

# A Connectionist Model May Shed Light on Neural Mechanisms for Visually Guided Reaching

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## Abstract

Formal principles of vision-based planning and control of arm movements are used to gain insight into the neurobiological mechanisms that underlie this important class of sensorimotor behavior. The primary conceptual tool used in this work has been a neurally inspired connectionist system called MURPHY that learns to reach for visual targets among obstacles, crudely based on the style of architecture and representations in sensory and motor areas of cerebral cortex. This system has provided a concrete implementation that demonstrates how

areas of cerebral cortex could in principle interact to direct both sensory-locked and internally planned reaching movements. We use MURPHY's simple, artificial "cortex" as a point of departure in the development of two high-level cortical models for visual limb control, involving the supplementary motor area (SMA), areas 5 and 7 of the posterior parietal lobe, and several visually responsive areas including V2, PO, and areas TPO and STP in the upper bank of the superior temporal sulcus. ■

## INTRODUCTION

The goal of this work has been to gain further insight into the neural basis for the planning and kinematic control of limb movements, an important systems-level function of the brain that remains poorly understood. The control of reaching is a useful model problem in cognitive neuroscience because (1) it is of considerable ecological importance to humans, primates, and other animals, (2) it embodies several of the central elements of intelligent behavior, including complex coordinate transformations and sequence planning, (3) the abstract problem of guiding a multilink arm through a workspace is well understood mathematically, and algorithms exist for every aspect of its solution (i.e., kinematics, dynamics, and path planning), and (4) a large body of psychological, physiological, anatomical, and neuropathological data is available that bears directly on the brain's underlying approach to the problem.

In spite of all such advantages, the neural mechanisms for visually guided reaching remain complicated and obscure, distributed across a large number of multiply interconnected areas of the brain including the posterior parietal cortex (consisting of a dozen or so subareas), the primary motor, premotor, supplementary motor, and parts of the prefrontal cortices, the basal ganglia, and the cerebellum and its nuclei (Georgopoulos, 1986; Goldberg, 1985; Humphrey, 1979; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Wise, 1985). To further complicate the picture, these same areas participate in

the control of numerous other sensory, motor, and limbic functions. For example, the posterior parietal cortex (PPC) is intimately involved in the control of eye movements and visual attention (Andersen, 1987; Bushnell, Goldberg, & Robinson, 1981; Lynch, 1980; Mountcastle et al., 1975), the premotor cortices participate in the generation of speech and other movements, etc. (Goldberg, 1985; Wise, 1985). Likewise, clinical syndromes that arise from destruction of each of these areas are characterized by a wide range of behavioral deficits that are in many cases unrelated to the control of reaching, such as a generic lack of spontaneous movement (damage to SMA or basal ganglia) (DeLong, 1990; Goldberg, 1985; Taylor, Sladek, Roth, & Redmond, 1990), or the eerie hemilateral neglect phenomenon in which a patient inappropriately ignores events in half of extrapersonal space—in extreme cases to the point of denying ownership of his own limbs (damage to PPC) (Lynch, 1980).

In the current work we adopt an unusual approach to the understanding of a neurobiological system. We first review some of the basic computational issues that arise in the planning and visual control of arm movements. Second, we describe a neurally inspired connectionist robot motion planner that steers a multilink arm to visual targets in the presence of obstacles (Mel, 1988, 1989, 1990a). Beyond the goal to explore a novel engineering approach to a difficult real-world problem, the robot-camera system, called MURPHY, demonstrates how a handful of neuronal populations representing various aspects of an organism's "mental" state, interconnected in anal-

ogy with sensory, motor, and association areas of cerebral cortex, can function together to direct arm movements in a complex environment. The availability of a concrete solution to the problem, built from neurally inspired elements, provides a valuable conceptual tool that can guide the search for the true *biological* mechanisms of sensorimotor integration that underlie this type of motor control. Finally, we use MURPHY's simple, artificial "cortex" as a point of departure in the attempt to interpret aspects of the neural basis of the behavior in humans and other animals.

## VISUALLY GUIDED REACHING

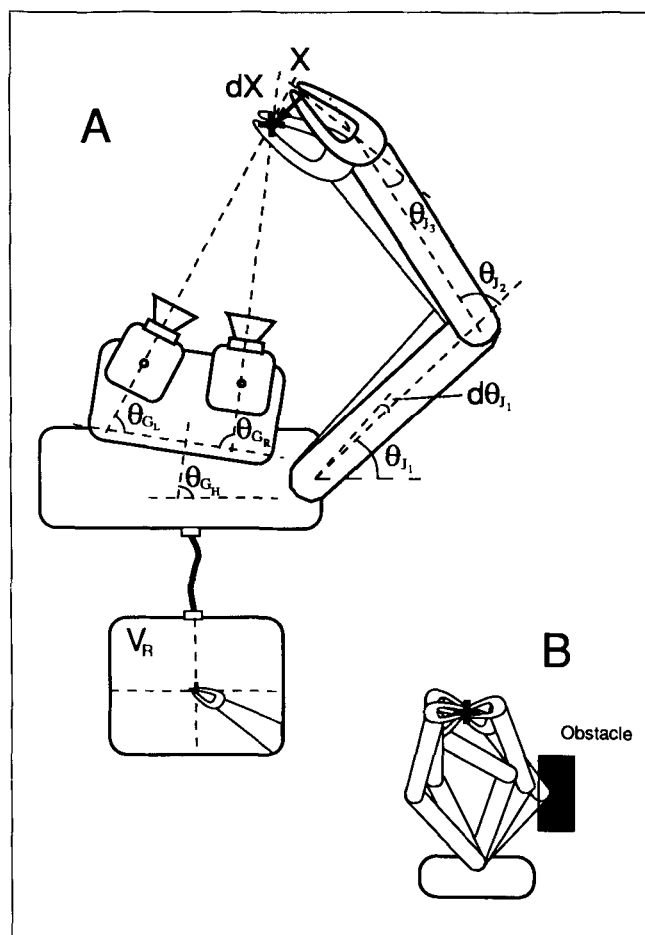
### The Computational Problems

The apparent ease with which we reach for objects in everyday experience does not imply simplicity in the underlying mechanisms. Both planning and control of a jointed arm using vision are in fact very difficult computational problems, requiring knowledge of the complex spatial relationships between the body and its parts and the coordinate systems and contents of the external world. As is true for the visual control of eye movements or locomotion, the ability to reach for visual targets requires that body parts be aligned through sequences of motor commands with an external environment that is specified only sensorially. A profound and very general problem thus exists as to how to relate information in these two different internal languages. In the following paragraphs, we introduce the basic concepts of kinematic control of a multilink arm. As the principal emphasis of this work is on motion planning, arm dynamics are not treated here (see Bullock & Grossberg, 1988; Flash, 1989; Hogan, 1984, 1988; Paul, 1981).

### Kinematics for a Multilink Arm

#### Forward Kinematics

The term *kinematics* refers to the geometry of the arm and its relationships to the workspace. Assume the posture of the arm is determined by a set of  $n$  joint angles  $\Theta = \{\theta_1, \theta_2, \dots, \theta_n\}$ , and consider for the moment only the position of the tip of the arm in the workspace  $X = \{x, y, z\}$ , hereafter referred to as the "hand" (Fig. 1). A set of straightforward trigonometric equations can be written that take joint angles as inputs and give as outputs the  $(x, y, z)$  coordinates for the hand in the workspace. These equations specify the *forward kinematic* relation for the arm, and depend on the type of joints (i.e., spherical, prismatic, rotational, etc.) and the lengths and shapes of each of the arm's links. Related equations can be written to generate the workspace coordinates for any other points on the arm, in addition to the hand. Thus, a system with a forward kinematic model can predict the spatial configuration of the arm in the workspace given a set of internally represented joint angles. Figure 2A



