by using the numerous connections between them and the spinal neurons that control the muscles. Neurons that encode movement in other coordinate spaces may also be recruited and work in parallel to control movement, but the stringent structure and multiple steps imposed by a serial processing scheme is not required.

While we suggest that different populations of MI neurons that represent movement in different spaces can each directly command muscles, an extreme interprettation of this is that only one fairly extrinsic population of neurons is needed to command muscles for certain movements. We examine the feasibility of this through a neural network model inspired by the work of Kakei et al. (1999) and Hoffman and Strick (1999), which are related studies that investigated how primate wrist muscle activity and MI neural activity varied during a 2 degree-of-freedom (DOF) wrist movement task. Using the model presented in this paper, we show that it is computationally possible for the population of extrinsic-like neurons to directly control muscles appropriately. The model produces muscle activation patterns that produce an end-point of movement near the desired targets and are similar to those recorded during the task. These results suggest that this may be a plausible coding scheme.

2 MI and Muscle Involvement in the Production of Wrist Movements

Hoffman and Strick (1999) and Kakei et al. (1999) recently described a step tracking task in which human and monkey subjects moved a manipulandum with the wrist in order to control the movements of a cursor 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 pronation, supination, or midrange posture (see figure 2). 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 upon the subject) which lay 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 wrist muscles. The muscles exhibited a typical two-phased behavior, with agonist muscle bursts initiating the movement; these were followed several hundred milliseconds later by antagonist braking bursts.

Examining the peak agonist phase muscle EMG level as a function of movement direction, Hoffman and Strick (1999) observed that muscle recruitment followed a cosine-like behavior. Figure 3 shows the muscle activity patterns for ECU and ECRB from a typical monkey subject. Also shown are the best-fit cosine functions for each case. The peak of the fitted cosine defines the muscles *preferred direction* (PD) of activation. The monkey ECRB muscle exhibited both positive and negative EMG levels; these levels were relative to a baseline of

Muscle	pronation	midrange	supination
1 Extensor Carpi Ulnaris (ECU)	89.4	159.4	218.6
2 Extensor Carpi Radialis Brevis (ECRB)	355.5	17.9	69.6
3 Extensor Carpi Radialis Longus (ECRL)	310.7	1.2	42.4
4 Flexor Carpi Radialis (FCR)	263.0	313.9	321.8
5 Flexor Carpi Ulnaris (FCU)	179.1	197.8	254.3
6 Abductor Pollicis Longus (APL)	280.5	341.4	8.1

Table 1: Average pulling direction for the six wrist muscles in each of the three wrist postures, as reported by Hoffman (1999). Pulling direction was measured by stimulating the muscle (on the right hand) and observing the direction of wrist movement within 50 msec of movement onset (Hoffman and Strick, 1999). Directions are in degrees within an extrinsic coordinate system where $0°$ is "up," $90°$ is "right," $180°$ is "down," and $270°$ is "left." This orientation is the same as a the numbers on a 12-hour analog clock. Wrist flexion in pronation cooresponds to a movement towards $180°$; wrist flexion in midrange corresponds to a movement toward $270°$; wrist flexion in supination corresponds to a movement to $0°$.

activity that was present when the monkey was holding the cursor at the starting location; the negative EMG was a decrease in activity relative to this baseline.

The contribution to wrist movement by each muscle, referred to as the *muscle pulling direction*, was determined by individually stimulating each wrist muscle as the monkey held the manipulandum at the central position and observing immediate cursor movement. Note the distinction between the muscle pulling direction and the muscle preferred direction, defined in the previous paragraph. Average pulling directions (in extrinsic space) for six muscles and three postures is shown in table 1 (Hoffman, 1999). As the wrist posture changed from pronation to supination (a rotation of $180°$), the pulling directions of the muscles rotated within the range of $74°$ to $130°$.

Of particular note, some muscles were recruited most strongly for directions that differed significantly from their pulling direction. Figure 4 shows polar plots of muscle activation as a function of movement direction. Measured pulling directions are indicated as short open arrows; calculated preferred directions are given as long closed arrows. The pulling and preferred directions of ECRB and ECU differed by as much as $45°$, whereas the pulling and preferred directions of ECRL and FCR differed by only a few degrees.

The wrist step-tracking task distinguished three coordinate spaces. *Extrinsic space* was represented by the movement of the cursor and was unaffected by wrist posture. An upward movement of the wrist in pronation (extension of the wrist) resulted in the same cursor movement as an upward movement of the wrist in supination (flexion of the wrist). *Joint* *space* was defined by wrist flexion/extension and radial/ulnar deviation. Flexion of the wrist in pronation resulted in an downward movement of the cursor while flexion of the wrist in supination resulted in a upward movement of the cursor. *Muscle space* was defined by how the muscle preferred directions (not their pulling directions) rotated as the wrist posture rotated. As the wrist rotated 180° from pronation to supination, muscle PDs rotated between 46° and 90°. (Kakei et al., 1999).

It has been suggested that the cosine tuning and other properties of muscle activity may be a reflection of the broad neural coding in MI (Hoffman and Strick, 1999). In order to understand the role of MI in driving the wrist muscles, Kakei et al. (1999) recorded the activities of single neurons in the hand area of MI. Of the 125 movement-related neurons recorded, 88 were directionally tuned in all three wrist postures. Neurons were labelled *extrinsic-like*, *muscle-like*, or *joint-like*, depending on how their PDs rotated as wrist posture rotated 180° from pronation to supination. Because categorization of neurons were based entirely on how their PDs rotated, the suffix "-like" was explicitly included. If the preferred direction of a neuron did not change much with wrist posture (between $-20°$ and $35°$), it was labeled extrinsic-like. The activity of some neurons in this category was modulated by wrist posture; their overall activity may be greater in one wrist posture than another. Extrinsic-like neurons comprised about 50% of the neurons recorded. If the preferred direction of a neuron shifted between 40° and 110° as the wrist rotated from pronation to supination, it was labeled muscle-like because of the similar shifts in muscle preferred directions. These neurons comprised about 32% of the neurons recorded. If the preferred direction of a neuron shifted about 180° as the wrist rotated from pronation to supination, it was labeled joint-like. None of the neurons recorded fell under this latter category. The remaining neurons were not easily categorized. Kakei et al. (1999) found no significant difference in the spatial distribution or the temporal dynamics of the extrinsic-like and the muscle-like neurons. The presence of both extrinsic and intrinsic neurons led Kakei et al. (1999) to suggest that a serial processing scheme was implemented in MI. This implies that only intrinsic neurons (such as the muscle-like MI neurons) can be pyramidal tract neurons (PTNs) and send direct projections through the pyramidal tract to the spinal motor neurons. If PTNs consisted of only intrinsic neurons, one would expect a spatial and temporal distinction between the intrinsic and extrinsic neurons. However, Kakei et al. (1999) found no such difference difference between the extrinsic-like and muscle-like neurons.

3 Description of the Model

As outlined in the introduction of this paper, we suggest an alternative to a serial processing scheme in which extrinsic MI neurons are merely an early stage in a series of coordinate transformations that result in MI neurons encoding movement in muscle space. The results of Kakei et al. (1999) can be interpretted to support the serial processing scheme. However, we suggest that it is computationally possible for populations of MI neurons recruited for a task, including extrinsic-like neurons, to each *directly* command muscles for certain tasks. To show this, we have created a neural network model in which a population of extrinsic-like neural units (referred to simply as "neurons" hereafter) directly activate muscle units (referred to simply as "muscles" hereafter). This model is based on the physiology and components studied in Hoffman and Strick (1999) and Kakei et al. (1999) and attempts to simulate the wrist step-tracking task described in these studies.

The architecture of this network is shown in figure 5. The extrinsic-like neurons used in this network behave like those recorded in Kakei et al. (1999): their PDs are in extrinsic space, but their activities are modulated by wrist posture. Therefore, some neurons are more active when the wrist is in pronation than when it is in supination and vice versa. To create this behavior, a population of purely extrinsic neurons representing direction of the target (labelled *Target Direction* in figure 5) and a population of neurons representing wrist posture (*Wrist Posture*) determine the activity of the population of extrinsic-like MI neurons (*MI*). Each extrinsic-like neuron sends projections (K) directly to each of six muscles (*Muscles*), representing the muscles recorded from in Hoffman and Strick (1999) and Kakei et al. (1999). Each muscle pulls the wrist in its pulling direction (see table 1), depending on which of the three postures the wrist is in. The activity of these muscles determine extrinsic movement (*Reaching Direction*), analogous to the movement of the wrist and hence the movement of the cursor in Hoffman and Strick (1999) and Kakei et al. (1999). Through an error term that includes accuracy of movement, K is modified so that the activity of the MI neurons produces appropriate muscle activations. This training process is described in detail later in this section.

