

# Modeling sensorimotor transformation in medial intraparietal area connectivity

CN740 Final Project  
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## 1. Introduction

How do monkeys and humans make reaching movements toward a visual target? This question has received much attention in neuroscience and the detailed neural mechanisms underlying visually-guided reaching remains an open question on many levels. One of the most important areas in the brain for sensorimotor transformation, with respects to visually-guided hand movements, is the posterior parietal cortex (PPC) - more specifically, the medial intraparietal area (MIP) residing in the PPC. Transformation signals in MIP are currently of particular interest to scientists and engineers due to their potential role in building better neural prosthetics (Andersen et al., 2005). One issue with attempting to decode MIP signals, however, is the dearth of information concerning the exact input and output structure of neurons in this region.

In this report I will review the somewhat sparse anatomical and neurophysiological literature on MIP inputs/outputs in order to sort out various types of neuronal activity found in this key reaching region, then discuss MIP's role in spatial planning and continuous updating of a reaching movement. The goal of this study is to construct a simplified first-pass neural model of MIP input connectivity and attempt to replicate the neural recordings of Gail and Andersen (2006). Adapting the Grossberg-like equations from Cisek (2006), a more detailed view of MIP neural activity is presented for insight into the experimental results of visually-guided arm movement shown by the Andersen lab and other MIP researchers.

## 2. MIP Inputs and Outputs

Before discussing the functional considerations of MIP it is important to point out where this area resides in the brain. MIP is located in the posterior half of the medial wall of the intraparietal sulcus (IPS), carved out of the former "PEa" area of the superior parietal lobe (SPL) and first named by Colby et al. (1988) as a parietal area sending

connections to area PO (now known as V6/V6A). To confuse matters more, the Andersen lab refers to MIP in functional terms as the parietal reach region (PRR) for obvious reasons. One issue with this is that these researchers associate the area with reach-related activity which may involve V6a as well, so there could be some overlap between MIP and V6A that is coined "PRR".

As for inputs, there is strong evidence that MIP receives inputs from the parietal occipital area (PO) which is receives inputs from most primary visual areas as well as MT (Colby & Duhamel, 1991; Johnson et al., 1996; Caminiti et al., 1999). Area PO is considered to be homologous with areas V6 and V6A combined, all of which show important connections with MIP (Shipp et al., 1998) to the point of being lumped together into one functionally-defined region - PRR. Another primary input area to MIP is the ventral intraparietal area (VIP) which is a highly polymodal and direction-of-movement specific region (Colby, 1988; Lewis & Van Essen, 2000a). There is also the possibility that MIP has reciprocal projections with LIP, an area which codes saccade goal planning, on the lateral wall of the IPS. Lastly, there is speculation and hand-waving that PMd sends its projections from the frontal lobe back to MIP, however, most studies refer only to MIP's projections to PMd. Given MIP's activity during target selection, there is strong evidence that PMd is indeed sending projections reciprocally (Scherberger & Andersen, 2007).

The outputs from MIP are better studied than its inputs, with the most important projection being to PMd, presumably sending extrinsic reach plans to the more intrinsic, motor planning-based premotor cortex (Caminiti et al., 1999; Cisek, 2006). More specifically, projections to PMd are to more trunk- or arm-related areas along the somatotopic mapping of PMd. It is also believed that output to M1 occurs in addition to PMd. Lastly, as mentioned earlier, V6a receives axon collaterals from MIP. Figure 1 below gives an anatomical map of the PPC.

As for the MIP itself, it is known to be highly plastic and modified by learning, expected value, and other high-level cognitive factors which seems a logical conclusion when looking at which inputs project to it. Within this highly plastic region, anterior MIP is more concerned with motor information whereas posterior and ventral MIP is more visuomotor tuned. I propose in the last section that in order to simulate neurons in this area one must take into account the gradient of visual-to-motor encoding in MIP and that this gradient may reflect the spatiotemporal activity here. This is based on the timed inputs from various regions which are integrated in a dorsal-caudal to ventral-rostral direction over spatial location and time.

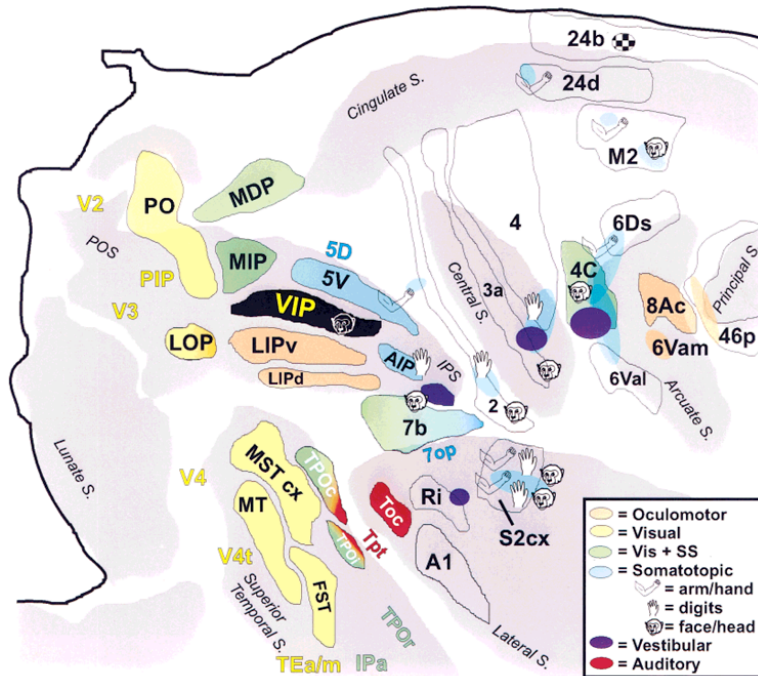


Figure 1: Cortical areas near PPC (Lewis & Van Essen, 2000b)