**Figure 1.** (A) Representation of several variables relevant to the kinematic control of a multilink arm, including  $X$ , the position of the hand in the workspace,  $dX$ , the vector designating the direction and amplitude of a small change in hand position,  $\Theta_G$ , direction-of-gaze variables, including both head and eye-position components,  $\Theta_j$ , joint angles,  $d\Theta_j$ , infinitesimal changes in the joint angles, and  $V_R$ , a binocular retinal image of the arm in the workspace. (B) When the arm has excess degrees of freedom, a given target can be reached, in general, with many different configurations of the arm. Some may be impossible given the layout of obstacles in the workspace.

shows an iconic representation of the forward kinematic relation for a multilink arm. Input and output variables depicted as boxes may be actually represented using numbers, computer memory locations, or neurons. The arrow represents the forward kinematic function and may be implemented in several ways, such as with equations, a computer program, or a neural net. Figure 2B shows a more biologically relevant instantiation of forward kinematics that takes into account the ability to orient the head and eyes and the wide incidence of visuotopically mapped representations in the visual systems of higher vertebrates. An additional input vector  $\Theta_G$  specifies the orientation of the head and the directions of gaze for the two eyes. These variables combine with the joint angles  $\Theta_j$  to produce an output vector  $V_R$ , a retinotopically mapped visual image of the arm in the workspace as it reaches for targets.<sup>1</sup> Note that a full visual

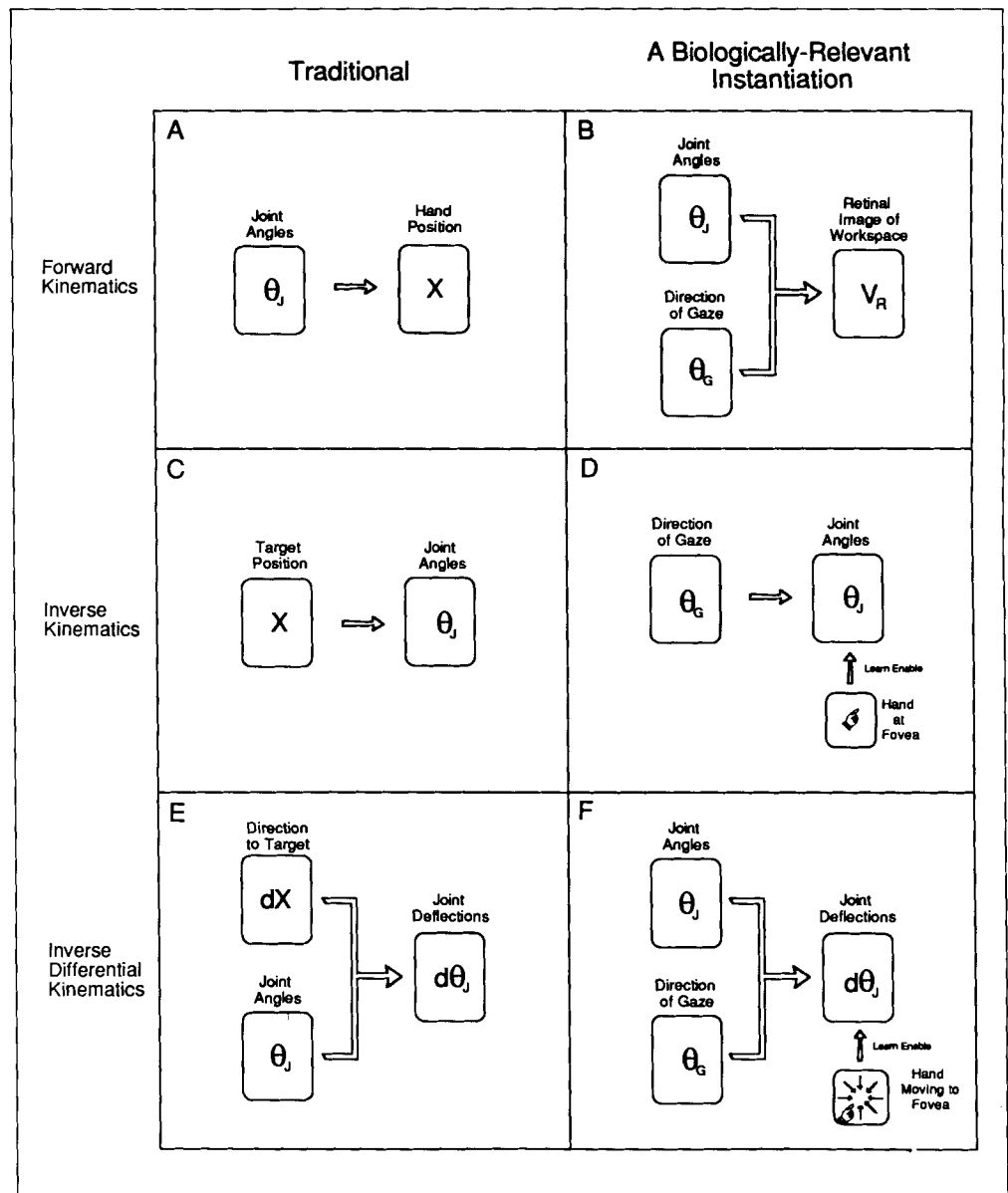
image of the arm is a much richer “output” than is traditionally associated with the forward kinematic map (Fig. 2A). The visual representation of Figure 2B could have been chosen to be in head- or body-centered coordinates,<sup>2</sup> though the biological evidence for true head- or body-centered visual representations is currently lacking (but see Andersen, 1987; Andersen & Zipser, 1988; Andersen, 1989).

### Inverse Kinematics

A much more difficult problem is that of deriving the *inverse kinematic* relation, i.e., equations that take a desired final position  $X$  of the hand as input, and generate a set of final joint angles  $\Theta_j$  that place the hand at the desired location, such as to grab a target (Fig. 2c). This is usually conceived as the most direct means for dis-

patching a jointed arm to a target when no obstacles are present. One reason the problem is so difficult is that, in a system with excess degrees of freedom, such as the human arm, there are generally very many different ways to configure the arm such that the hand is in contact with a target. The inverse kinematic mechanism, however represented, must therefore choose one among multiple inverse solutions (Fig. 1B). A further complication arises when there are obstacles in the workspace, since many configurations of the arm that correctly place the hand at the target may be disqualified due to the layout of obstacles. In general, in the case of cluttered workspaces, it is necessary to explicitly plan a collision-free path from start to finish (see section on motion-planning below). Figure 2D shows an instantiation of the inverse kinematic map, once again based on biologically relevant variables. Assuming the target is fixated, direction-of-gaze variables

**Figure 2.** Iconic representation of traditional kinematic functions (left column) and a biologically motivated instantiation for each (right column). Input and output variables are depicted as boxes; arrows represent the functional relations that hold between them. Special additional variables may be used as “gates” during learning, signaling those states of the system when the input and output variables are in their proper relation (**D**, **F**). See text for additional details.



$\Theta_G$  substitute for the explicit coordinates of the target  $X$ . In addition, a new variable, that signals the presence of the hand at the fovea, specifies when the correct relation holds between the principal input and output variables  $\Theta_G$  and  $\Theta_J$  during movement of the arms. In other words, the eyes can be fixated anywhere in extrapersonal space, but only when they fixate the hand is the relation between direction-of-gaze and joint angles a correct instance of this inverse kinematic map. The hand-at-fovea variable can thus be used as a “gate” that selects for well-formed training examples during learning (the issue of learning is taken up again below). Kuperstein (1988) developed an interesting neurally inspired connectionist system that learns inverse kinematics in essentially this way.

### Differential Kinematics

If the forward kinematic equations are differentiated, a *differential kinematic* relation results, which specifies how small changes in joint angles are mapped into small changes in the position of the hand in the workspace. On the other hand, the inverse of this differential relation can be used to calculate appropriate small changes to the joint angles  $d\Theta_J$  (Figs. 1A, 2E) if it is desired to push the hand in a particular direction  $dX$ , such as toward a visual target. This relation is thus a useful mechanism for aiming at and/or tracking a visual target. Once again, a biologically motivated instance of this function is shown in Figure 2F. The direction from the hand to the target is implicit in the combination of direction-of-gaze variables, which encode the location of the fixated target, and current joint angles, which encode the location of the hand. The appropriate differential joint commands  $d\Theta_J$  may thus be written as functions of only the joint and gaze variables. As in Figure 2D, an additional variable is included that specifies when the correct kinematic relationship holds between input and output variables, if the map is to be learned: When the gaze is fixed at a point in extrapersonal space, a commanded change in joint angles  $d\Theta_J$  is a “correct” instance of this inverse differential map if the hand moves toward the point of fixation. A population of motion-sensitive visual cells with radially inward direction preference is one approximation to this “hand-moving-to-fovea” function.