In the following paragraphs, vectors and matrices are in bold type while scalers and the elements of the vectors and matrices are in italics. For example, the array of MI neurons is denoted by **MI**, a vector of which element i is the activity level of neuron MI_i. The neurons in this model are non-spiking; their activities are a real value between zero and 1. This can be thought of as the firing-rate of the neuron. The Target Direction array has N neurons (we choose $N = 48$). Each unit is most active when the target direction is the same as its preferred direction (θ_{PD}) in extrinsic space. The preferred directions of these neurons are evenly distributed throughout the array. T_i, the activity of neuron i in the target direction array, is

$$T_i = e^{-\left(\frac{\theta_{PD_i} - \theta}{SD}\right)^2},$$

where θ is the direction of the target and SD defines the width of this Gaussian-like function (analogous to the standard deviation). This model uses an SD of 1.3 units, which produces a width at half maximum of 120°. We discuss the implications of this broad tuning function in the discussion. The N neurons in the target direction array project to the MI neuron array **MI**, which has $2N$ neurons. Each target direction neuron i projects to only two **MI** neurons (i and $i+N$). All connections from the target direction neurons to **MI** neurons are assigned a weight of $+1$.

The wrist posture is represented by a 2 element array of neurons, **wp**. **wp** depends on wrist posture and is assigned the following values:

$$\mathbf{wp} = \begin{cases} \begin{pmatrix} 1.0 \\ 0.0 \end{pmatrix} & \text{if pronation wrist posture} \\ \begin{pmatrix} 0.5 \\ 0.5 \end{pmatrix} & \text{if midrange wrist posture} \\ \begin{pmatrix} 0.0 \\ 1.0 \end{pmatrix} & \text{if supination wrist posture.} \end{cases} \tag{1}$$

Wrist posture neuron 1, wp_1, projects to **MI** neurons 1 through N and wrist posture neuron 2, wp_2, projects to **MI** neurons $N+1$ through $2N$. All projections from **wp** to **MI** have a weight of $-1/2$. Through the projections of the target direction array and wrist posture array to **MI**, the extrinsic-like behavior of **MI** is hardwired to represent both target direction in extrinsic space and wrist posture. The activity level of any **MI** neuron is determined as follows:

$$MI_i = \begin{cases} T_i + wp_1 & \text{if } T_i + wp_1 > 0 \quad \text{AND } 1 \leq i \leq N; \\ T_{i-N} + wp_2 & \text{if } T_{i-N} + wp_2 > 0 \quad \text{AND } N+1 \leq i \leq 2N; \\ 0 & \text{otherwise.} \end{cases} \tag{2}$$

The pattern of activity of the **MI** neurons behave similarly to the extrinsic-like neurons modulated by wrist posture recorded in MI by Kakei et al. (1999). Figure 6 shows how the activity level of an **MI** neuron varies with extrinsic target position. Although the activity of this neuron is modulated by wrist posture, its preferred direction is not modulated by wrist posture (and hence fits the "extrinsic-like" neuron catagory). Figure 7 shows the activity of the array of neurons in **MI** when the target is at $\theta = 180°$. As shown, the activity of the array of MI neurons is different for the three different wrist postures.

The $2N$ MI neurons, **MI**, directly project to an array of six muscles, **a**. The connection matrix from **MI** to **a** is referred to as **K**. There are no imposed constraints on the elements of **K**; they can be any positive or negative real value. Muscle activity is determined by MI neuron activity and **K** as follows:

$$\mathbf{a} = (\mathbf{K})(\mathbf{MI})$$

Figure 8 shows the muscle pulling directions for the six muscles of interest as unit vectors in the direction of their pulling directions. The extrinsic direction of action of each muscle can be described as a 2-element column vector, $\mathbf{P}_i^\rho$, where ρ is the wrist posture (pronated, midrange, supinated), and i is the muscle index ($1 \leq i \leq 6$). The distribution of pulling directions in extrinsic space is not uniform nor consistent between the three wrist postures. In addition, as the wrist rotates 180° from pronation to supination, the pulling directions only rotate between 74° and 130°. The pulling directions of each muscle are represented in figure 5 as the matrix $\mathbf{P}$, which changes with wrist posture.

Muscles contribute to the end-point of movement along their vector of action, where the length of the vector is proportional to the muscle's activation level, a_i. This is analogous to the muscle EMG level. Muscles are assumed to contribute to the movement end-point independently of one-another. Thus, the end-point of movement, $\mathbf{x}$, is determined by the weighted sum of the muscle pulling directions as follows:

$$\mathbf{x} \;=\; \sum_{i \in A} \mathbf{P}_i^\rho a_i,$$

where A is the set of six muscles. Note that only the end-point of wrist movement, not the actual path of movement itself, is simulated in this model.

In figure 5, $\mathbf{K}$ represents a plastic linear transformation from MI neuron activation to muscle activation. While $\mathbf{K}$ is modifiable, the the muscle pulling directions matrix, $\mathbf{P}$, is fixed to one of three matrices, depending on wrist posture. Thus, to produce appropriate muscle activity from MI neuron activity, the model iterively updates $\mathbf{K}$ based on an error term including three factors as follows: *i.* minimize error between movement end-point and target, *ii.* constrain all muscle activations to be positive, and *iii.* minimize total squared muscle activation. While criterion *i.* is an obvious goal, we included criterion *ii.* and *iii.* to ensure unique muscle activations for a desired movement as there are an infinite number of ways six muscles can produce as 2-DOF movement. Justification for the these criteria are described in detail in Fagg et al. (2001). Briefly, minimizing total muscle effort (criterion *iii.*) is a plausible strategy the brain might use in setting muscle activation patterns. Studies by Pedotti et al. (1978) and, more recently, Collins (1995), investigated different types of muscle-based optimization criteria and found that minimizing total squared force of the muscles provide reasonable predictions of muscle activity during one phase of movement. The constraint for keeping all muscle activities positive (criterion *ii.*) simply prohibits the muscles from pushing.

The initial elements of $\mathbf{K}$ are randomly chosen from a uniform distribution between $-1/2$ and $1/2$ (though a broader range yields similar results). A random $\mathbf{K}$ yields a random muscle activation pattern produced by **MI** and hence a random (and inaccurate) end-point of wrist movement. **K** is updated for each of 12 evenly spaced targets located on a circle of unit radius for each of the three wrist postures. This yields a total of 36 distinct conditions per epoch to be used in modifying **K**. Note that each condition is accompanied by a unique **MI** activation. The following paragraphs describe in detail how **K** is updated for each of the 36 conditions.

Optimization criteria *i.* and *iii.* lead to the following error function:

$$E(\mathbf{a}) = \frac{1}{2}\left\|\mathbf{x_t} - \sum_{i \in A} \mathbf{P}_i^{\rho} a_i\right\|^2 + \frac{\lambda}{2}\left\|\mathbf{a}\right\|^2, \tag{3}$$

where $\mathbf{x_t}$ is the target location, λ is a regularization parameter which has been set to 0.02 for the results reported in this paper, and $\mathbf{a}$ is the muscle activation vector.

To determine muscle activation values that satisfy the error criteria, a gradient descent method is employed. The error gradient with respect to muscle activation, a_j, is as follows:

$$\frac{\partial E}{\partial a_j} = -\left(\mathbf{x_t} - \sum_{i \in A} \mathbf{P}_i^{\rho} a_i(t)\right)^T \mathbf{P}_j^{\rho} + \lambda a_j. \tag{4}$$

To constrain muscle activation levels to positive values, the error in muscle j is defined as:

$$e_j = \begin{cases} -\frac{\partial E}{\partial a_j} & \text{if } a_j > 0, \\ -a_j & \text{otherwise.} \end{cases} \tag{5}$$

If the muscle activation a_j is already positive, then the error e_j is $-\partial E/\partial a_j$. However, if a_j is negative, then e_j is set to $-a_j$ to force a_j towards zero activation (criterion *ii.*). In turn, e_j is used to modify the connection matrix **K** as follows:

$$\mathbf{K_{new}} \leftarrow \mathbf{K_{old}} + \eta(\mathbf{e})(\mathbf{MI}^T),$$

where η is a learning rate set to 0.02 in this model. This is not intended as a biologically based learning approach.

