

Distributed motor processing in cerebral cortex

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Responding to a visual cue requires processing throughout many areas in the brain. The anatomical pathways connecting these diffuse areas are numerous. One way to study the cognitive processing associated with volitional movement is to identify common physiological properties in each area. Recently, the discovery that neuronal activity is broadly tuned in many of these cortical areas has led to new insights into the physiological structure of the process underlying cognition in this distributed system.

Current Opinion in Neurobiology 1994, 4:840-846

Introduction

While the desire to move can originate in the absence of overt environmental stimuli, it is much easier to study movement generation when it is linked to known cues. The processing by successive CNS structures of the sensory cue leads to the action embodied in the desired movement. A cold glass of water on a hot day, for instance, may be considered both a target and a cue. It is necessary for its behavioral significance to be recognized along with its position in space. This information might then be used to plan a movement trajectory of the arm, from an initial position, to the glass of water. The trajectory is a function of the desired behavior, as it would differ, for instance, if the objective was to swat a fly in the same position.

In step with the trajectory generation, a sequence of joint angles and muscle activations need to be specified to displace the arm. Inherent in this description is the idea of parameters — physical quantities that can be measured and represented in the activity of neurons. Typically, sensory parameters are those aspects of the environment that act on the individual, whereas motor parameters are measurements of the actions taken by the individual to act on the environment. As soon as movement occurs, both types of parameters change together and the nervous system processes them simultaneously. Movement changes the environment, altering the sensation used to generate the next portion of the movement. This cyclic interaction blurs the boundary between sensory and motor, a distinction that becomes more artificial when considering neuronal connections that are a few synapses away from the periphery. The known anatomical connectivity between visual and motor cortical areas will be reviewed. Some physiological

properties and analytical approaches to the information contained in these structures will also be discussed.

Parameter coding

Most investigations of volitional movement rely on the representation of task-related parameters within a pattern of neuronal activity. In the past twenty years, several key features of parameter representation in such activity have become clear. In almost all sensory and motor systems, parameters are represented by a broad single-peaked function between the parameter's value and the discharge rate of individual cells. Such a function was termed the neuronal response function by Erickson [1]. These functions are poor descriptors of parameters because they are ambiguous: each discharge rate codes for two values of the parameter. Also, the functions are susceptible to noise, especially at the peak discharge rate where small changes in firing frequency can lead to large changes in the parameter value. This was one of the reasons why the idea of population coding was invoked. The same conclusion was reached from psychophysical and neurophysiological studies of sensation. Population activity has been implemented to encode vibration intensity [2], limb position [3•] visual motion [4••], selective visual attention [5], faces [6] and body location in space [7] — abilities that emerge from concerted activity of individual neurons.

Humphrey (see [8]) was the first investigator to show the value of considering a population response as a representation of motor parameters. Using monkeys, he measured angular position, angular velocity, torque and change in torque during a simple wrist movement

Abbreviations

AIT—anterior inferotemporal area; IT—inferotemporal area; LIP—lateral intraparietal area; M1—primary motor cortex; MIP—medial intraparietal area; MST—middle superior temporal area; MT—middle temporal area; PET—positron emission tomography; PMd—dorsal portion of premotor area; PMv—ventral portion of premotor area; PO—parietal-occipital cortex; SMA—supplementary motor area; VIP—ventral intraparietal area.

and found a poor or inconsistent relationship between these parameters and the discharge patterns of individual motor cortical cells. This relationship improved when the weighted contributions of 5–7 cells were combined through the task. The evidence that parameters were encoded in groups of cells was further substantiated by Georgopoulos and colleagues [9] who found that motor cortical activity was broadly tuned to movement direction when recorded from monkeys performing planar reaching movements. This novel experiment examined movement direction explicitly for multi-joint movements in a center→out task. The function between discharge rate and direction was described with a cosine function characterized by a 'preferred direction' of movement where the cell fired at its maximal rate. This simple, coarse relationship spanned all movement directions and suggested that many cells were active simultaneously during each movement. These findings were remarkable because the mechanics of the freely moving arm are quite complex, yet the relationship between motor cortical discharge rate and the direction of movement is simple and robust. A population algorithm based on weighted vector contributions in each cell's preferred direction was used successfully to predict the direction of arm movement [10]. These findings were elaborated by tasks performed in three-dimensional space [11–13], with static loads [14] and in adjacent workspaces [15]. The responses of cerebellar cells [16], parietal [17,18] and premotor (D Karluk, TJ Ebner, Soc Neurosci Abstr 1989, 15:787; [19]) cortical cells were studied during the performance of the center→out task and all were found to follow the same cosine tuning function.