### 3. Experimental Data

Reaching towards an object seems to be a simple task at first glance, yet the ability to perform such a “simple” task requires a vast network of brain regions. Not only must one worry about the actual online movement of the limb, but there is also the issue of goal-directed behavior which integrates rules in order to carry out abstract motor goals. There is also the problem of integrating eye coordinates and hand coordinates in the brain. MIP has been shown to be highly involved in this parietofrontal network for planning a reaching movement. More specifically MIP integrates visual information with abstract motor goals and somatosensory feedback of the limb in a manner which is still poorly understood.

The Andersen lab in particular continues to be a key investigator of how intended movements goals are stored in the parietofrontal network. Recently, this lab looked into the context-specific visuomotor mappings for visually guided reaches by spatially dissociating the cue from the motor goal via a memory-guided anti-reach task (Gail & Andersen, 2006). Two male rhesus monkeys performed the task and extracellular neural recordings were made from up to five microelectrodes. Single-cell spiking activity from successful memory reach trials were analyzed for spatial selectivity on a cell-by-cell and population level. Figure 2 shows the task where a monkey fixated on a

small central red dot throughout the trial, then at the cue a green (reach) or blue (anti-reach) dot appeared, letting the monkey know whether it should make a reach or anti-reach to the target after a variable memory period (MEM). Visual feedback (FDB) appeared only after the monkey touched the correct goal on the screen. Figure 2C shows the typical delay period tuning in MIP. The example neuron in Fig. 2C shows a selective firing during the time between the CUE and MOV periods for movements to the right.

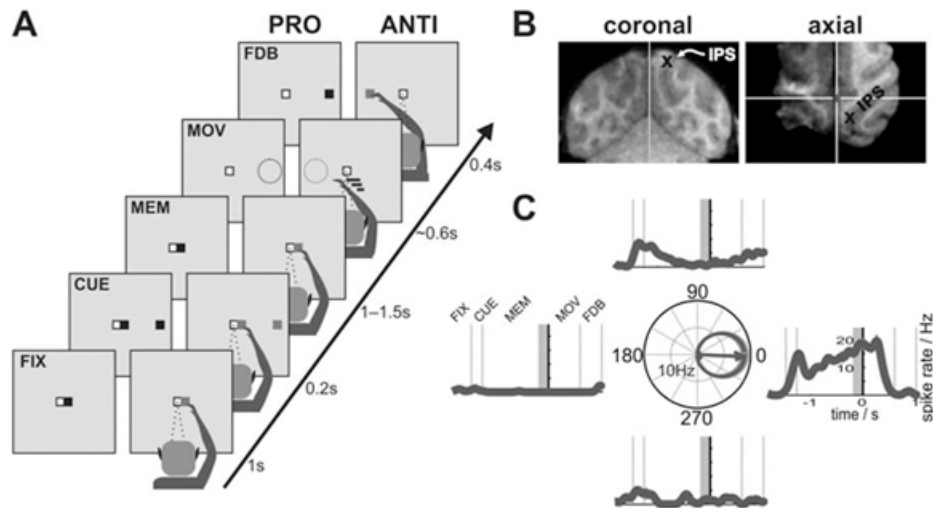


Figure 2: Memory-guided anti-reach task (Gail & Andersen, 2006).

From these results the researchers point out that during the delay period of a memory reach task MIP represents *motor goals* more than “visual memories”. Results from 143 MIP neurons rendered two primary neural response categories as seen in Fig. 3, allowing one to discriminate visual sensory information (CUE response) from motor goal information (MEM & MOV response). Neuron A represents the location of the monkey’s motor goal during the MEM period as seen in the neural response in Fig. 2C. Note that this cell is only active for “up” motor goals giving it *motor goal tuning*. Neuron B, on the other hand, responds to the spatial location for the dot during the CUE period yet changes to selectivity for the spatial location of the motor goal during the MEM period giving it *visuomotor tuning*.