4 Results

Training **K** to within a reasonable movement accuracy and little change in its elements occurred within 100,000 epochs. Although different initial conditions did not yield a unique **K**, they did yield very similar muscle activation patterns, indicating a unique solution for muscle activation. This indicates that the error term the model used provided sufficient criteria to produce a stereotyped muscle activation pattern for a given movement. As will be shown in the following paragraphs, these muscle activation patterns are similar to EMG recordings, suggesting that the criteria used may represent a plausible strategy the central nervous system uses in controlling movements.

Figures 9 and 10 illustrate how the activity of modeled muscles ECRL, ECRB, FCR, and ECU vary with target direction with the wrist in the midrange posture. These four muscles were analyzed in Hoffman and Strick (1999) and the format of these figures are similar to figures 3 and 4 for comparison of model muscle activations with actual EMG recordings. Muscle activity versus target direction follows a cosine-like shape for all six muscles in all three wrist postures. Figure 9 shows normalized model muscle activity versus target direction for muscles ECU and ECRB in the midrange wrist posture. This figure includes the best fit of the function $B\cos(\theta - C) + D$ to the muscle activity. The preferred direction of the muscle is defined to be the parameter C. As in Hoffman and Strick (1999), low muscle activation levels (< 0.05 in our analyses) were given a zero weight in the fitting process. This is done because muscle activity levels are not allowed to fall below zero.

Figure 10 shows normalized model muscle activity versus target direction as polar plots for muscles ECRL, ECRB, FCR, and ECU in the midrange wrist posture. Included are the pulling directions (short open arrow) and calculated preferred directions (long closed arrow) of the muscles. In all four cases, the preferred direction deviates from the pulling direction. This discrepancy between pulling directions and preferred directions is also seen in the EMG recordings from Hoffman and Strick (1999). This difference is the result of the uneven distribution of pulling directions of the muscles (Fagg et al., 2001). If there is a large gap between the pulling directions of two muscles, then the muscles have to devote additional activity to pulling against each other in order to reach a target located within the gap. Thus, the preferred direction of a muscle will tend towards this gap.

The range of target directions for which a muscle is at least moderately active (referred to as the "range of activation") is not the same for all muscles. In figure 10, the range of activation of muscle ECRL is less than that of muscles ECRB, FCR, and ECU. Interestingly, a similar range of activation for the same four muscles is seen in figure 4. Comparison of figures 9 and 10 with figures 3 and 4 shows how the muscle activation patterns produced by the model are similar to those produced by recorded EMG activity of monkey muscles during the step-tracking task (Hoffman and Strick, 1999).

Figure 11 compares the preferred direction of the muscles ECRL, ECRB, FCR, and ECU in the midrange wrist posture as calculated by this model with those calculated from EMG recordings from human and monkey wrist muscles (including inter-subject variation) during the step-tracking task (Hoffman and Strick, 1999). Although there are differences between the model preferred directions and those recorded by monkey and human subjects, there is reasonable agreement between experiment and model.

5 Discussion

In this paper, we suggest that populations of MI neurons that encode movement in different coordinate spaces can each directly control muscle activations. This coding scheme challenges a serial processing scheme in which extrinsic MI neurons provide input to more intrinsic MI neurons and only MI neurons whose activities covary with muscle activities could command muscle activations. A visual comparison of the two schemes is shown in figure 1. To show that our scheme is computationally possible, we have developed a neural network model in which extrinsic-like neurons rather than muscle-like neurons directly activate muscles in a simulated 2-DOF wrist movement task. The task, muscle action, and neural behavior used in the model are based on the results of recent studies by Kakei et al. (1999) and Hoffman and Strick (1999). In these studies, stereotyped muscle activation patterns, muscle pulling directions, and MI neurons that were described as "extrinsic-like" or "muscle-like" were identified. We chose to model only extrinsic-like neurons in controlling the muscles to show that neurons that code in spaces more abstract than muscle space can also command muscles. This is an extreme view in that only one type of neuron is used; populations of MI neurons that encode movement in other spaces working in parallel would facilitate control of movement.

The task to be modelled involved moving the wrist joint in one of 12 directions. The neurons used in this model behaved like the "extrinsic-like" neurons recorded in Kakei et al. (1999). They are capable of directly activating six muscle units, which represent the dominant wrist muscles identified by Kakei et al. (1999) and Hoffman and Strick (1999). These muscles are represented as vectors in the direction of the experimentally determined muscle pulling directions. A linear combination of muscle units, in turn, determines the end-point of wrist movement in this model. By modifying the connections between the MI neurons and muscles of the model, the array of extrinsic-like neurons produced muscle activation patterns that resulted in the desired end-point of movement and were similar to the EMG patterns recorded in Hoffman and Strick (1999). These results suggest that it is computationally possible for the extrinsic-like MI neurons to directly command muscle activation patterns as opposed to merely providing inputs for more intrinsic neurons.

An extreme interpretation of the serial processing scheme is derived from analogy with the robot control domain. In controlling the movements of a robot, it is often necessary to transform an extrinsic representation of movement (such as a visual cue) to a kinematic representation (joint position) and then into torques to be applied at the joints (via actuators). Many forms of robot control require some explicit representation of the different stages of the transformation. Although parallels can be drawn between the control of robot movement and human movement, the two systems may not necessarily employ the same method of control. There is no reason that the central nervous system should explicitly show evidence of the calculations required to transform extrinsic space into muslce space. The transformation process in MI can be simplified by taking advantage of the distributed processing nature of the central nervous system. Through population coding and cosine tuning, a large number of neurons encode a single variable (such as direction of movement). However, if a serial processing scheme is used, the only advantage in using population coding is to have redundancy in the system; a population of neurons encoding one variable is equivalent to one neuron encoding one variable. The serial processing scheme does not require a distributed system. Although the complete transformation from an extrinsic target representation to signals that drive the muscles must be computed for movement to occur in animals, intermediate steps of movement need not be explicitly expressed in neural activity. In particular, because there are so many more neurons than limb state variables, it is possible that the excess degrees of freedom can be leveraged to construct an expansive representation of the state, which in turn simplifies the transformation process.

Taking advantage of distributed processing would allow different populations of MI neurons to each directly control movement. MI neurons recruited for different tasks may represent movement in different spaces. For some types of movements, an extrinsic representation is most useful. Hogan (1988) reviewed evidence that planning simple hand movements, which involves many brain regions other than MI, in an extrinsic space fits a wider range of data than planning in an intrinsic space. Georgopoulos (1988) suggested that MI generates an abstract representation of movement. If the movement is well known or simple, the extrinsic neural activity may be sufficient to produce the proper muscle activation pattern, as demonstrated in this paper.

However, for some movements, a more intrinsic representation of movement may be most useful. Rather than reaching a certain target, the goal of the movement may be to deviate a joint angle. In this case, an intrinsic representation of movement in joint space, in which neural activity varies with joint angle deviation, would be recruited. An extrinsic representation of limb movement is not needed. Figure 12 illustrates how different pools of MI neurons, each of which directly commands muscles, may be recruited for different tasks. For some tasks, neurons from both pools may be recruited. In addition, two different tasks might require the same movement. In this case, two different populations of neurons would be recruited for controlling the same movement.

A single population of MI neurons that represents movement in one coordinate system may not be entirely sufficient for some movements. For example, the error between target and end-point of movement produced by the model was small, but non-zero. While adding more extrinsic-like neurons in this model would reduce this error by adding more DOF with which to work, adding neurons that encode movement in other coordinate spaces that work in parallel with the extrinsic-like neurons would also reduce error. The more flexible coding scheme allows for this and the fact that both extrinsic-like and muscle-like neurons were recorded in Kakei et al. (1999) may be taken as evidence supporting parallel processing.

The results of several experimental and modeling studies, outlined in the introduction of this paper, have been used to argue that MI encodes movement in a certain coordinate frame. While these studies show under which coordinate system MI neural activity during a particular task can be best described, one must be careful in forming a coding scheme based on them. In the model described in this paper, MI neurons that are described as "extrinsic-like" directly command muscles. While the activity of the MI neurons alone only indicates extrinsic target direction and wrist posture, one can directly calculate muscle activations from the MI neuron activity and the weights of the connections from the neurons to the muscles.