The ability of these cells to predict movement trajectory was tested explicitly when the directional properties of motor cortical cells were used to construct population vectors during drawing movements [20•]. A time series of population vectors predicted the changes in direction and speed of the hand continuously as figures were drawn. The shape of the drawn figure was recovered by adding the population vectors tip-to-tail. The ability to extract accurate trajectory information from cortical activity not only shows that this information is present in motor cortical activity but provides insight into the process underlying drawing. Psychophysical properties such as the 2/3 power law (where speed and curvature are inversely related) and trajectory segmentation are evident in this neural representation, and show that these properties are the result of central processing [21•]. The latency between the population vector and the corresponding portion of the trajectory is variable, for example, as spirals are drawn, the latency in the outer, straighter portions of the spiral is near zero or negative and at a threshold level of curvature it rises quickly to 100–120 ms. This has been interpreted as a sign that the trajectory formation process bypasses the motor cortex when movement direction is constant during drawing.

Information flow

The widespread observations of broad tuning in different neuronal (brain) systems and the ability to detect external parameters using population algorithms in these systems suggest the exciting possibility that we may soon begin to understand how information about the external world is transformed to a state where it is used to trigger and control movement. In the case of volitional movement this process may be considered cognitive. The flow of visual information to motor cortical areas will be reviewed as an example of this process (see also Fig. 1).

Visual information has been described as projecting through the neocortex in separate pathways [22••]. Spatial information flows from layers 4b and 6 of cortical areas V1 and V2 to the medial temporal area (MT) in a dorsal pathway. The pathway then projects to the medial superior temporal area (MST). The ventral pathway is believed to involve cortical areas V1–V2, V4 and the inferotemporal area (IT), structures that are involved in object identification.

Cells in MT are broadly tuned to the direction of visual motion. Dot patterns moving in different directions generate discharge patterns that when mapped to direction result in tuning functions that are very similar to those found in the motor cortex for different directions of arm movement [23]. Whether these neuronal responses can be summed to produce population responses or operate individually in a 'winner-take-all' mechanism [24] is presently somewhat controversial. MT cells project to MST. Cells in the dorsal portion of this area, MSTd, respond to more complex motions composed of rotation, expansion, and translation [25]. These are components of 'visual flow', that is, information experienced when moving through the environment. The responses of individual cells are related to combinations of the three components and have been fit with coarse tuning functions in a way that suggests that many cells respond simultaneously as this type of visual information is processed [4••]. For instance, when the random dot patterns moved in a spiral motion (combination of expansion/contraction and rotation), many of the cells responded with high discharge rates and would respond to other motions with lower rates. Displaying these patterns in other portions of the receptive field did not have a great influence on the cellular responses, suggesting that they were position invariant. Positional invariance is not a property of MT cells and probably is a function of the integration of MT inputs in MST. In addition to visual flow, MST discharge could be used to process information during manipulation because these cells respond when an object in the foreground moves against a background.

MST and MT project to cortical area 7a and to areas within the intraparietal sulcus (lateral intraparietal area [LIP] and ventral intraparietal area [VIP]). Cells in these regions respond broadly to spots of light moving from the periphery toward the fovea (at which point the cells