### Motion Planning

The differential kinematic relation discussed above embodies a minimal notion of the arm’s *path*, however, an explicit representation of the reaching problem as a whole, including the layout of targets and obstacles, is still needed to plan collision-free movements for the entire arm. The conceptually simplest way to plan a path for a multilink arm is to use heuristic search. For example, from the starting posture of the arm, a set of neighboring postures are internally generated as possible candidates for the arm’s next position. Then, by run-

ning the forward kinematic map internally, i.e., without moving the arm, it can be determined for each candidate posture (1) the remaining distance from the hand to the target and (2) whether the arm remains clear of obstacles. The posture that results in the greatest progress toward the target without causing a collision is accepted. The search cycle is then repeated from this new, simulated position until the hand either reaches the target, or becomes trapped in a “local minimum.” If the target was reached, the complete stored path is physically executed; if the search was caught in a local minimum, the most recent internal move is rejected and the search loop continues. Much more sophisticated algorithms have been devised that eliminate illegal arm configurations before the search begins, conduct the search at variable resolution, etc. (for review see Latombe, 1991; Mel, 1990a). However, the dependence on some form of search is a feature common to all global path planning algorithms.

### Two Types of Reaching

As is implicit in the above discussion, two distinct types of vision-based reaching may be identified. In *type-1*, or “sensory-driven” reaching, motor commands are generated as direct functions of sensory variables, i.e., joint and gaze angles and target locations. According to this definition, both inverse and inverse-differential kinematics are type-1 reaching algorithms. Without implying a commonality of underlying mechanism, a *type-1* reaching movement that sends the hand to a visual target may be compared to a visual saccade, which sends the *fovea* to a visual target. No obstacles are assumed to be present in either case, making path planning unnecessary. The ecological relevance of type-1 reaching derives primarily from the fact that it is fast to compute, useful for grabbing, swatting, fighting, catching, etc.

In the presence of obstacles, however, a hand plunged directly toward a visual target may result in a collision. A means of choosing among alternative paths to the goal is thus necessary. *Type-2* reaching describes arm movements that are planned, i.e., that involve an internal search process using a model of the arm and the workspace that evaluates alternative movements against their predicted workspace consequences. During planning, those paths that involve collisions or other inconveniences are “mentally” discarded in favor of those that bring the hand efficiently and uneventfully to the target.

### HOW MURPHY WORKS

MURPHY is a kinematic controller and vision-based robot motion planner that learns from experience, based on a neurally inspired connectionist architecture [see Mel, (1990a) for complete description]. The problem of central concern in this work was to guide a multilink arm to visual targets in a workspace cluttered with obstacles.

In contrast to other formulations of the motion-planning problem (e.g., Brooks, 1983a,b; Favrejon, 1984; Khatib, 1986; Lozano-Pérez, 1987), emphasis in this work was on finding ecological solutions, more relevant to the typical visually guided reaching behaviors of humans and animals in natural environments, than to the highly structured demands of an industrial setting. For example, we desired algorithms that would work well in unfamiliar workspaces whose effective layouts with respect to the body can change from moment to moment with movements of the eyes, head and limbs. Further, exact kinematic tolerances were considered less important than the flexibility associated with the ability to learn sensorimotor relationships through active practice. While not intended as a strict model for a particular neural subsystem in a particular animal species, MURPHY's data structures and algorithms were also constrained to adhere to the *style* of representation and computation seen in biological sensory and motor systems to the greatest extent possible. In consequence, no a priori analytic model (i.e., kinematic equations) of the arm-camera system were included—instead MURPHY was to learn these quantities “by doing.” Complex, special-purpose algorithms and data structures for motion planning with obstacles were also avoided in favor of a simple search procedure using visual “mental” images of the arm.

The internal connectionist architecture was designed to emulate aspects of the organization of cerebral cortex. Several guidelines were adopted: (1) to create a set of neural populations, each of which represents some aspect of the organism's sensory, motor, or internal state, (2) to define the semantics (i.e., response properties) of individual neurons in these populations in keeping with known electrophysiological response properties of cortical neurons, and (3) to allow for plastic interconnection pathways between any two (or more) of the neural populations. It was envisioned that within such a framework, an organism could simply *behave*, and while doing so, profit from a rich set of associative learning opportunities. Once learned, these associative mappings could act as mental models that could be run internally to guide future behavior. Only a brief overview of MURPHY's representations and algorithms is presented here; for more details, see Mel (1988, 1989, 1990a).

### The Physical Setup

MURPHY's physical setup consists of a computer-controllable robot arm with wrist, elbow, and shoulder joints, and a camera that looks at the arm. The three joints move only in the frontal plane of the camera, such that the reaching problems MURPHY faces are two rather than three dimensional. Figure 3 shows MURPHY's view of his arm, a target (white cross stuck to backdrop), and obstacles (other white paper cutouts). MURPHY's *internal* image of his arm is reduced, for reasons of visual processing efficiency, consisting of only those parts covered with

white spots or markings (Fig. 5). Intermediate regions of the arm are explicitly computed internal to the program. During reaching, the target is “acquired” when the hand is visually superimposed with the target from the perspective of the camera. A collision is said to occur when any part of the arm falls into superposition with any of the backdrop obstacles.

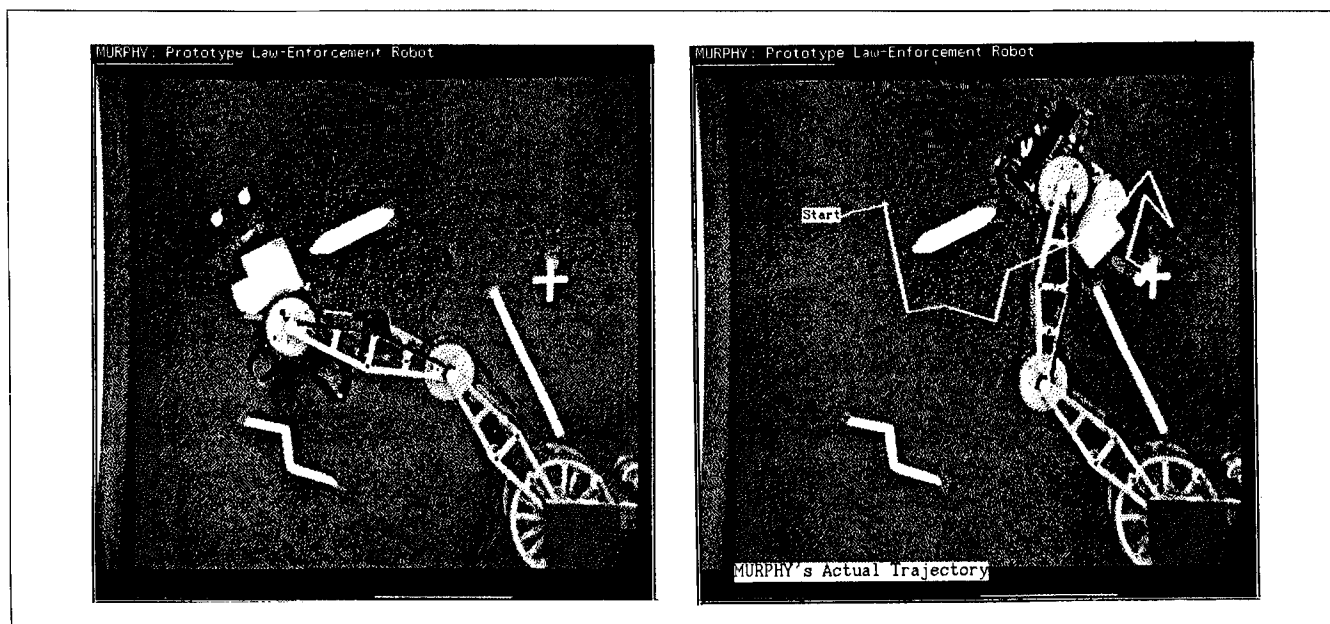
### The Connectionist Architecture

MURPHY's connectionist architecture is based on four interconnected populations of neuron-like units (Fig. 4), encoding visual position, visual velocity, joint position, and joint velocity. All four are coarse coded, i.e., consist of units with peaked receptive fields that overlap among neighboring units, and whose peak sensitivities vary systematically from unit to unit across the population. This type of coarsely tuned representation is ubiquitous in biological sensory systems and has a number of representational advantages, including finer stimulus discrimination and increased immunity to noise and unit malfunction (Ballard, Hinton, & Sejnowski, 1983; Hinton, 1986; Erikson, 1984; Baldi & Heiligenberg, 1988; Sejnowski, 1986; Mel & Omohundro, 1991), as well as contributing to local generalization during learning (Ballard, 1987; Walters, 1987; Moody & Darken, 1989; Mel, 1988; Mel & Omohundro, 1991).