Several studies have used correlation methods to argue that neurons in the red nucleus directly code muscle activity (Gibson et al., 1985; Houk et al., 1987; Miller et al., 1993; Miller and Houk, 1995; Miller and Sinkjaer, 1999). MI and the red nucleus may be connected through positive feedback loops (Houk et al., 1993) and project towards similar areas of the spinal cord, indicating that these two areas may process movement similarly (Miller and Sinkjaer, 1999). In these studies, a monkey (in Houk et al. 1987, a cat was used) performed a reaching task and single neuron activity in the red nucleus and EMG signals from several muscles were recorded. Analog cross correlations between the neuron firing rate and kinematic variables and muscle EMGs over a period of several minutes for various time delays between the signals were performed. The correlations between neuron-muscle pairs were higher than correlations between neuron-kinematic variable pairs. For each neuron, a "functional linkage vector," of which element i was the peak cross correlation between the neuron and muscle i, was identified. This represented the activity of a neuron in muscle space. By studying how correlation values vary with time delays, how the functional linkage vectors behave with the task, and comparing neuron-muscle correlations with each other, these studies argued that neurons in the red nucleus may directly encode muscle activity. The results of Miller and Sinkjaer (1999) are consistent with the theory that the summed activity of red nucleus neurons determine the dynamics and activation of the muscles they control and that no additional transformation is needed. These studies provides evidence that red nucleus neurons may directly command muscles through motor neurons.

To determine what correlations could be found in the model presented in this paper, in which the behavior of MI neurons is "hard-wired" to be extrinsic-like, correlation coefficients were calculated for each MI neuron-muscle pair over all three wrist postures and all 12 target directions (36 conditions). The formula used to calculate the correlation coefficient between

MI neuron i (MI_i)and muscle j (a_j) is

$$crcf(MI_i, a_j) = \frac{\sum_{\theta \in \Theta}(MI_i - \mu_{MI_i})(a_j - \mu_{a_j})}{\sigma_{MI_i}\sigma_{a_j}},$$

where μ_{MI_i} is the average activation of neuron MI_i over all 36 conditions, μ_{a_j} is the average activation of muscle a_j, σ_{MI_i} is the standard deviation in MI_i neuron activation, σ_{a_j} is the standard deviation in muscle a_j activation, and the sum is over all target positions and wrist postures in the set Θ. This expression is a normalized correlation coefficient, so $-1 \leq crcf \leq +1$ for all pairs. A high positive correlation indicates that neuron MI_i is highly active over the same range of target positions as muscle a_j, while a high negative correlation indicates that neuron MI_i and muscle a_j are highly active at essentially opposite target positions. The correlations ranged fairly evenly between -0.5 to almost 1.

While a high positive correlation might be interpreted as the MI neuron coding in muscle space, in this model it merely indicates that the neuron and muscle happen to have similar preferred directions. For example, a high correlation ($crcf = 0.8488$) was found between neuron number 92 (out of 96) and muscle APL (number 6). Because the neurons were defined to have equally spaced preferred directions, MI neuron number 92 has a preferred direction of 345° while the preferred directions of muscle APL are 316.6° (in pronation wrist posture), 320.6° (midrange), and 354.9° (supination). Figure 13 is a scatter plot of the activities of muscle APL versus the activities of MI neuron 92 for all three wrist postures and all twelve targets. Simply put, as the neuron's activity rises, so does the muscle activity. This does not mean that the activity of the neuron and the muscle are modulated in the same coordinate frame. The **MI** array was explicitly defined to be directionally tuned in extrinsic space; the preferred directions of all the neuron units are in extrinsic space and do not vary with wrist posture or muscle activity. The neuron is activated in an extrinsic manner, but it directly drives the muscle. The high $crcf$ is a coincidence in this model.

It should be noted that this model has no time varying aspects, is very abstract, and thus the correlation coefficient is a simple calculation. The studies referred to above (Gibson et al., 1985; Houk et al., 1987; Miller et al., 1993; Miller and Houk, 1995; Miller and Sinkjaer, 1999) calculate correlations between neural activity and muscle activity over a time span of several minutes with a much more complex system, a more complex task, and performed a more complex analysis. In the case of this model, the high correlation alone may be misconstrued to indicate a similarity in coding schemes of the neurons and muscles. If the distribution of $crcf$s was heavily weighted towards $+1$ and the extrinsic-like behavior of the MI neurons were not known, then it would be reasonable to suggest that the MI neurons and muscles encode movement in the same coordinate frame. However the wide distribution of correlations from the results of this model discourages that reasoning.

The distributed processing nature of the central nervous system allows for seemingly hidden coordinate transformations to take place. This enables different populations of neurons, recruited for different tasks, to each participate in directly commanding muscles as in figure 12. A theoretical study by Sanger (1994) shows how a distributed representation of a variable (such as how direction of movement may be represented by the activities of a population of neurons) does not necessarily lead to a particular coordinate system. A simple linear mapping, which is used in this model, may be sufficient for transforming the representation of a variable from one coordinate system to another if certain conditions are met (for more, see Sanger 1994). As shown in this paper and Sanger (1994), the functional characteristics of MI neurons (how activity varies with movement) does not necessarily lead to a causal relationship (how movement is encoded).

The width of the tuning function for the motor cortical neurons in this model are set to have a full width at half maximum of about 120°, which corresponds to an SD of 1.3 in the Gaussian-like function used to define the tuning profile. The width of the tuning function was derived from a study by Thoroughman and Shadmehr (2000), which investigated how learning to reach in one direction in a viscous force field affects reaching in other directions. It should be emphasized that Thoroughman and Shadmehr (2000) investigated motor primitives, not the tuning properties of MI neurons. this study was used as a guide, but the tuning properties of cortical neurons is still an area of active research.

Several studies have investigated how the tuning function of neurons might affect the population code. A recent theoretical analysis (Zhang and Sejnowski, 1999) investigated how population coding accuracy is affected by the width of tuning functions of neurons. Zhang and Sejnowski (1999) found that for one dimensional features, such as direction, a sharper tuning curve provided greater accuracy. For two dimensional features, the tuning width had no effect on population coding accuracy (also see Zhang et al. 1998). For features that had three or more dimensions, a broader tuning curve increased accuracy. Zhang and Sejnowski (1999) also pointed out that a narrower tuning curve might require less energy as fewer neurons would be active. Another theoretical study showed that how distribution of noise varied with the tuning width had an effect on accuracy for neurons that encode one dimensional features (Pouget et al., 1999). The finding that sharper tuning curves increased accuracy for one dimensional features fits well with recent experimental work investigating tuning properties of MI neurons. Amirikian and Georgopoulos (2000) systematically studied the shape of the directional tuning profiles of monkey MI neurons while the monkey performed a center-out reaching task in 20 directions (every 18°). They determined that the full width at half maximum of the activities of MI neurons as a function of direction varied between 30° and 90°, with a median of 56°, which is much sharper than the cosine function originally used to describe them (Georgopoulos et al., 1982).

As shown by Zhang and Sejnowski (1999), a sharper tuning function provides a more accurate population code for neurons that encode one state variable. In the model described in this paper, the visual input neuronal units encode the single feature of direction of target. These neuronal units, along with wrist posture units, determine the activations of the MI neurons in the model. If tuning functions of the MI neurons are sharpened, the model will produce more accurate reaching movements. This is because there is less "cross-talk" between the input vectors that represent the activities of the array of MI neurons; changing the weights from MI neurons to muscles to correct errors for one target direction has less effect on changing the weights from MI neurons to muscles for another target direction. If more MI neurons were highly active for a given direction (as would be the case with a broad tuning function), it would be harder to develop an appropriate connection matrix to satisfy all error criteria. However, a broader tuning function increases the system's ability to generalize to tasks not explicitly learned (Thoroughman and Shadmehr, 2000), such as reaching in a target direction not previously trained with. Because a wide tuning function allows for generalization and makes the transformation harder, we used broadly tuned neurons in thie model to test its capabilities.

Future Work adn Conclusions

The level of abstraction of this model is very high. A model of muscle recruitment, described in detail in Fagg et al. (2001), was used to determine the muscle activation pattern for each target and wrist posture. This study investigated what strategy the brain employs in setting the activation levels of muscles to achieve the desired movement. To introduce as few assumptions as possible about muscle dynamics, we focused only on agonist activity and ignored the time-course or EMG activity. Hoffman and Strick (1999) showed that during the agonist phase of muscle activity during the step-tracking task, the peak EMG activity of each muscle occurred at the same time relative to movement onset. The magnitude of this activity was modulated by target direction. Thus, it seemed that this magnitude and not the timing determined wrist movement for this task. In the model presented in this paper and in Fagg et al. (2001), individual muscles are assumed to pull along straight lines in joint space, parameterized by wrist flexion/extension and radial/ulnar deviation. The model produced muscle activations as a function of reaching direction that were similar to those recorded in Hoffman and Strick (1999). However, there are also *time varying* activities of muscles involved in the wrist movement (Hoffman and Strick, 1999). Hoffman and Strick (1999) described other time varying properties of muscle activity that the model presented in this paper does not take into account. One area of future research with this model is to incorporate dynamical changes in muscle activity.