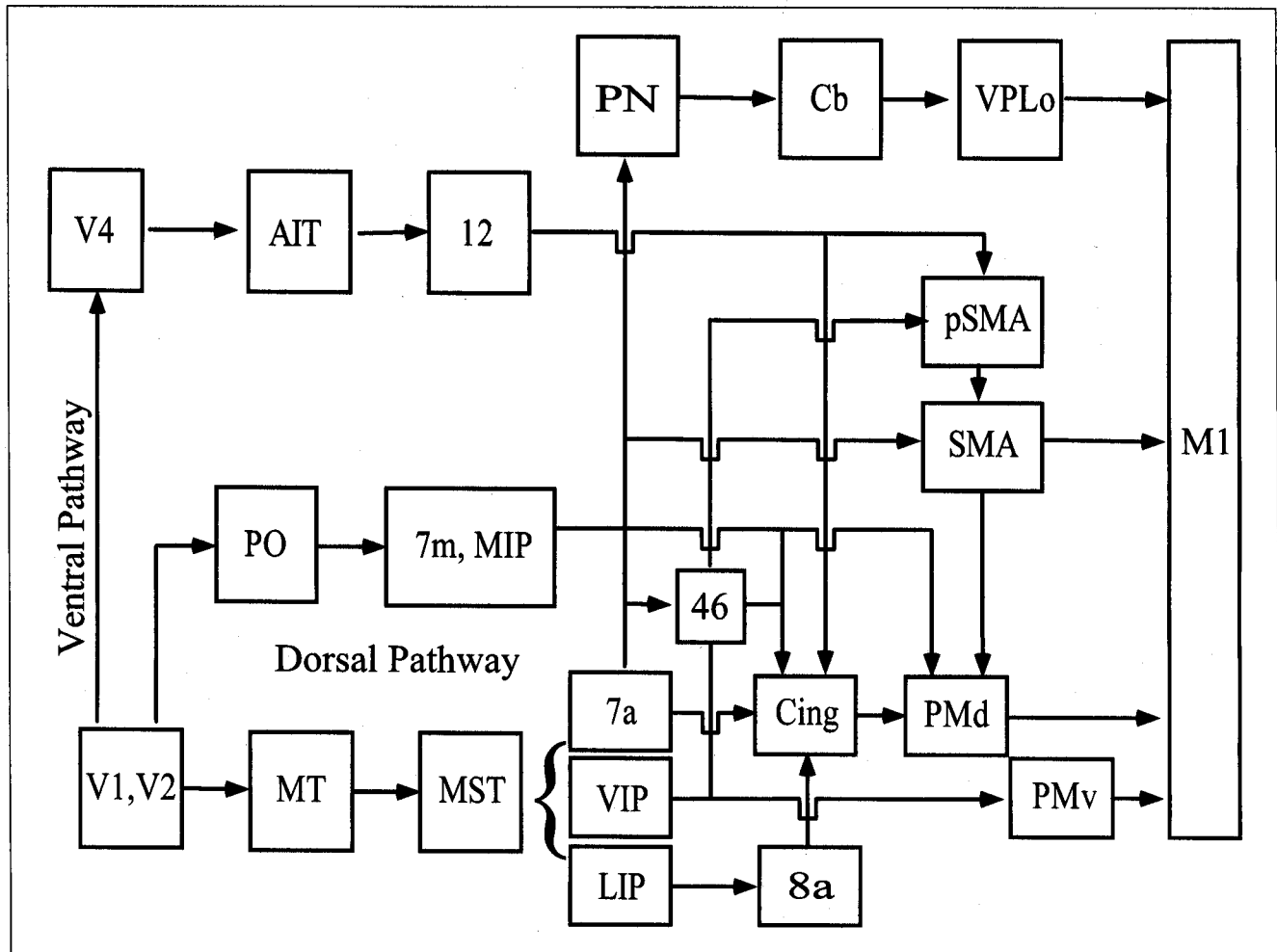


Fig. 1. Summary of connections between visual cortical areas (V1, V2) and primary motor cortex (M1). Abbreviations: Cb, cerebellum; Cing, cingulate cortex; PN, pontine nuclei; pSMA, pre-SMA; VPLo, oral portion of ventral posterior lateral thalamus.

stop firing) in different directions [5]. When applied to these directional responses, the population vector algorithm predicted accurately the direction of the moving stimulus. These cells probably play a role in the visual guidance of the hand as it approaches a foveated target. In an experiment where monkeys gripped and manipulated different objects, the responses of cells in this area were modulated preferentially for specific types of grip [26]. Although more active with vision, many of these cells were also responsive in the dark. Cell responses in VIP were also broadly tuned to moving stimuli [27]. Some of these responses were selective for movement directed toward a specific spot on the face.