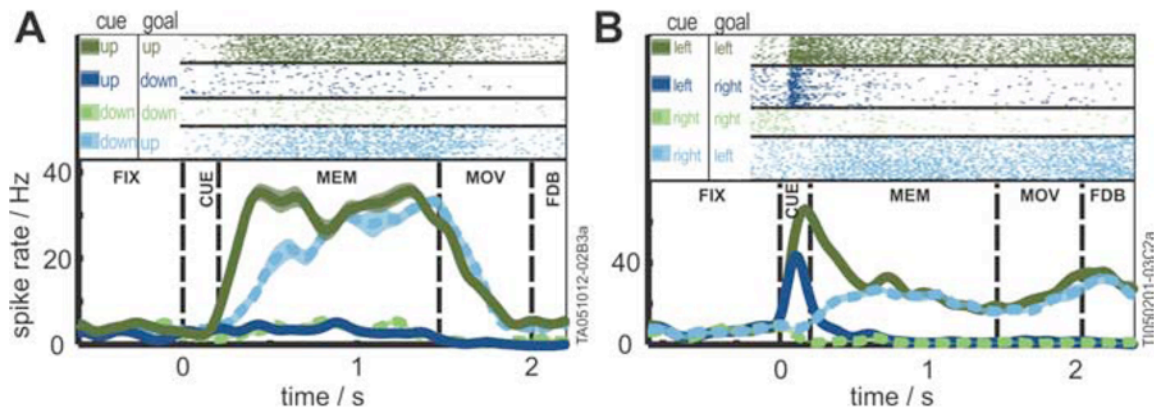


Figure 3: A) Example neuron with sustained motor goal tuning and B) example neuron with visuomotor tuning. Green traces represent reaches and blue traces anti-reaches (Gail & Andersen, 2006).

These results suggest that sensory representation is quickly replaced by a motor goal representation in MIP neurons; in fact, only 13% of MIP neurons recorded showed visual tuning and most of these adapted to motor tuning over the trial period whereas 52% showed motor goal tuning throughout. It is evident here that MIP is integrating both visual and motor information and based on its neurons' tuning properties and that this area temporally shifts between sensory and motor tuning based on the current or most relevant incoming signals.

In another paper involving the Andersen lab (Buneo & Andersen, 2006), the relation of MIP to the PPC as a whole is addressed. In particular, does MIP correlate to arm movement goals in the same way LIP does for saccade preparation? The researchers pose this question by discussing *separable* PPC neurons where hand and target signals are independently coded. *Inseparable* PPC neurons, then, are dependently encoded for both hand and target variables. With this framework in mind a "separability gradient" of responses (Fig. 4) are found in the superior parietal lobe where MIP neurons seem to show both separable and inseparable qualities. Buneo and Andersen interpret this by saying MIP encodes "hand position in eye coordinates" where motor error and body position signals are multiplexed then transmitted to the frontal lobe. Further, PPC may map three-dimensional target and hand positions in eye-centered coordinates to the four-dimensional space of arm postures. Lastly, Fig. 3 shows that, as a part of PPC, MIP is involved in the inverse kinematics problem of converting sensory information into motor commands. Recent evidence also shows MIP may be important for the forward kinematics process of integrating sensory input with previous or ongoing motor commands during an arm movement. The neuron activity in Fig. 2 seems to imply that MIP is indeed involved in both computations.

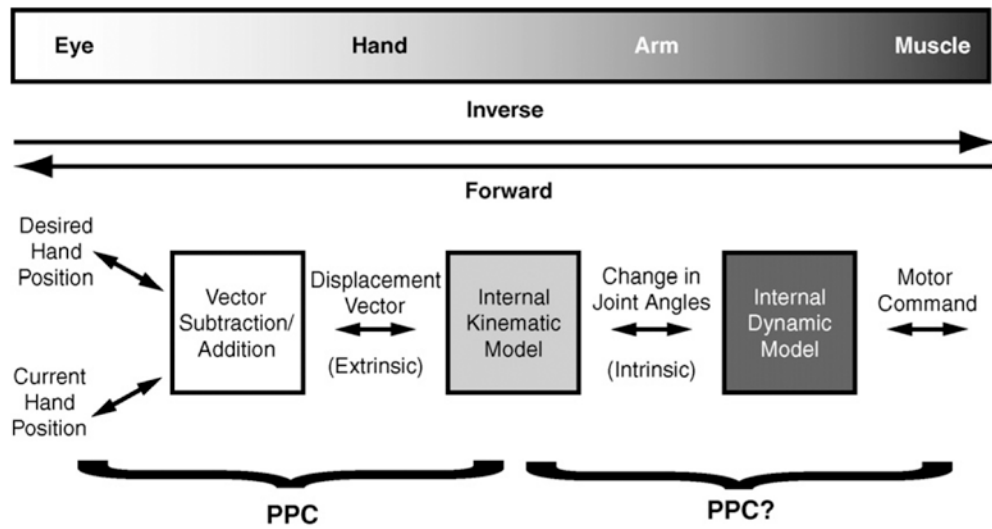


Figure 4: PPC's possible roles in reach planning (Buneo & Andersen, 2006)

To verify Buneo and Andersen's intuition concerning a correlation between LIP saccade goal activity and MIP arm movement goal activity, one study (Quiroga et al., 2006) shows that MIP tunes for reaches in a similar manner as LIP's saccade tuning. For this experiment, a monkey performed interleaved delayed reach and saccade trials. Figure 5 shows that activations for both PPC areas occur during the delay period and have similar neural responses for planning movement in the upper right direction.