In this model, all muscles pull with equal strength in their pulling directions. However, it is likely the case that some muscles pull with greater strength than others. Several studies which estimate the force of wrist muscles (Buchanan et al., 1993; Chadwick and Nicol, 2000) could guide us in making the relative pulling strength of muscles more accurate. However, even with setting the pulling strengths of the muscles equal to each other, the model presented in this paper produces muscle activation patterns comparable to those recorded from monkey muscles. In addition, as shown in Fagg et al. (2001), the qualitative relationship between the muscle pulling direction and preferred direction remains largly intact when adjusting the relative strengths of certain muscles.

Several studies indicated that some MI neurons may encode several movement-related parameters (Caminiti and Johnson, 1992; Ashe and Georgopoulos, 1994; Fu et al., 1995; Moran and Schwartz, 1999; Schwartz and Moran, 2000). One key target parameter missing from neuronal representation in this model is distance to target. Although the error term includes a target position, which includes direction and distance, only direction and wrist posture are represented by the activity of the **MI** neuron array. Because each target is of unit distance away from the starting position in the task, a representation of distance is not required. However, in order to deal with more complicated movements, additional represenations of movement may be needed.

This paper describes the testing of only one part of the coding scheme we suggest MI may use: neurons directionally tuned in extrinsic space directly commanding muscles for simple movements. We also suggest that intrinsic neurons may be recruited and work in parallel with the extrinsic-like neurons. Different populations of MI neurons are recruited depending on the task. While multiple populations of MI neurons commanding muscles directly would facilitate movement, how would the brain determine when such a recruitment is necessary and what representation is most important? A more detailed model investigating how different types of neurons are used would add credence to this coding scheme.

6 Acknowledgments

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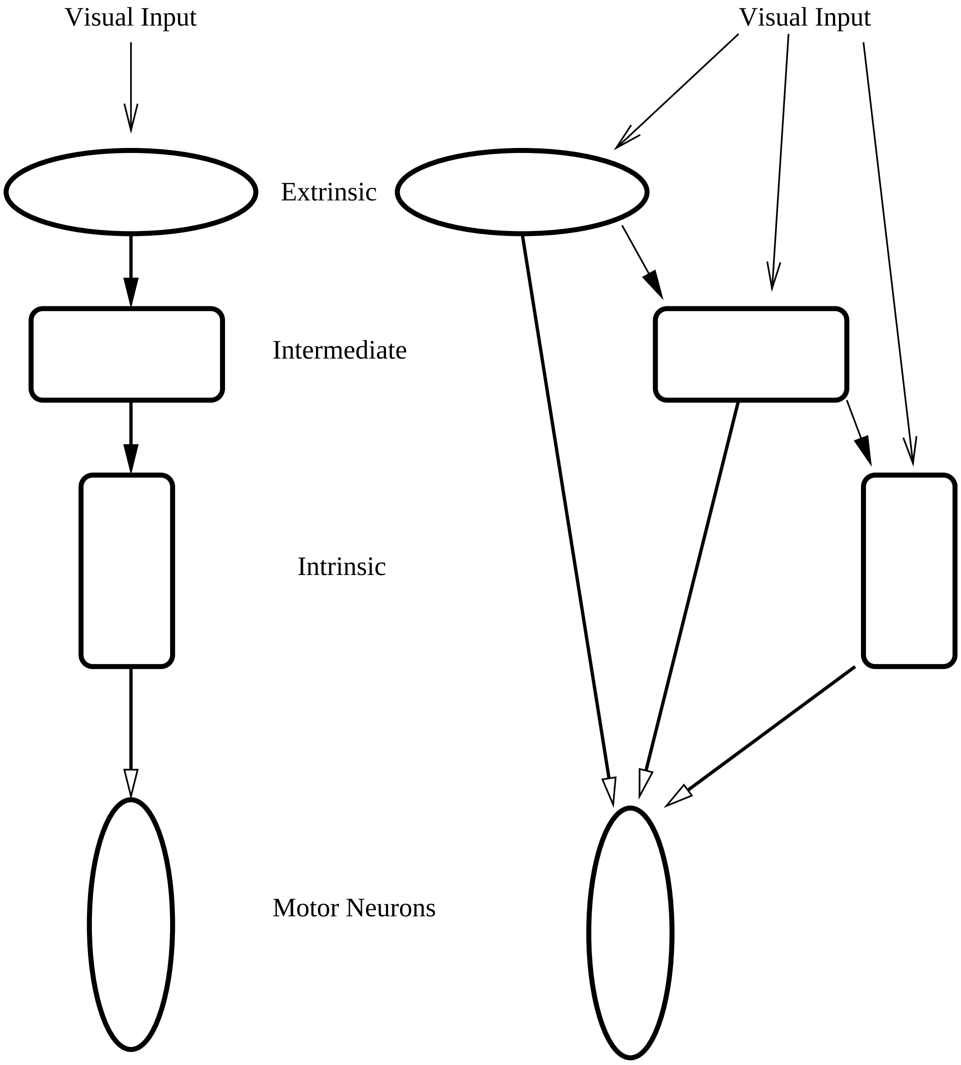

Figure 1: Graphic representation of a serial processing scheme (left) and a more flexible processing scheme (right). The different shapes represent seperate populations of neurons that code movement in different spaces, labled by the text in the middle. "Extrinsic," "Intermediate," and "Intrinsic" shapes represent MI neural populations; "Motor Neurons" shapes represent spinal motor neurons. The coordinate spaces on top are more extrinsic than the coordinate spaces on the bottom; vertical arrangement does not denote the passge of time. Open arrows represent projections from visual input to neural populations, closed filled arrows represent projections between MI neuron populations, closed unfilled arrows represent projections to spinal motor neurons.

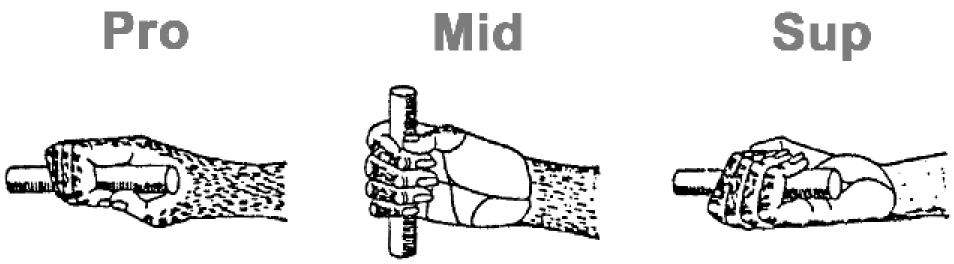

Figure 2: A schematic showing a monkey right hand gripping a stick in the pronation (left), midrange (middle), and supination (right) wrist postures. Adapted from Kakei et al. (1999).

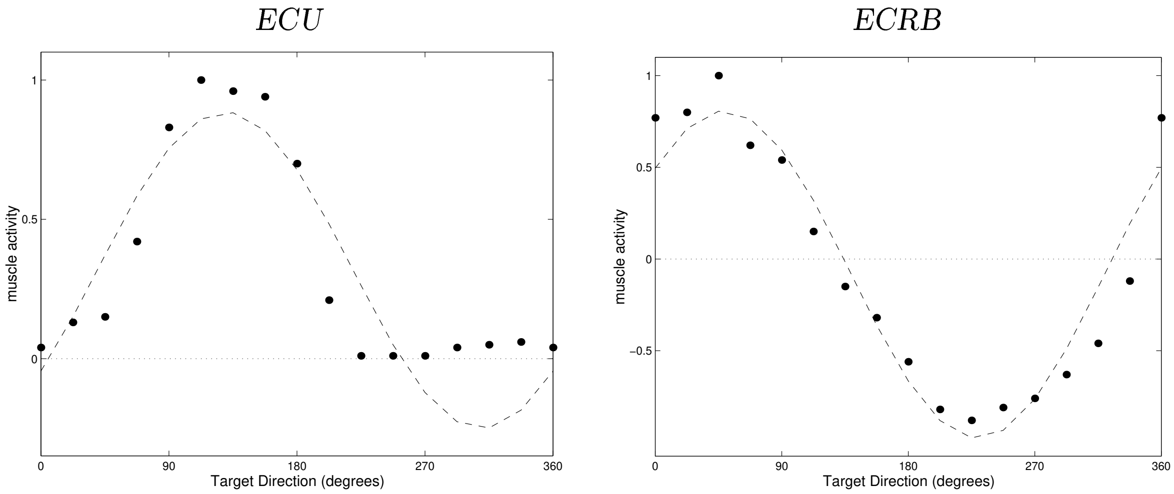

Figure 3: Peak agonist muscle EMG (normalized) as a function of target direction for muscles ECU and ECRB in the midrange wrist posture. Solid circles are muscle EMG recordings from a monkey subject performing the wrist step-tracking task. Dashed line is the best fit function $B\cos(\theta - C) + D$, where θ is target direction. Muscle preferred direction is defined to be the parameter C. Points where muscle EMGs are below 0.05 are given a zero weight in the fitting process. Horizontal dotted line at muscle activity = 0 is the baseline muscle EMG when wrist is in the neutral position (target is at center of circle). Negative activity for muscle ECRB represents a decrease from this baseline value. EMG data from Hoffman and Strick (1999) and Hoffman (2001).