Many of the areas in and around the intraparietal sulcus project to the frontal cortex. Some of these projections terminate in the premotor areas [28]. Output from the posterior-medial superior parietal lobule projects to the dorsal premotor cortex (PMd). These parietal regions include the medial surface of the hemisphere (7m) and the medial wall of the intraparietal sulcus (MIP) [29,30]. Area 7m receives input from parietal-occipital cortex (PO), an area that processes visual stimuli in the peripheral field [31–33]. MIP cells have visual and motor

responses [34,35]. PMd also receives cortical input from supplementary motor area (SMA) and cingulate areas 23 and 24 [29].

Cells in PMd are broadly tuned to the direction of arm movement with the same tuning function as cells in primary motor cortex (M1) [36]. As with M1 activity, a population algorithm applied to PMd activity formed accurate neural trajectories (A Kakavand, AB Schwartz, Soc Neurosci Abstr 1992, 18:502). One characteristic of these cells is that a subpopulation appeared to be inhibited for curved trajectories [37]. These cells tended to have maintained discharge during an instructed delay task and were classified as set-related [38–40]. This activity was dependent on the characteristics of the instructed movement, but independent of the visual cue. This contrasts to the findings in SMA where the set-related cells are better related to the visual stimulus than the instructed movement.

Cells in ventral premotor area (PMv) receive their major cortical input from the fundus of the intraparietal sulcus — area VIP [29]. This parietal area receives input from MT and MST and contain cells responsive to visual motion. Prefrontal area 46 also projects heavily to

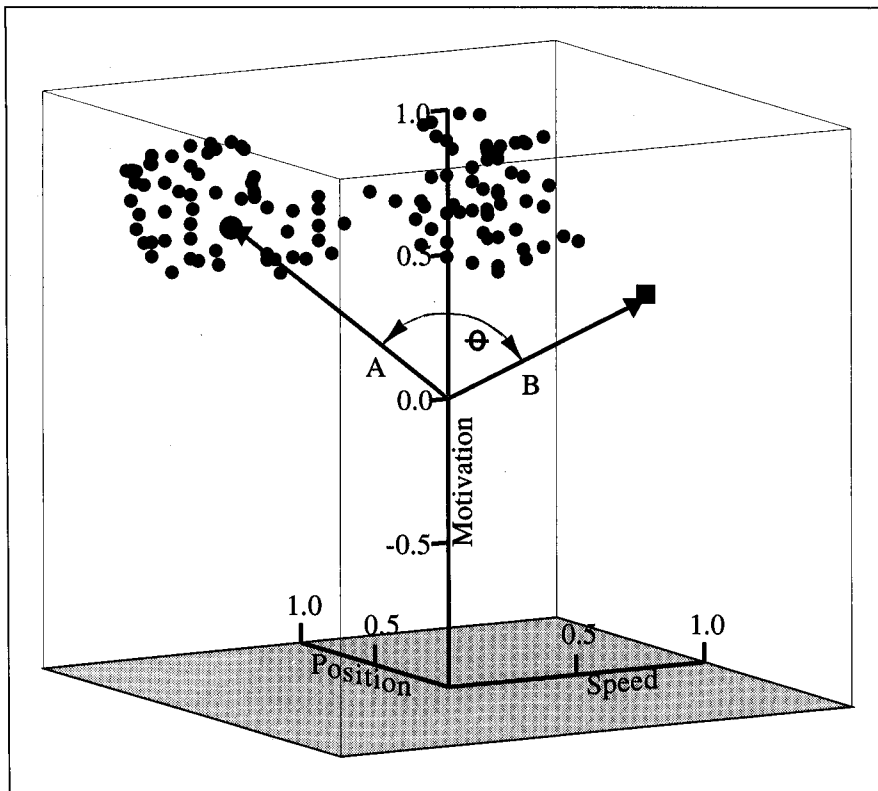


Fig. 2. Representation of cortical activity and behavior. For visualization, a three-dimensional parameter space is illustrated for the parameters speed, motivation and position. Vector A points to a cell in this space and vector B points to a behavior comprising a set of values for each parameter. During this behavior, the cell pointed to by vector A should fire at a rate that depends on the $\cos \theta$. See text for further description.

this region [41•]. PMv cells have set-related activity but their responses were not as dependent on the action to be taken as PMd cells [40]. PMv cells may be gaze specific, in that their activity changes when static stimuli are fixated in different parts of the visual surround [42•], but seem to be gaze independent for moving stimuli [43]. These cells also are preferentially responsive to particular arm trajectories but are less pervasive than those in M1, SMA or PMd [37].