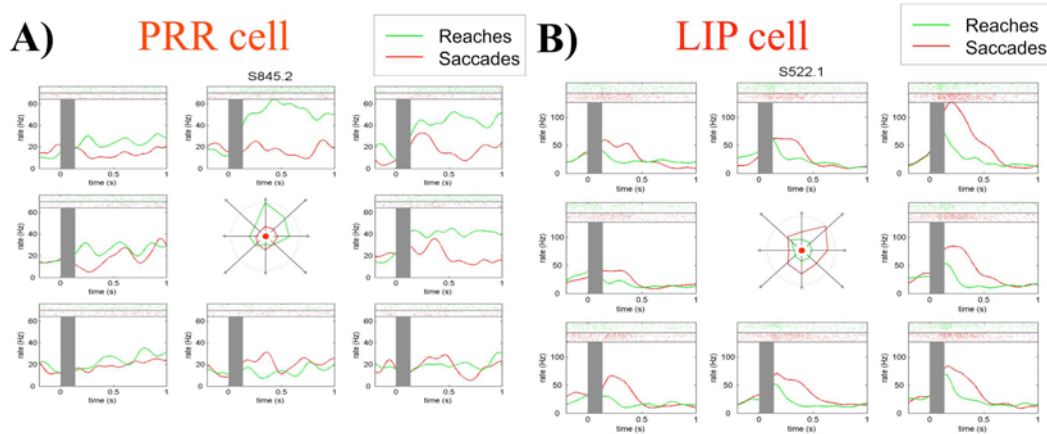


Figure 5: Response of A) PRR cell and B) LIP cell to delayed reach and delayed saccade trials (Quiroga et al., 2006)

Another study (Eskandar & Assad, 1999) has shown that MIP neurons are selectively modulated by the direction of hand movement when a monkey is trained to use a joystick for guiding a spot of light to a circular target while fixating. Figure 6 shows that an example MIP neuron was active for occluded trials with the hand moving in one direction but not the reverse direction, irrespective of the direction of stimulus movement. The researchers conclude that MIP uses extraretinal direction selectivity related to the direction of hand movement. One thing to note here is that recording was *at the start* of the joystick movement, thus the response over time would probably have been different between the visible and occluded trials had they started recording at cue onset.

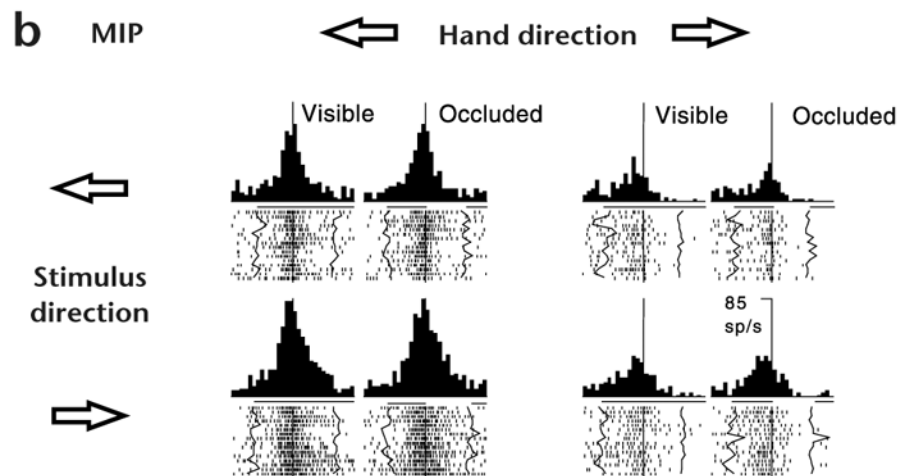


Figure 6: Single neuron response in MIP (Eskandar & Assad, 1999)

The last study I want to present here discusses what happens in MIP neurons when a monkey selects one of two visual stimuli as a movement reach target (Scherberger & Andersen, 2007). Similar to results shown above, MIP neural activity initially reflects the visual target stimulus then changes into a motor goal tuning over time. For choice between two targets, T1 and T2, this representation is either up- or down-modulated according to which stimulus of the two is chosen. Representation of T2 is suppressed in the population of T2-selective cells if the network is strongly active for T1 and vice versa. After this target selection process, the population activity represents the selected movement that is eventually executed (Fig. 7). Timing of the second target is important during this selective competition because the further the plan to move to T1 has evolved, the harder it will be for T2 to compete against the existing T1 movement plan. MIP activity as shown in Fig. 7, say Scherberger & Andersen, can be interpreted in terms of a race or mutual competition model such as the one proposed by Cisek, Kalaska, Wang and others. In conclusion,

this experiment is conducive with the idea that MIP integrates top-down choice preferences with bottom-up visual stimuli for the selection of reach targets. Further, MIP is part of a larger “decision network” for reach movements and has important reciprocal connections with PMd and other PPC areas.