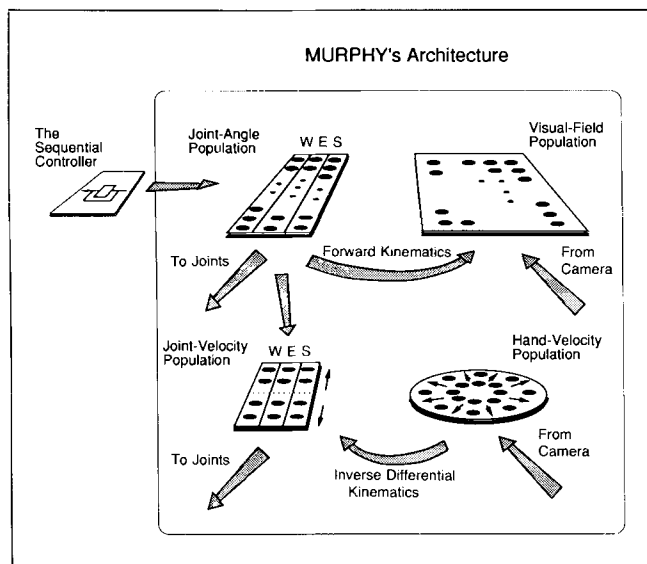
MURPHY's four “neural” populations were chosen to allow the learning and representation of both forward and inverse-differential kinematic relations. The *visual-field* population is organized as a rectangular, camera-topically mapped  $64 \times 64$  grid of visual units encoding  $V_R$ , whose responses to a view of the arm are shown in Figure 5 at upper right. The *joint-angle* population of 273 units encodes  $\Theta_C$  and consists of three subpopulations, one for each of the three joints. Each unit in a joint subpopulation is coarsely tuned, with a peak response at a specific joint angle. Peak responses within a joint subpopulation are distributed across the entire range of joint angles. The *hand-velocity* population consists of 24 visually activated units that encode  $dX$ . These units are “fired” only by the distinct visual image of the moving hand, and are selective for the direction and amplitude of hand motion through the visual field as MURPHY moves his arm in the workspace. The hand is detected as the largest contiguous blob of activity on the retina; however, any other distinctive cue could be employed. The *joint-velocity* population of 24 units encoding  $d\Theta_j$  also consists of three subpopulations, each encoding the *velocity*, i.e., change in angle during a unit timestep, for one of the three joints.

### How MURPHY Learns

The forward kinematic function that relates MURPHY's joint angles  $\Theta_j$  to visual images of the arm  $V_R$  is a smooth nonlinear function that can be learned from examples.



**Figure 3.** The physical setup. MURPHY's view of his arm in a typical starting configuration. Target (white cross) and obstacles (other white shapes) are paper cutouts stuck to backdrop 6" behind the plane of the arm's movement.



**Figure 4.** MURPHY's connectionist architecture. Four interconnected populations of neuron-like units implement MURPHY's forward-kinematic and inverse-differential kinematic mappings. Visual input from camera enters at right. A sequential controller (upper left) drives the joint-angle population during both learning and performance phases of operation.

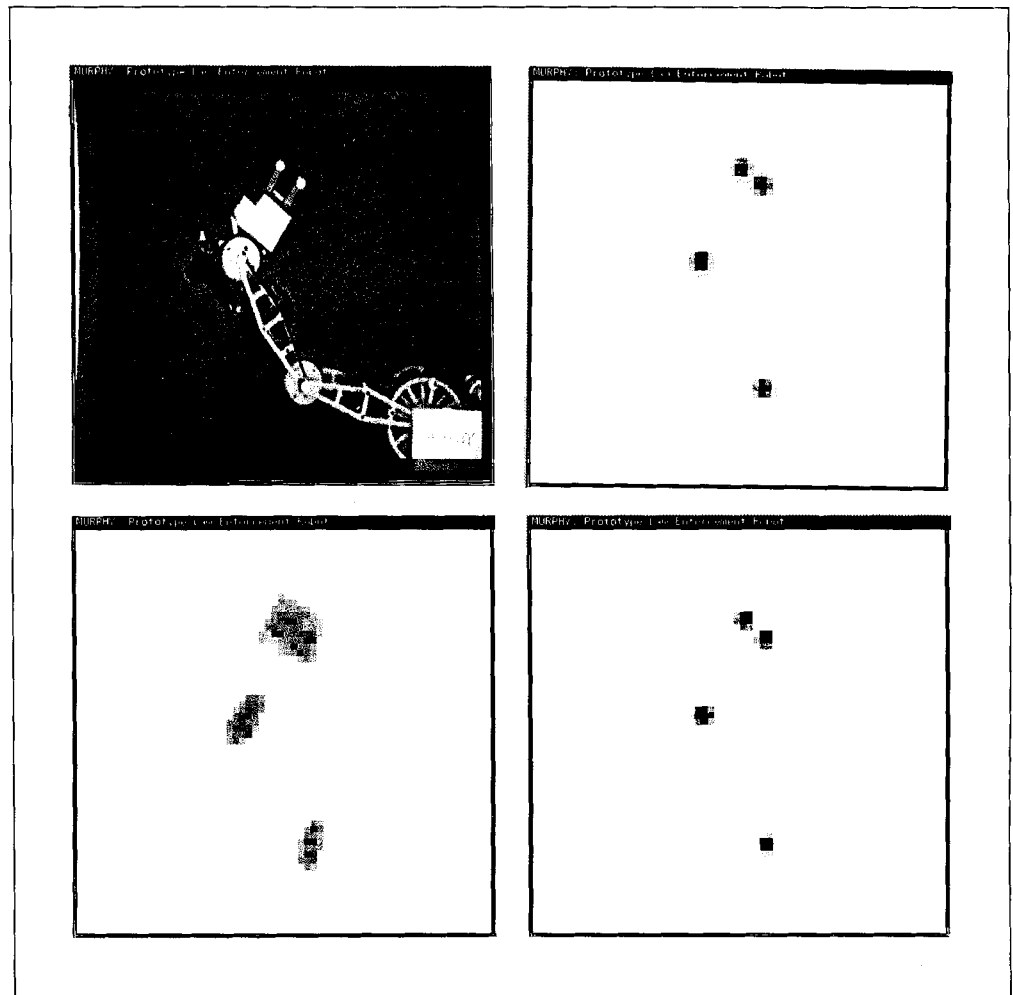
(Since the camera is fixed relative to the arm, the direction-of-gaze variables of Fig. 2B are not needed here.) MURPHY learns this map by stepping his arm through a small, uniform sample (approximately 17,000) of 3.3 billion legal arm configurations. During this training period, each unit in the visual-field population is occasionally activated when a portion of the arm falls into its visual

receptive field. Its pattern of "unconditioned" visual activation, driven by its input line from the camera, is thus a function that depends on the angles of the three joints. The unit's goal is to learn this function, i.e., learn to respond directly to its joint inputs with an intensity equal to that of its unconditioned visual input. Learning for each visual-field unit may thus be viewed as the establishment of an additional complex joint "receptive field." Learning is complete when each of the 4096 visual-field neurons can be fired "associatively" by its synaptic inputs from the joint-angle population, in a pattern that consistently predicts its visual input. The strength of synaptic connections between joint-angle units and their visual-field targets is variable and is that which encodes the forward kinematic functions. The details of the synaptic modification rule used in this standard neural-network learning problem are omitted here, as this paper is primarily concerned with the problems of reaching per se [see Mel (1990a) for description; see also Mel (1990b) for a discussion of the biological plausibility of synaptic learning rules].