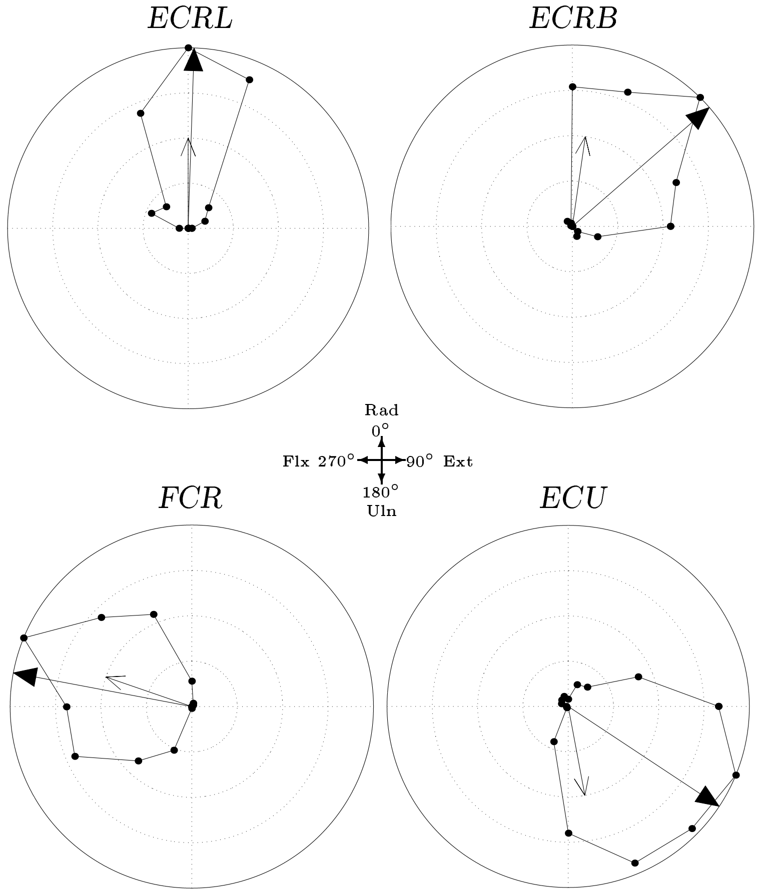

Figure 4: Normalized polar plots of peak agonist muscle EMG as a function of target direction for muscles ECRL, ECRB, FCR, and ECU in the midrange wrist posture. Solid circles connected by a solid line are muscle EMG recordings from a monkey subject performing the wrist step-tracking task. Short open arrows are muscle pulling directions. Long closed arrows are muscle preferred directions. The pulling directions are from a specific monkey and thus are not exactly the same as those from table 1. The 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 from Hoffman and Strick (1999) and Hoffman (2001).

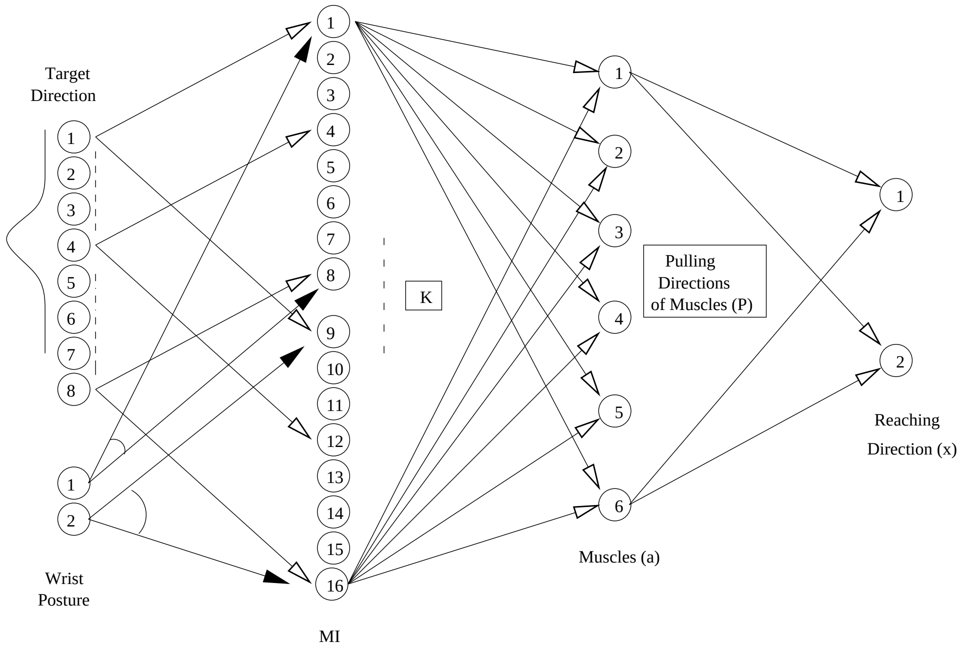

Figure 5: Architecture of this model with $N = 8$ for clarity. The "Target Direction" array represents neurons that encode extrinsic target direction. The curve to the left of the Target Direction array approximates th activation of the array of neuron units for a target direction near $\theta = 180°$. Each Target Direction neuron unit i connects only to the **MI** neuron units MI_i and MI_{i+N}. The "Wrist Posture" array represents the posture of the wrist. Wrist Posture unit 1 connects to **MI** neuron units MI_i through MI_N, while Wrist Posture unit 2 connects to **MI** neuron units MI_{i+N} through MI_{2N}. The "MI" array represents the **MI** neuron units. The "Muscles" array represents the muscle units (labeled **a** in the equations). Each **MI** neuron unit connects to each Muscle unit through the connection matrix **K**. The "Reaching Direction" array represents the wrist movement direction. Each Muscle unit is connected to each Reaching Direction unit through the connection matrix **P**. Full connections are not illustrated for clarity. Open arrows indicate excitatory connections while closed arrows indicate inhibitory connections. All units have linear activation functions except **MI**, which has a lower threshold of zero.

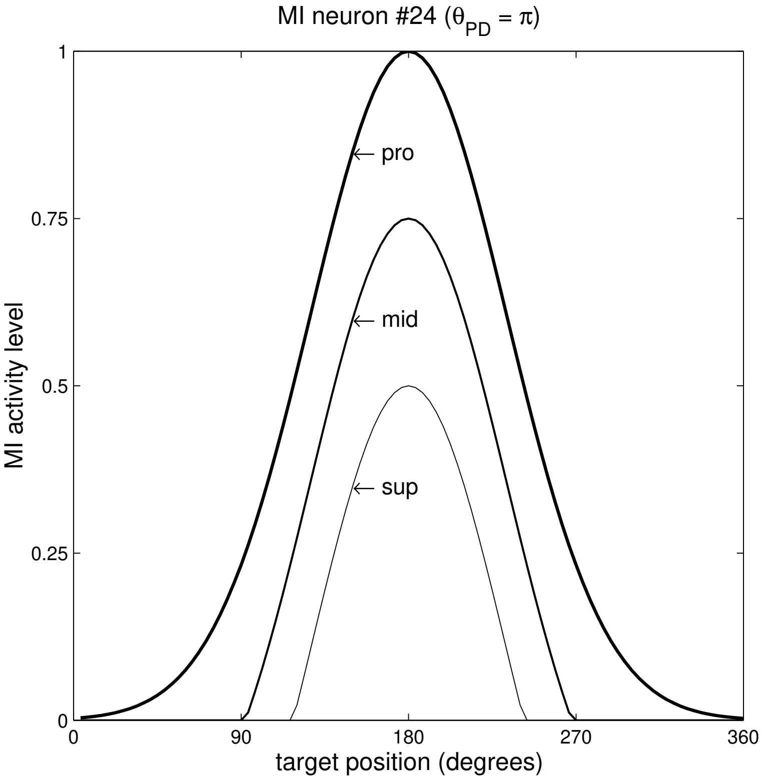

Figure 6: Activity of **MI** unit 24 ($\theta_{PD} = 180°$) as a function of extrinsic target position for wrist posture pronation (pro, thickest line), midway (mid, mid-weight line), and supination (sup, thinnest line). For this neuron, the curves are defined by the equation $e^{-((\theta_{PD_i} - \theta)/SD)^2}$, which defines the "Target Direction" array with an $SD = 1.3$. The equation is added to either 0 (for pro), -0.25 (for mid), or -0.5 (for sup), with the minimum value floored to zero. The PD of the neuron does not change with wrist posture, though the magnitude of activity does.