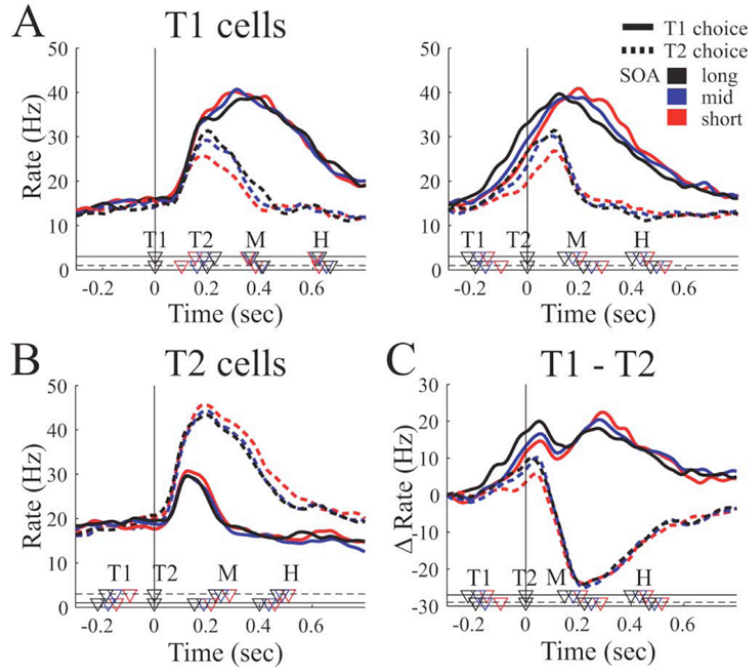


Figure 7: Influence of stimulus-onset asynchrony on choice activity (Scherberger & Andersen, 2007)

All of the experimental studies above illuminate various pieces of the sensorimotor transformation puzzle in order to find what kinds of neurons are firing in visual, somatosensory, motor, or cognitive domains. All of these types of signals are present in MIP and by looking at neural response over the time span of an entire delayed reach trial one can get a better intuition about what types of neurons are firing and at what location within MIP itself.

#### 4. Modeling Efforts

In 1999 a review article (Burnod et al., 1999) proposed a model for explaining the parieto-frontal network’s organization along with its importance for visually-guided arm-reaching movements. The review was extensive and made several important steps toward building a computational model of this



network using a parallel, neurophysiologically-sound approach. Also noted by the authors was the concept of combinatorial domains matching different sources of signals when discussing sensory-motor transformations in particular. The core of the model simply states that there is optimal activation in one region of the network when two inputs are parallel or “matching”, where neural nets align distributed sensory and motor representations. Figure 8 shows the full parieto-frontal network for visually-guided reaching. The areas most important for the matching criteria are found in what Burnod and colleagues call iM and iP, or intermediate motor and intermediate parietal, where the green connections between them are reciprocal and primarily arm-related in signal type. The authors, however, do note that this structure is a loose approximation and that areas along a divide such as that between iP and pP will see mixtures of neural response. For the iP/pP border scenario one would expect to see arm- or gaze-related activity and this is indeed the case...as is recorded in MIP.

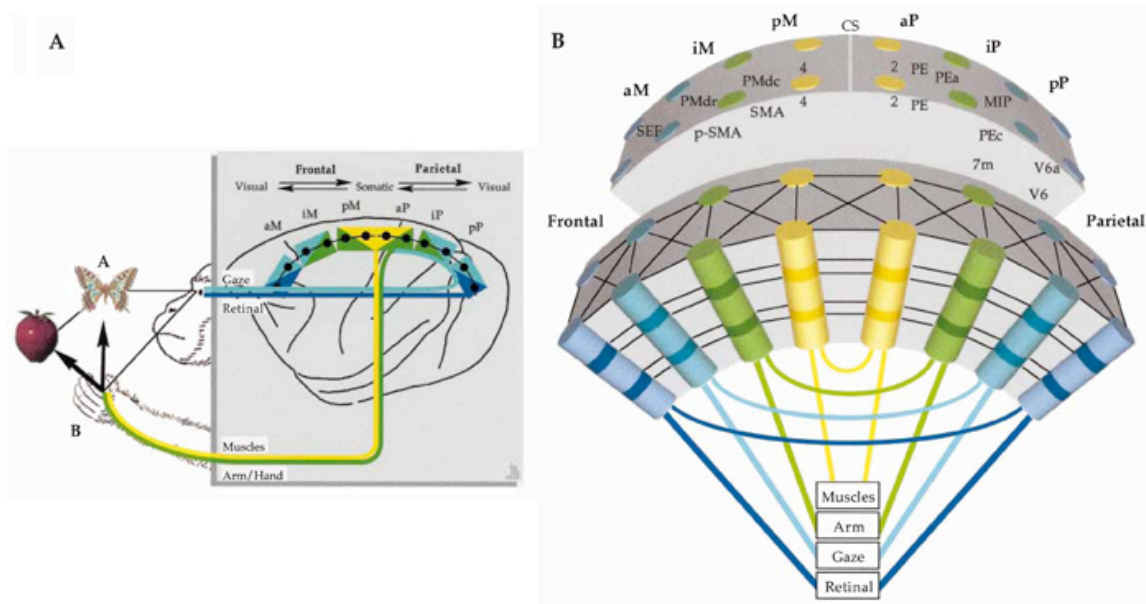


Figure 8: A) A monkey chooses to move its hand from either a butterfly or an apple with the appropriate network shown (dark blue, retinal; light blue, gaze; green, arm; yellow, muscles); B) architecture of the cortical network underlying reaching with reciprocal connectivity among each of the four major categories.