Once learned, running the forward model involves first setting up a state of activity on the joint-angle population that encodes some arm configuration, and then allowing the synaptic projection to the visual-field population to generate a "mental image" of the arm in that configuration (Fig. 5). For visually specified problems, such as sending the hand to a visual target in the presence of obstacles, this type of *analogical* visual representation is a powerful, natural data structure.

The inverse differential relation is learned in a similar way. Each movement of the arm provides an example of

**Figure 5.** Four visual representations. Upper left frame shows the unprocessed camera view of MURPHY's arm. White spots have been stuck to the arm at various places, such that a thresholded image contains only the spots. Upper right frame shows the resulting pattern of activation over the  $64 \times 64$  grid of coarsely-tuned visual units as driven by the camera input pathway. Lower left frame depicts an internally-produced "mental image" of the arm in the same configuration, as driven by weighted connections from the joint-angle population. Note that the mental image is a sloppy but recognizable approximation to the camera-driven image. The last frame shows the mental image generated instead using k-d trees (Bentley, 1975), a more conventional computer science technique that has the advantage of far greater run-time efficiency during simulation than the neural network (Omohundro, 1987). The lower two frames thus exhibit the output of the forward-kinematic map under two different representational conditions. From (Mel, 1990a).



the relation between small changes in joint angle  $d\theta_j$ , represented by the joint-velocity population, and the direction (or desired direction) of hand movement through the visual field,  $dX$ , represented by the hand-velocity population. As before, the map has been successfully learned when initial states on the joint-angle and hand-velocity populations give rise, via the learned synaptic projection, to a set of commanded changes to the joint angles that push the hand in the desired direction through the visual field. Note that MURPHY's representation of the direction from hand to target is explicitly encoded as *retinal error*, i.e., as the vector pointing from the hand to the target, carried by a population of hand-centered, "direction-selective" visual units.<sup>3</sup> It is thus different from the movable-gaze system of Figure 2F, in which  $dX$  is *implicit* in the combination of direction-of-gaze variables, which determine the position of the target, plus joint angles, which determine the position of the hand. Reflective of considerable leeway in the design of sensorimotor systems, MURPHY could equally well have been designed to use visual-field *position* to code target locations, in analogy with direction-of-gaze, and in lieu of retinal error.

## MURPHY in Action

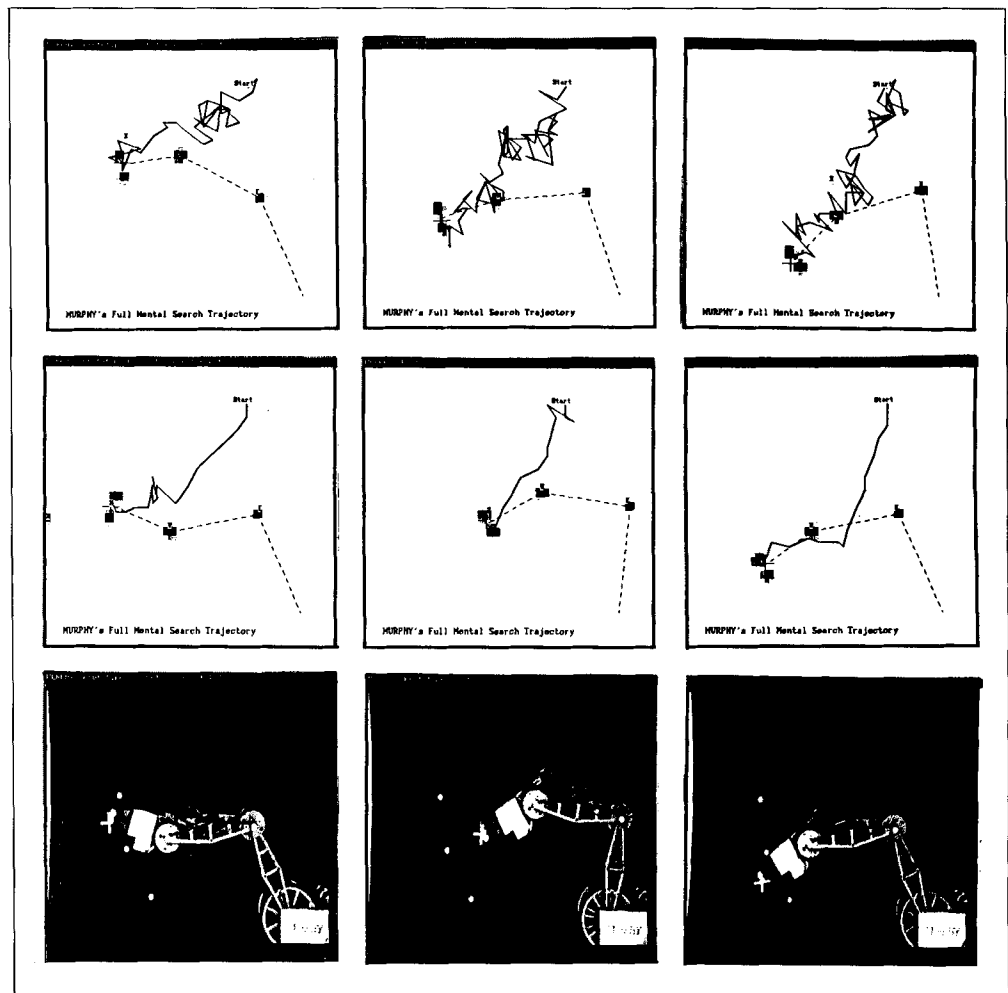
### *Sensory-Driven Reaching (Type-1)*

The bases for both type-1 and type-2 reaching are thus in place. Type-1, or visually driven, reaching movements are simplest, in that motor commands are generated as functions of the immediate sensory variables. Figure 6 shows the improvement in MURPHY's reaching performance when type-1 control comes on line after learning. Initial hand trajectories to a target are generated by a simple hill-climbing search process (top row). Each move of the arm acts as a training example for the inverse-differential map, as discussed above. After these three practice reaching trials the inverse-differential map is brought on line, generating sequences of "joint saccades" that lead to three new visual targets (bottom row).

### *Planned Reaching (Type-2)*

When obstacles are present in the workspace, arm movements must be planned in order to find trajectories that bring the hand to the target while avoiding collisions. MURPHY's planning mechanism is based on a simple

**Figure 6.** Type-1 reaching. Frames in the top row represent practice reaches to three visual targets (corresponding to the white spots in frames in the lower row), where each step in the random search acts as a training example for the inverse-differential kinematic (type-1) map of the arm. Frames in the second row show how the need to flail is mostly eliminated as the type-1 mechanism is brought on line; frames in the bottom row show the final configuration of the arm in three actual reaching trials.



search procedure. In addition to the forward kinematic map, MURPHY is endowed with a handful of simple, task-relevant visual operations including the ability (1) to distinguish target from obstacles, (2) to compute the distance from the hand to the target, and (3) to recognize when any part of the arm is in visual superposition with an obstacle, indicating a collision. The search procedure works as follows:

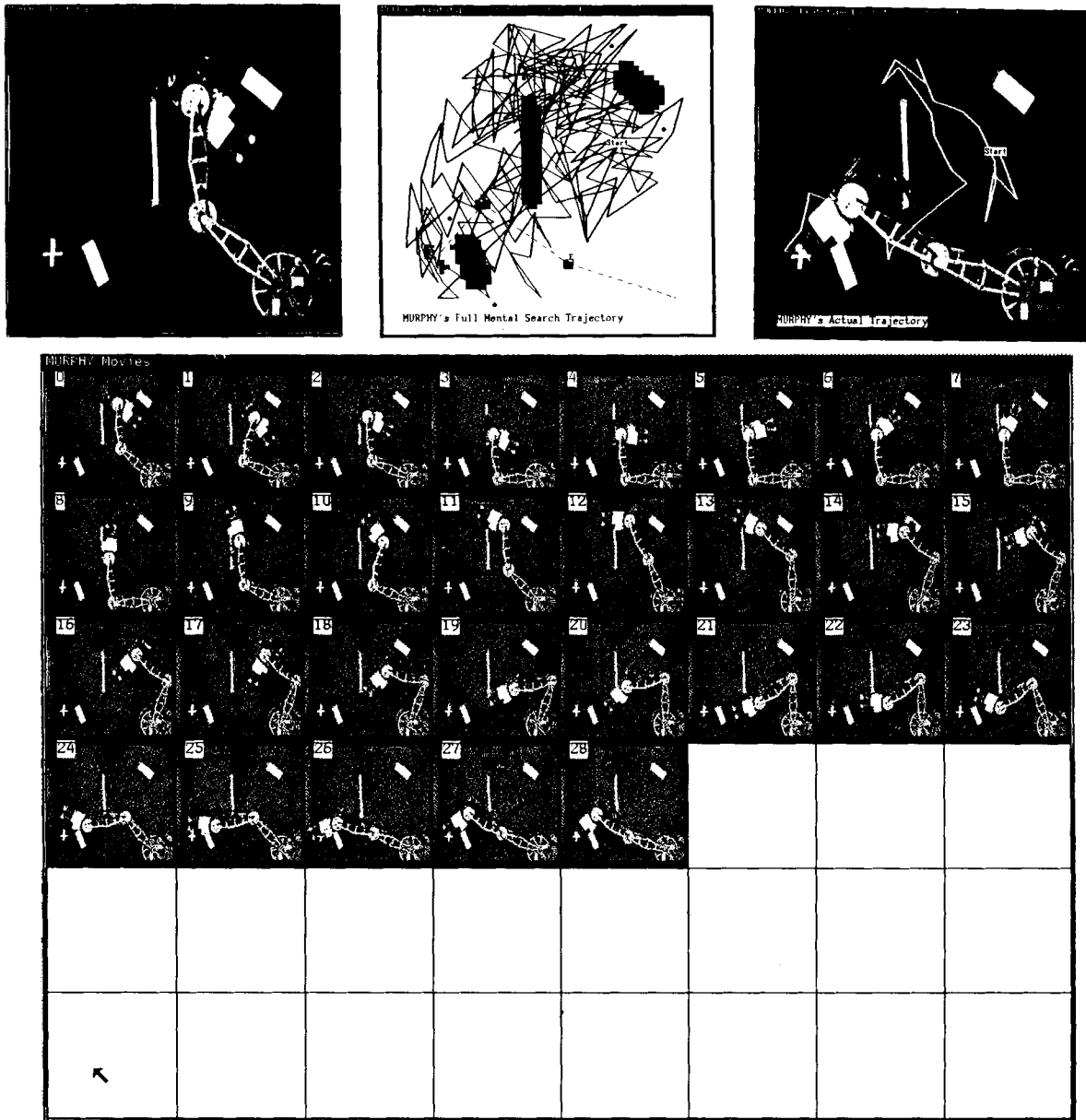
1. Label the target and any obstacles present in the visual field.
2. Generate a mental image of the arm in the initial joint configuration.
3. Measure the distance from hand to target.
4. Mentally move the arm in a random direction. This involves randomly perturbing the internal joint-angle representation, and regenerating the mental image of the arm—all without allowing the arm to move physically. If this arm configuration either has been tried before, pushes the hand out of the field of view, or causes a collision with an obstacle, then reject it and try another move. If there are no more moves to try from here, go back a step and try the next-most-promising move. If all paths are exhausted, give up.

5. Measure the new distance to the goal. If it has decreased, loop to 4 and continue moving closer. If it has increased, temporarily reject it, i.e., push it on the stack of things to try later, and go back to 4 for another try.

6. If and when the image of the hand reaches the target, move the arm physically to the target following the remembered path, dispensing with backtracking dead-ends.

Figure 7 demonstrates the path found in an example reaching problem (see caption for details). This problem is particularly difficult since the arm must be unwound in a cramped space before the target may be acquired, involving a complete traversal of the arm's joint space. In the process of unwinding, MURPHY is temporarily lured toward what appears to be a promising (but impossible) path over the top of the vertical obstacle (frames 8–12). As is the nature of heuristic search, the solution path is not optimal (e.g., as short as possible), but is usually a reasonable, if naive, path according to aesthetic criteria. Unfortunately, the level of “intelligence” necessary to understand *how* the paths are suboptimal is beyond MURPHY's current ability to reason.





**Figure 7.** Reaching for a target in the presence of obstacles. The left frame at top shows an initial configuration of the arm relative to a visual target (white cross) and obstacles. The second frame shows the sequence of intermediate hand positions generated during the mental search process. Once a complete, collision-free mental trajectory was found, MURPHY moved his hand physically to the target along a path pruned of backtracking dead-ends encountered during the search process (third frame). The lower panel shows a "movie" of intermediate steps in the physical execution of the plan, read from left to right by row.

### Two Other Connectionist Approaches

Two other connectionist schemes have addressed the learning of robot arm kinematics (Kuperstein, 1988; Reeke, Finkel, Sporns, & Edelman, 1989) that bear certain similarities to MURPHY. Reeke et al. (1989) describe a simulated automaton (Darwin III) based on an elaborate system of interconnected neuronal populations, includ-

ing rough analogues for motor cortex, two subgroups of cerebellar cortex, kinesthetic and tactile representations, analogues for visual cortex and superior colliculus, and various drive-reinforcement populations. The emphasis in this work has been learning based on Darwinian selection acting on initially unstructured patterns of neural connections. The task for which this approach appeared most successful was in the learning of the inverse-differ-

ential kinematic relation mapping a visual-field vector into perturbations to the joint angles, allowing the simulated 2-joint robot to acquire visual targets. In these early experiments, the authors do not, however, address the problem of motion planning in the presence of obstacles.

Kuperstein (1988) described a connectionist architecture that directly learns the inverse kinematics of a robot arm. This system is based on highly decoded populations of sensory and motor units, including binocular eye-muscle and direction of gaze maps, a binocular retina with orientation-selective responses, and a set of joint-muscle units. The 5-*dof* robot arm strikes a series of random poses in view of a binocular vision system with a cylindrical target object in hand. The inverse kinematic map is learned, taking the three-dimensional spatial coordinates and orientation of the target cylinder into corresponding joint angles for each of the 5 joints. The standard problem of multiple inverse solutions is not addressed in this work, however (see Fig. 1B). In addition, the architecture does not appear to be extensible to the case of reaching in the presence of obstacles.

## NEURAL MECHANISMS FOR VISUALLY GUIDED REACHING

As was stated in the previous section, MURPHY'S organization and behavior, while "biologically inspired," have not been intended as specific neural, psychological, or biomechanical models for the control of limb action in a particular animal species. Most obviously, in respect to primates, MURPHY'S possession of a single, fixed camera rather than independently orientable head and eyes has exerted a clear nonbiological influence on the choice of internal representation. Nor was any attempt made to model the psychophysics of biological limb motion, such as joint velocity and acceleration profiles characteristic of rapid arm movements. MURPHY'S psychology is also quite unlike that of his natural counterparts in a number of ways: (1) motor learning in humans and animals is not typically accomplished during a single uniform practice session over the space of actions, (2) where learning and performance phases of activity are distinct for MURPHY, they coexist in biological organisms, (3) in reaching for obstructed targets, humans and other primates clearly make more informed guesses in choosing initial candidate paths for their moving arms than does MURPHY, (4) likewise, there is no evidence that primates precompute entire complex trajectories mentally before actually moving their arms; a much more realistic scenario would have the mental model keep *just ahead* of the physical arm trajectory in order to avert collisions, and (5) MURPHY lacks any interesting treatment of goals and subgoals, clearly a crucial aspect of intelligent manipulation.