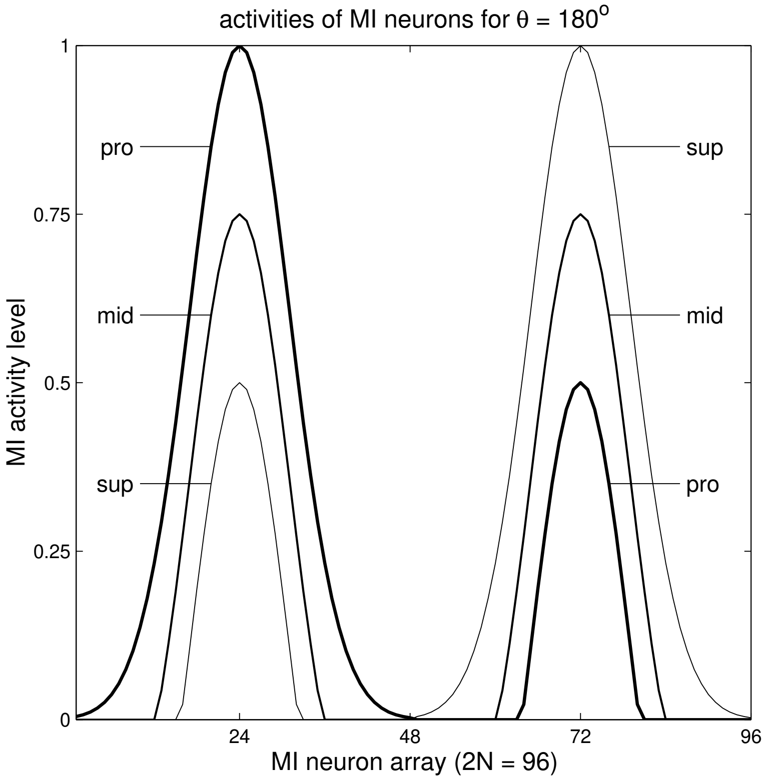

Figure 7: Activity of the array of **MI** neurons ($2N = 96$) for pronation (pro, thickest line), midway (mid, mid-weight line), and supination (sup, thinnest line) wrist postures when the target direction is $\theta = 180°$. For **MI** neurons 1 through 48, the activity in pro position is greater than the activity in mid, which is greater than the activity in sup. For **MI** neurons 49 through 96, the activity in sup position is greater than the activity in mid, which is greater than the activity in pro. Both extrinsic target direction and wrist posture is represented by the activity of this array of neurons. These curves are defined by $e^{-((\theta_{PD_i}-\theta)/SD)^2}$ with an $SD = 1.3$, with inhibitory inputs of 0, -0.25, or -0.5, depending on wrist posture. Activities have a lower limit of zero.

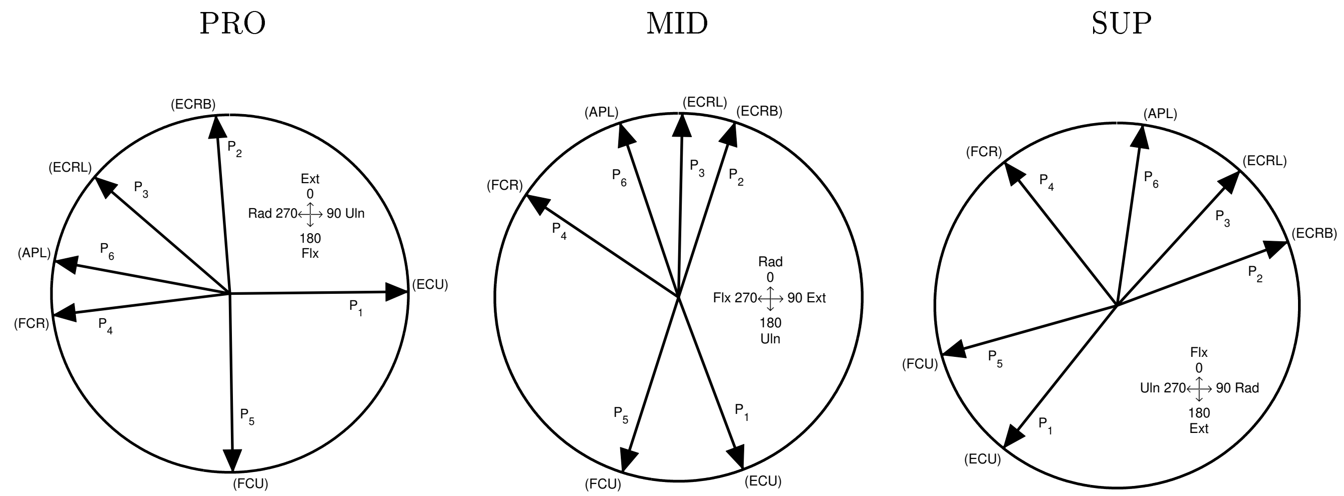

Figure 8: Pulling directions of the 6 muscles for pronation (left), midway (center), and supination (right) wrist postures. This represents the muscle contributions if each muscle pulled in its pulling direction in a straight line with a magnitude of one. Extrinsic wrist movement is a linear combination of these vectors. The legend in each circle indicates extrinsic direction (degrees) and joint movement (Rad, radial; Uln, ulnar; Flx, flexion; Ext, extension). Data from Hoffman (1999).

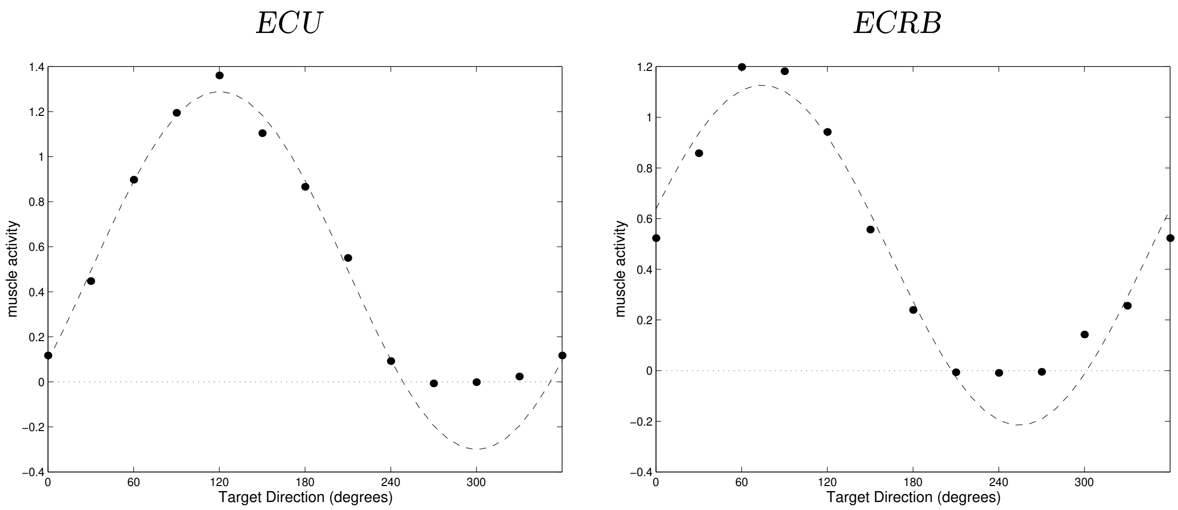

Figure 9: Muscle activity as a function of target location as produced by the model for muscles ECU and ECRB in the midrange wrist posture. Solid circles are the muscle activations; dashed lines are the best fit function $B\cos(\theta - C) + D$. Muscle preferred direction is defined to be the parameter C. Points where muscle activity is below 0.05 is given a zero weight in the fitting process. Horizontal dotted line is at muscle activitiy $= 0$. Compare with monkey data of figure 3.