Although the Burnod et al. review provides an excellent foundation for framing the major problems and strategies of planning a visually-guided movement, the model obviously falls short by

way of generalization in each area's network function. Unfortunately, few (if any) models since this review have provided a computational account of MIP that explains the experiments discussed earlier. Before going into the details of this current project's more MIP-specific model, I will briefly discuss two predominant variations relating to the computational foundations of sensorimotor transformation in the past decade.

The first approach uses the basis function where sensory information is recoded into "a flexible intermediate representation to facilitate the transformation into a motor command (Pouget & Snyder, 2000)." The basis function is a form of population code which the authors believe is able to adequately transform and encode information from multiple reference frames. In a basis function map, each neuron contributes to multiple frames of reference making these neurons ideal for coordinating different behaviors such as eye and hand coordinates. In Fig. 9B a model for a nonlinear arm movement - as is required due to the geometry of the joints - has an intermediate layer of units for learning the sensorimotor transformation where learning is performed in two stages. First, the unsupervised layer self-organizes because the basis functions depend only on the input and not the motor command output. Second, the weights for predicting a motor command can be learned using an error signal typical of most radial basis functions.

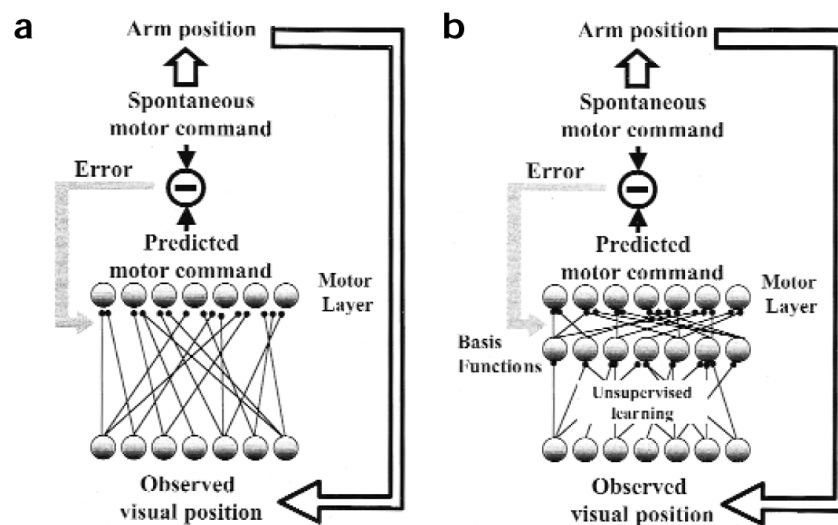


Figure 9: A) Learning spontaneous motor commands; B) Nonlinear arm movements with intermediate layer

Lastly, a recent article (Cisek, 2006) has put forth a computational framework for how an animal would decide which of two objects to reach for (action selection) and plan the movement (action specification) in an integrated manner. Just as the Burnod et al. and Pouget/Snyder articles looked at an overall systems-level model, so does Cisek, with each population of cells organized as a layer of neurons tuned to spatial directions of “potential actions” (Fig. 10).

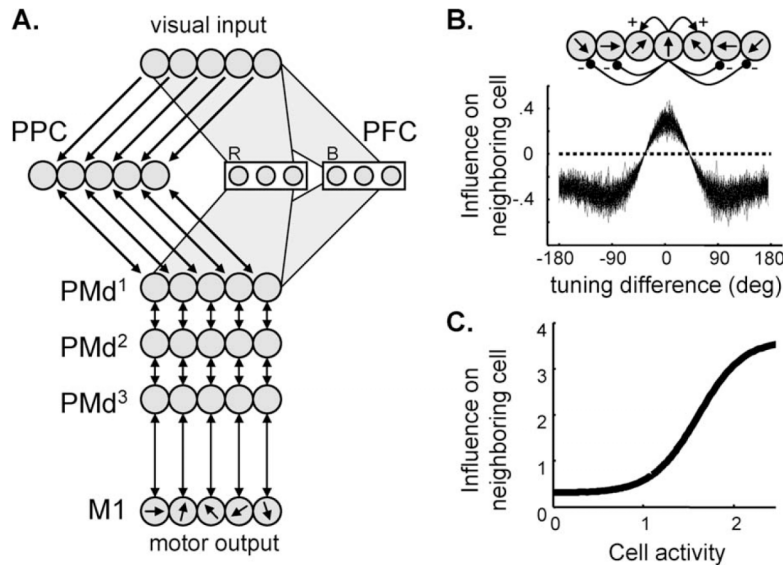


Figure 10: A) Network architecture, B) Cells with directional preferences in a frontoparietal layer (Cisek, 2006)

Rather than use Bayesian or basis functions in the model, Cisek implements a Grossberg-style equation,  $dX / dt = -\alpha X + (\beta - X) \cdot E - X \times I + \Theta$ , to represent each neuron’s activity. There are 90 such “neurons” in each layer where  $dX / dt$  is the change in mean firing rate of a neuron over time,  $E$  is the excitatory input,  $I$  is the inhibitory input,  $\alpha$  is a decay rate,  $\beta$  is the maximum activity of the neuron,  $\gamma$  is the excitatory gain, and  $\Theta$  is Gaussian noise. As shown in Fig. 10B, the cells compete to learn tuning preferences in a population of cells and Fig. 10C shows that higher cell activity accounts for more neighboring cells being influenced.