In spite of these differences, important similarities exist as well that are most evident at a more abstract level of description: (1) basic sensorimotor learning requires

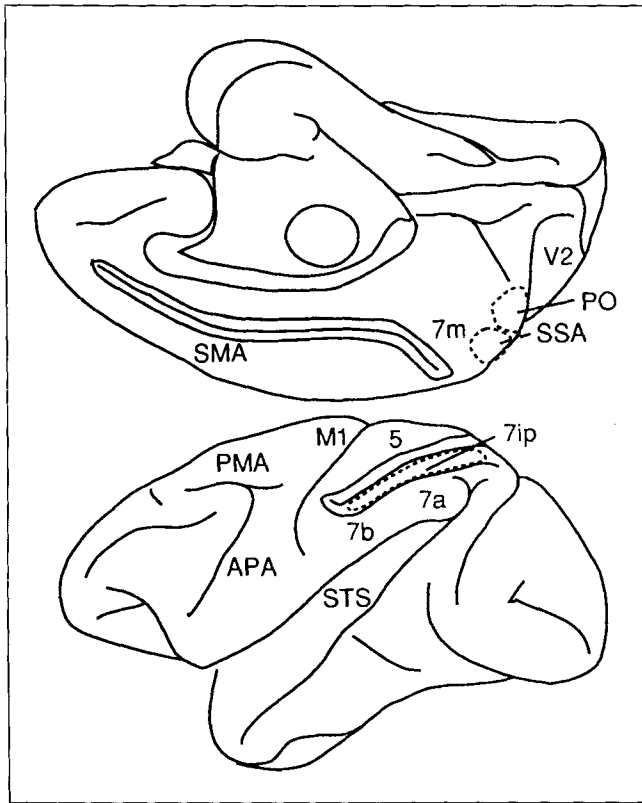
an extended period of active physical practice (Held, 1965; Schmidt, 1988), (2) two modes of vision-based arm control can be distinguished, one a sensory-locked subsystem for direct visually driven control, and the other subsystem for the programming of more complex movement patterns (Goldberg, 1985; Paillard, Jordan, & Brouchon, 1981), (3) analogical sequences of mental images can be used to solve difficult spatial reasoning problems (Finke & Shepard, 1985; Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989; Kosslyn & Shwartz, 1977; Kosslyn, Pinker, Smith, & Shwartz, 1979; Kosslyn, 1987; Mel, 1986; Shepard & Cooper, 1982), and (4) preprogramming of motor sequences takes longer as a function of task difficulty (Henry & Rogers, 1960; Klapp, 1977). Below, we explore in greater depth what can be learned about neural mechanisms from our current vantage point.

## Review of Basic Anatomy

Drawing from a number of independent lines of evidence, it has emerged that in primates, a large portion of the control of visually guided arm movements can be accounted for in a relatively well-defined complex of cortical areas, in addition to involvement of the basal ganglia and cerebellum (see Alexander & Crutcher, 1990a; Georgopoulos, 1986; Goldberg, 1985; Humphrey, 1979; Wise, 1985 for reviews). The cortical areas are shown in Figure 8 and include area 6 of Brodmann, comprising the ventrolateral (APA) and dorsolateral (PMA) premotor and supplementary motor (SMA) areas located just anterior to the primary motor area (M1), and both areas 5 and 7 of the posterior parietal lobes. Unfortunately, this complex of cortical areas is far from exclusively dedicated to the control of visually guided reaching: the SMA and the premotor areas have been implicated in numerous other integrative sensory and motor functions, such as the control of eye movements and the production of speech (Goldberg, 1985; Wise, 1985), while the posterior parietal regions play critical roles in the direction of attention and spatial perception and memory (Lynch, 1980). The array of behavioral deficits resulting from damage to the posterior parietal lobes is particularly daunting, making it inappropriate to attempt to treat these areas comprehensively within a single-function computational model. Our scope in the following discussion is therefore highly selective, limited to data specifically relevant to the control of visually guided reaching.

## Evidence for a Type-1/Type-2 Distinction

According to Goldberg (1985), a primary organizational feature of the neural substrate for the control of action is that it appears to be split into two distinct subsystems implementing two different modes of control. In a tantalizing analogy to the distinction between MURPHY'S



**Figure 8.** The complex of cortical regions implicated in the control of limb movement in the brain of the rhesus monkey. Areas include the primary motor cortex (M1), the supplementary motor area (SMA), the dorsolateral (PMA) and ventrolateral (APA) premotor areas, and areas 5 and 7 of the posterior parietal cortex. Several visual areas are also putatively involved, including V2, PO, and areas TPO and STP in the upper bank of the superior temporal sulcus (STS).

type-1 (sensory-driven) and type-2 (planned) control modes, Goldberg (1985) distinguishes the “medial” SMA-based neural subsystem from the “lateral” APA-based system:

The medial [SMA] system operates in “projectional” action or action that is driven forward by prediction derived from an internal model of the world composed from previous experience which permits the creation of a probabilistic model of the future (Bernstein, 1967). The lateral [APA] system is part of a system responsible for recognizing and associating motivational significance with external objects and, in relation to action, operates in a responsive mode in which each action is dependent upon an explicit external input.

Thus, the author argues, the lateral subsystem associated with the APA may dominate in tasks requiring an arm to swoop out reactively to an identified, motivationally significant target (type-1), in contrast to the medial system associated with the SMA for the control of complex navigational arm movements associated with reaching in the presence of obstacles (type-2).

A fascinating bit of evidence that accentuates the functional distinction between planned movements and direct visually driven control, but confuses Goldberg’s anatomical distinction, is reported by Moll and Kuypers (1977), who demonstrated that monkeys with premotor lesions, including *both* the SMA and the lateral premotor area, will reach directly and accurately toward food even when their reach is blocked by a transparent barrier. They therefore retain the ability to reach in a sensory-locked fashion, but lose the ability to plan an appropriate circuitous trajectory. It may thus be concluded that normal limb control in primates is achieved through the transparent superposition of at least two modes of control—one sensory-locked and one planned. The pattern of development in human infants of the ability to reach for visual targets seems to support this notion: The ability to reach around barriers develops only late in the first year of life in humans (Lockman, 1984), 4 to 6 months after the onset of highly effective reaching to unobstructed visual targets (Trevarthen, 1982). Furthermore, older infants have more trouble reaching around transparent than opaque barriers (manifested by their tendency to reach straight toward the target, in spite of the transparent barrier), suggesting poorly regulated competition among two modes of control.

### Toward a Neural Basis for Sensory-Driven Reaching (Type-1)

We briefly review here the key components of type-1 control, considering both inverse and inverse-differential kinematic modes together since their dependence on input and output variables is similar (see Figs. 1 and 2D,F). Both depend on target position, which may be encoded by direction-of-gaze  $\Theta_G$ . The inverse-differential mode of control additionally depends on the static arm configuration  $\Theta_j$ . Both modes produce motor commands, the former positional,  $\Theta_j$ , the latter directional,  $d\Theta_j$ . If the kinematic maps are to be learned, both require an additional visual variable that enables learning when, during normal behavior, gaze and joint variables are in their proper kinematic relations.