The ventral visual pathway terminating in the anterior inferior temporal cortex is thought to be specialized for pattern and object recognition [44]. Population vectors based on anterior inferotemporal area (AIT) cells, tuned to specific physical features of the face, were constructed and selective for particular faces. The analysis used multi-dimensional scaling to group the responses which were broadly tuned to a combination of physical features [6]. Cells in IT project to area 12 inferior of the principal sulcus in the prefrontal cortex [45•]. Cells in this region respond to foveal input and project to pre-SMA [46,47] and PMv [48].

Prefrontal cells also receive input from the dorsal stream [49]. Axons from area 7a terminate in area 46, LIP projects to area 8a and area 45 receives input from area 7b.

Area 7 output can also reach motor cortical areas through a cerebellar circuit [50,51]. There is a large projection from this region to the pontine nuclei, lateral cerebellar cortex, dentate nucleus, ventrolateral thalamus and the primary and premotor cortices. Cerebellar cells are sen-

sitive to moving visual stimuli and are also broadly tuned to the direction of arm movements [16].

Conclusions

There is no direct route from visual cortical areas to M1. There are, however, several pathways through ipsilateral cortical sites and subcortical structures from visual areas around the intraparietal sulcus to M1. This route is characterized by motion processing of visual stimuli. Visual information associated with object recognition may reach the motor cortex more indirectly from a pathway projecting from IT to prefrontal, then premotor and supplementary cortices. However, caution must be used when interpreting this type of anatomical routing. First, almost all of the premotor cortical areas have direct spinal projections independent of M1 [52,53]. Second, functional imaging studies repeatedly find that these pathways do not function independently [54•]. Third, it is difficult to assign discrete functions to particular anatomical substrates as the properties of their cell activity during movement are similar [55–57].

With these problems, how might we gain a realistic understanding of the processing responsible for the development of volitional action based on visual stimuli? It is likely that parameters used in this process are represented with broad tuning functions in every structure of the pathway. One approach would be to record the activity of many cells simultaneously from different structures

in the pathway. Each cell could be mapped analytically to an n -dimensional space based on its response to a variety of parameters. The dimensions of this space can be any aspect of the experiment that can be measured, even those that are relatively abstract [6]. It is likely that cells mapped this way will not fall along particular axes. Rather, they should be distributed homogeneously through the parameter space, as these cells encode multiple parameters [4**,36*,58]. If this mapping were done with a large sample from many of these structures, a time-series of n -dimensional population vectors through this space calculated at intervals throughout the task should reflect accurately the processing subserving the volitional action.

The response of each cell can be represented as a point in the parameter space (Fig. 2). The coordinates of this point could be considered the coefficients of multiple regression performed on each of the parameters and the cell's discharge rate. When normalized, these coordinates could function as the direction numbers for an n -dimensional vector, A . A behavior can be described by a set of parameters with specific values and these normalized values can be used to describe another vector, B . The discharge rate of the cell would be the projection of vector A onto vector B calculated by taking their dot product. A population vector could be built weighing each cell vector (vectors A_1, \dots, A_n) and summing their values. The resultant population vector will point to the behavior, if the cell responses are independent, homogeneously distributed in the space and broadly tuned to each parameter. If cells within a structure are involved in movement generation in a similar way, they should form clusters in this space and the evolution of these clusters throughout the task could explain how cellular activity in one structure interacts with that of another. This is one example of a new variety of analysis (see [54**,59*]) that can be applied to distributed systems.

Acknowledgement

This research was supported in part by USPHS NS26375.

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