## 5. A Detailed MIP Model

The experimental data in Section 3 provide a truncated list of the different ways in which MIP neurons behave over time. Gail and Andersen showed that there are most probably two major categories of cell response in MIP based on their goal-tuning properties – motor-tuned and visuomotor-tuned. My conjecture is that this variation in response may be due to combining visual inputs coming in the posterior and ventral regions of MIP with motor-related inputs arriving in the anterior and dorsal portions of MIP. The change of visuomotor-tuned cells to motor tuning properties over time in posterior MIP may be due to the influence of anterior MIP cells across the entire MIP area over time in preparation for a reaching movement. In the Buneo and Anderson review the notion of separable versus inseparable neurons was discussed where MIP neurons seemed to show a mixture of these two types of cells. This hypothesis fits well with the idea of visuomotor versus motor-tuned responses in MIP. Eskandar and Assad's results showed that MIP uses extraretinal direction selectivity related to the direction of hand movement, thus certain MIP neuron populations may be coding for the different goal-based directional movements. Lastly, Scherberger and Andersen accounted for selection between two objects for a reach-related movement in MIP, taking into account temporal and spatial dynamics.

This data raises several important questions. Do MIP neurons respond differently based on 1) preference of goal information, 2) variation of inputs from different regions at different times, 3) more visual cue-based MIP being complimented by the later arrival of motor goal tuning neural activity during the “MEM” period of the Gail and Andersen task, or 4) a mixture of these elements? A computational model of MIP must account for these questions and the neural responses in MIP data thus far. For this project I consider the two basic types of neural response in MIP based on the Gail and Andersen experiment by modeling a gradient of cell responses in MIP, emphasizing the fact that a majority of neurons have a more motor- rather than visually-related reaching plan response. The eventual motor-tuned responses in all MIP neurons may be acting as an output stage to its reciprocally-connected regions in order to strengthen the weights for various reaching-related goals.

So in what order does the MIP receive its numerous inputs? It is believed that PO is the first region to activate MIP as shown in the numerous activity profiles of this area, followed by VIP which may be involved with selecting the actual *direction* of a goal-tuned movement since VIP is highly sensitive to motion direction information across numerous sensory modalities. PMd inputs, then, may arrive after MIP sends output to PMd which then projects the

intrinsic motor plan back to MIP for updating of its synaptic weights. Implied here is the idea that MIP initially possesses no object selection preference until it receives feedback from PMd after learning. Over time, MIP-encoded weights are adapted for fast updating of a desired movement goal as well as online adapting to effector target trajectories – a concept that correlates with this area’s high level of plasticity. Lastly, MIP neurons receive mutual excitation from neighboring cells with similar preferred direction (PD) and inhibitory input from cells with different PDs via an on-center off-surround architecture.

For this project I have adapted the Cisek (2006) model of sensorimotor transformation between brain regions using the following equation for each neuron:  $dX_i^R / dt = -\alpha X_i^R + (\beta - X_i^R) \cdot E_i^R - X_i^R \cdot I_i^R + \Theta(0, \eta)$  which is similar to the Cisek equation shown earlier only  $X_i^R$  here refers to the particular region of activity and  $\eta$  is simply the variance with mean zero for the Gaussian noise. The medial intraparietal regions ( $R$ ) for this project are 1) MIP1 that represents the posterior, visuomotor-tuned neurons and 2) MIP2 that represents the anterior, motor-tuned neurons. The output of each neuron has a threshold which is determined by  $Y_i^R = [X_i^R - \Gamma]$ . No parameter values are given for these equations since no simulation is being completed for this project. For these equations 25 MIP1 cells and 125 MIP2 cells are used in order to account for the predominance of MIP2-type cells.

Excitatory input to MIP1 is calculated by

$$E_i^{MIP1} = V_i^{PO} + \sum_j w_{ji}^{MIP1 \leftrightarrow MIP2} \cdot Y_j^{MIP2} + \sum_j KE_{ji} \cdot f(Y_j^{MIP1})$$

where  $V_i^{PO}$  is the PO area input, the second

term sums the weights and output activity from MIP2 to MIP1, and the final summation refers to the excitatory kernel representing lateral connections between cells [defined as a Difference-of-Gaussians (DOG) function] within that region multiplied by the transfer function which is sigmoidal. The

inhibitory input to MIP1 is  $I_i^{MIP1} = \sum_j KI_{ji} \cdot f(Y_j^{MIP1})$  where  $KI$  is also a DOG function. Lastly, MIP2

$$E_i^{MIP2} = V_i^{VIP} + V_i^{PMd} + \sum_j w_{ji}^{MIP2 \leftrightarrow MIP1} \cdot Y_j^{MIP1} + \sum_j KE_{ji} \cdot f(Y_j^{MIP2})$$

where  $V_i^{VIP}$  is the VIP area input and  $V_i^{PMd}$  is the PMd area input to MIP2. The inhibitory input to MIP1

is defined as  $I_i^{MIP2} = \sum_j KI_{ji} \cdot f(Y_j^{MIP2})$ .