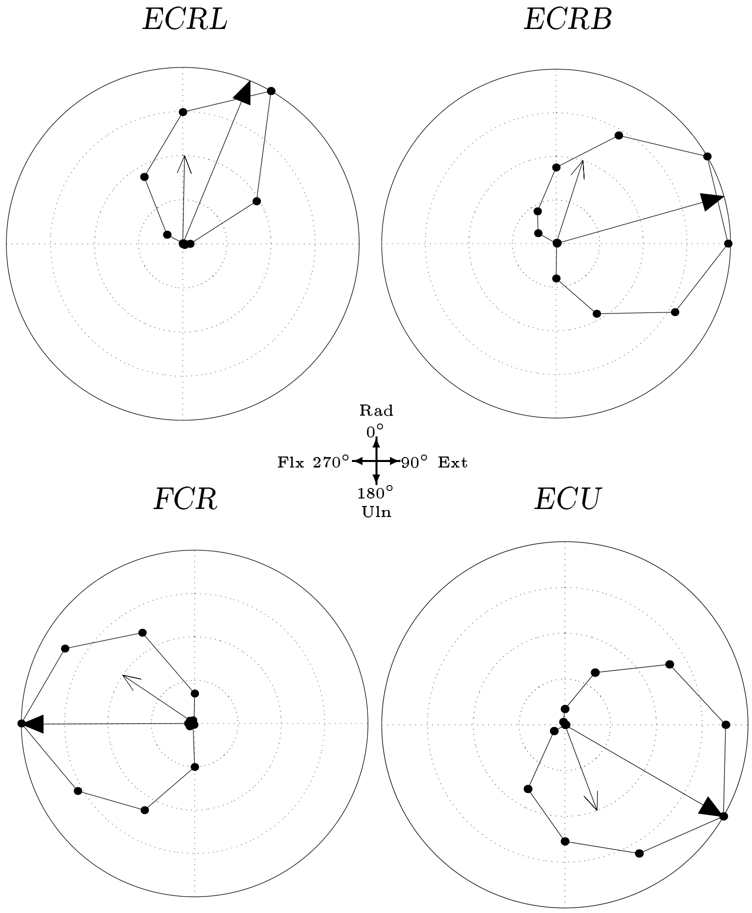

Figure 10: Normalized polar plots of as a function of target direction for muscles ECRL, ECRB, FCR, and ECU in the midrange wrist posture. Solid circles connected by a solid line are muscle activity as produced by the model. Short open arrows are muscle pulling directions. Long closed arrows are muscle preferred directions, calculated from fitting the function $B\cos(\theta - C) + D$ to the data, giving points less than 0.05 a zero weight in the fitting process. Preferre direction is the parameter C. The legen 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. Compare with monkey data of figure 4.

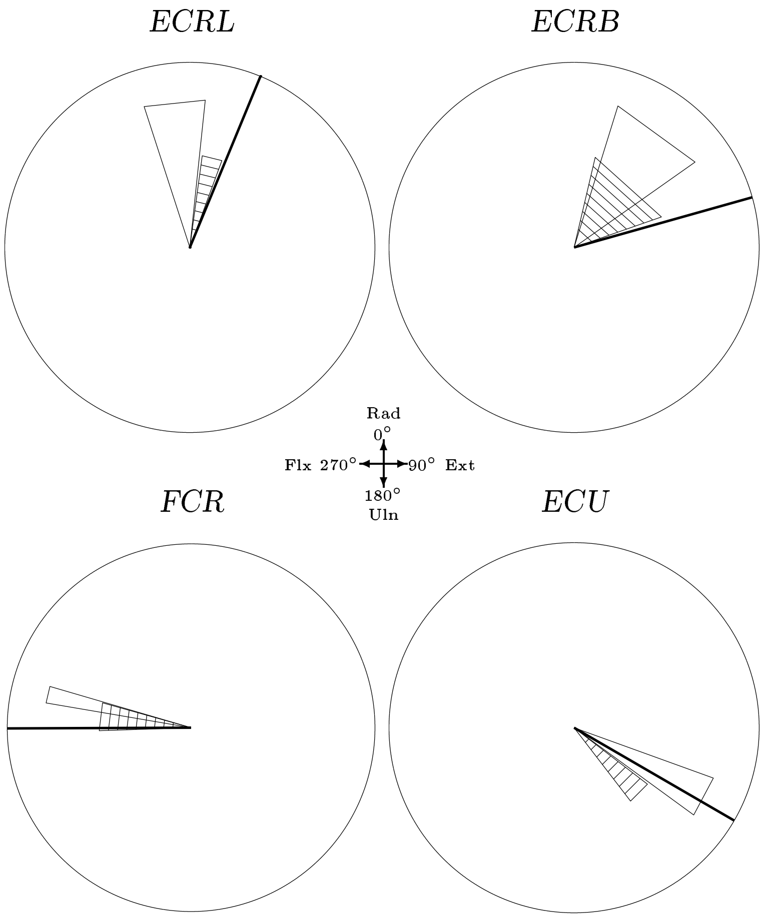

Figure 11: Preferred directions of human, monkey, and model muscles ECRL, ECRB, ECU, and FCR in the midrange wrist posture. Long solid lines indicate preferred direction produced by the model. Unfilled triangles represent the preferred direction, including inter-subject variation, produced by monkey EMG recordings. Hashed triangles represent the preferred directions, including inter-subject variation, produced by human EMG recordings. Monkey and human data from Hoffman and Strick (1999).

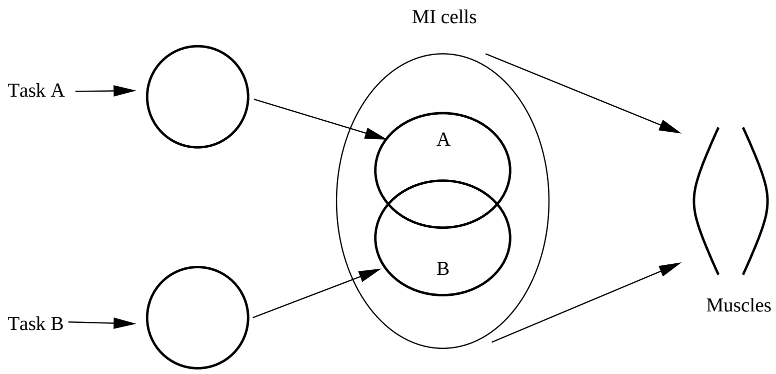

Figure 12: Illustration of two pools of MI cells, each directly activating muscles. Pool "A" is recruited for task "A," while pool "B" is recruited for task "B." The overlap between pools indicates that in some cases, members of both pools are recruited.

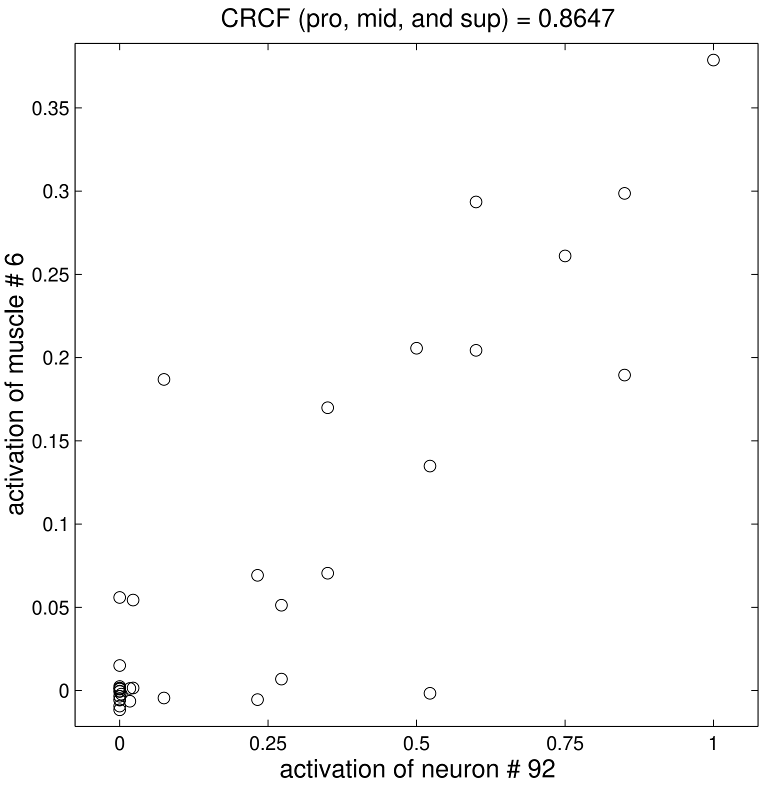

Figure 13: Activation values of muscle APL (6) versus activation values of neuron 92 including all three wrist postures. The correlation coefficient ($crcf$) between the muscle and neuron is 0.8647.