This system of equations is described visually in Fig. 11 where yellow circles represent visuomotor goal tuning and orange circles are motor goal tuning. Each circle is a small population of cells. Even though the cartoon shows a gradient of response I have depicted this in only major categories - MIP1 (yellow circles) and MIP2 (orange circles). Also note that LIP connections to MIP are purely speculative at this point thus they were not added to the equations above.

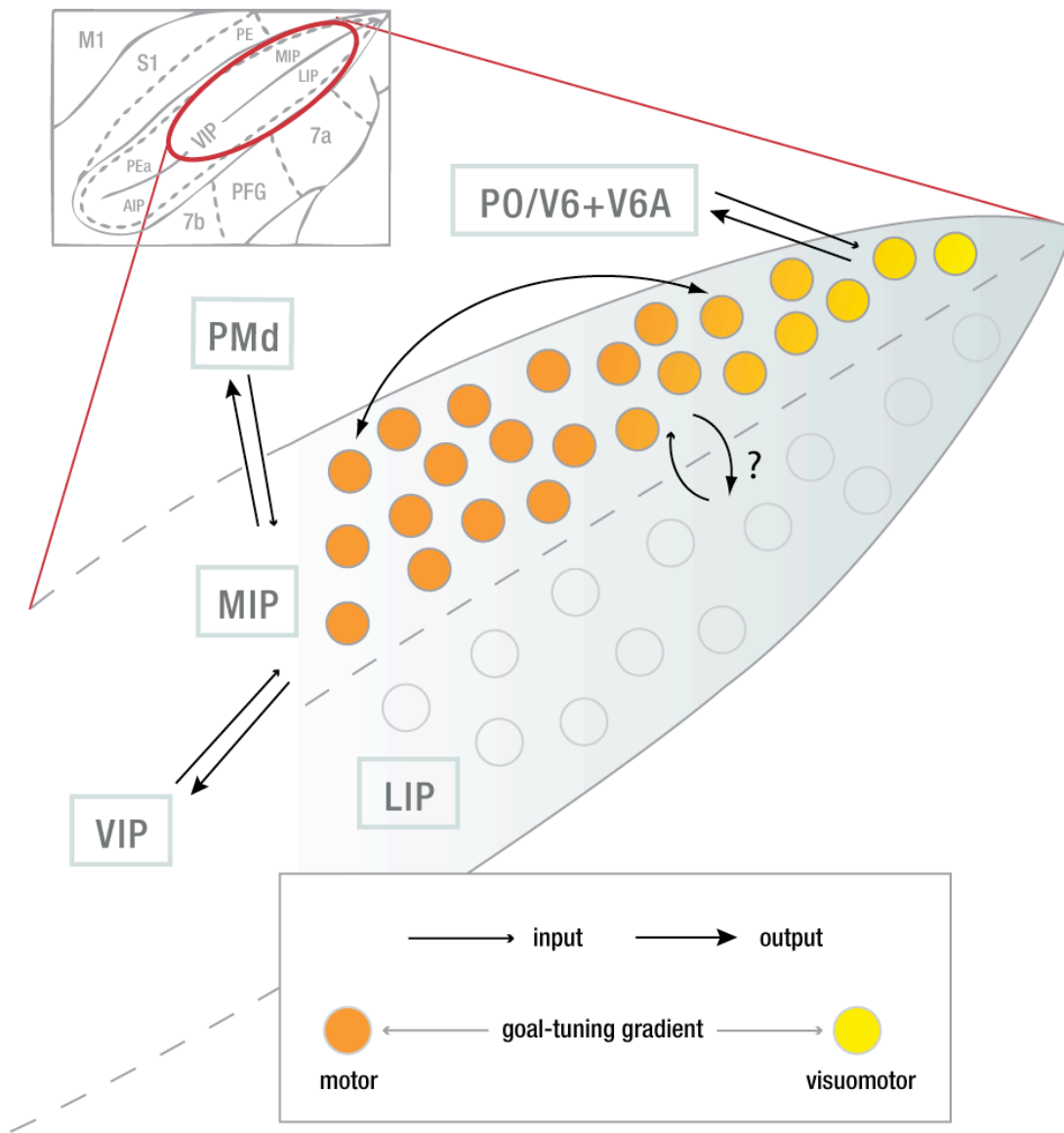


Figure 11: Proposed MIP input and output architecture based on goal-tuning neuron population features

## 6. Conclusion

Since the proposed model was not simulated fully as of yet, the expected results would hopefully be similar to the neural responses of Fig. 3, given that the inputs to the model are analogous to the task setup shown in Gail and Andersen. In conclusion, the model presented here gives more detail than the widespread schemas of Burnod, Cisek, or Pouget however the close attention paid to MIP begs the question as to how the hard-wired inputs from PMd, VIP, and PO acquire their respective inputs before outputting to MIP. More detailed models of these areas linked together would give a more full explanation of sensorimotor transformation. Nonetheless, based on the experimental data and current models proposed thus far it appears that MIP is an integral part of the parietofrontal network, initiating visually-guided, goal-directed movements which are needed for quick, online adapting to effector target trajectories.

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