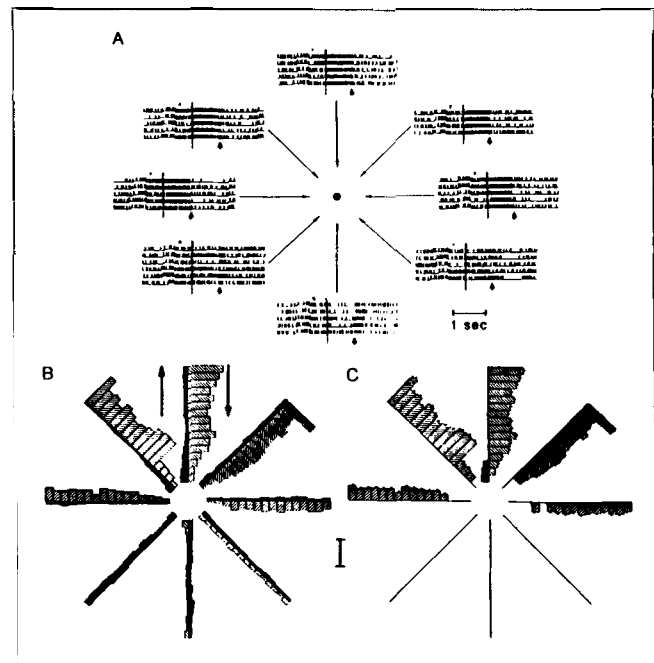
#### Cortical Representation of Kinematic Variables: Areas 7a and 7ip of the Inferior Parietal Lobe

Cells in area 7 of the posterior parietal lobe in monkeys exhibit several types of response properties of relevance to the visual control of limb movements. In the following discussion of area 7, we adopt the anatomical subdivisions of Cavada and Goldman-Rakic (1989a,b), which include 7a, 7b, 7ip, and 7m (Fig. 8). Areas 7a and 7b lie on the convexity of the inferior parietal lobe, corresponding to areas PF and PG of Von Bonin and Bailey (1947). Areas 7ip in the lower bank of the intraparietal sulcus corresponds to area POa of Pandya and Seltzer (1982); the posterior half of this area corresponds to the

ventral intraparietal area VIP of Maunsell and Van Essen (1983) and the lateral intraparietal area LIP of Andersen, Asanuma, and Cowan (1985) and Asanuma, Andersen, and Cowan (1985). Area 7m lies on the medial surface of the hemisphere and corresponds to area PGM of Pandya and Seltzer (1982).

Representation of direction-of-gaze is a crucial component in both type-1 mechanisms for visual limb control. A significant proportion of “fixation” neurons with “gaze fields” has been reported in areas 7a and 7ip of the posterior parietal cortex, among several other classes of neurons relevant to the control of eye movements and visual attention [see Andersen (1987) for review]. Fixation neurons are modulated by eye position in the sense that the responsiveness of their (usually) foveal receptive fields is greatest at specific orientations of the eyes in their orbits [see Andersen (1989) and Andersen & Zipser (1988) for more detailed discussion of the coding properties of these cells]. Further, Mountcastle, Motter, Steinmetz, and Duffy (1985) have shown that among area 7 visual neurons (as distinct from fixation neurons), receptive fields are very large, i.e., 10s of degrees in diameter, bilateral, and within the receptive field tend to show an unusual radially organized pattern of direction selectivity. Thus, a typical parietal visual neuron is maximally excited by a stimulus moving toward the fovea (Fig. 9). This type of response property appears ideally suited for encoding the hand-moving-to-fovea variable (Fig. 2F) needed during learning to signal that the ongoing motor commands  $d\theta$  are indeed pushing the hand toward the object of fixation. Mountcastle et al. (1985) have previously suggested a relevance of these radially organized visual receptive fields to the control of reaching. Evidence for parietal cells selectively responsive to the image of the hand at the fovea (useful for learning inverse kinematics—see Fig. 2b) is more limited: Leinonen, Hyvärinen, Nyman, and Linnankoski (1979) reported three neurons in area 7b that were maximally activated when the monkey was actively rotating and looking at its hand (and not other visual stimuli). Units responsive to images of hands have primarily been found in the inferotemporal cortex (Desimone, Albright, Gross, & Bruce, 1984), which projects to area 7ip (Cavada & Goldman-Rakic, 1989a,b), and units selective for faces and other complex visual stimuli that could include hands have been described throughout the upper bank of the superior temporal sulcus (Bruce, Desimone, & Gross, 1981; Perrett, Rolls, & Caan, 1982; Perrett, Mistlin, & Chitty, 1987), a region that has strong reciprocal connections to areas 7a and 7ip (Seltzer & Pandya, 1978, 1984; Cavada & Goldman-Rakic, 1989a,b).

Thus, the caudal region of the inferior parietal lobule (IPL), including areas 7a and 7ip, has a representation both of direction of gaze variables (esp. eye position) and of visual movement toward the point of fixation. Selectivity for a fixated image of the hand has been observed only in neighboring area 7b, but could exist as



**Figure 9.** Parietal visual neurons typically exhibit radially inward direction selectivity. Impulse replicas and radially oriented discharge histograms for a parietal visual neuron (PVN). The impulse replicas in **A** show the responses evoked during repeated trials when a  $10^\circ$  square visual stimulus moved in each of the eight radial directions through the visual field (long arrows) as the monkey fixated a small central target light. Vertical dashed lines indicated stimulus onset and small arrows the time at which the stimuli crossed the fixation point. In **B** and **C**, radially oriented stimuli were moved inwardly (diagonal shading) and outwardly (solid shading) from the fixation point in each of the eight directions. Bin size, 50 msec; vertical line = 100 impulses (imp)/sec; stimulus velocity,  $60^\circ$ /sec. (From Mountcastle et al., 1985.)

well in more caudal regions of the IPL, based on dense interconnectivity with temporal areas involved in the processing of complex visual patterns, including hands.

#### Area 5 of the Superior Parietal Lobe

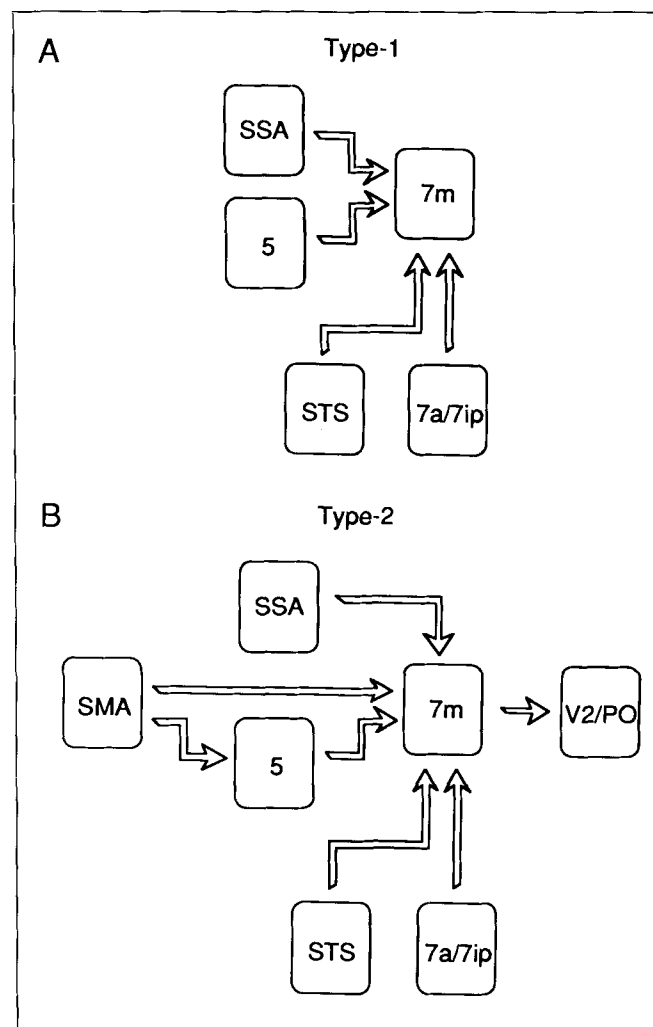
Additional variables encoding joint angles are needed to drive the inverse-differential map (Fig. 2F). Mountcastle, Lynch, Georgopoulos, Sakata, and Acuna (1975) reported that two-thirds of neurons in area 5 in the superior parietal lobule respond to joint rotation (Mountcastle et al., 1975). Responses were much brisker to active rather than passive movement of the joints, and 82% were related to single joints. Many were found to be sensitive indicators of the steady joint position, others selective for the direction of joint movement (i.e., flexion vs. extension) (Kalaska, Caminiti, & Georgopoulos, 1983; Chapman, Spidalieri, & Lamarre, 1984). Kalaska, Cohen, Prud'homme, and Hyde (1990) report that the responses of area 5 neurons are relatively insensitive to loading conditions during arm movements in different directions (in comparison to primary motor neurons in M1), implying that area 5 as a whole encodes primarily kinematic

parameters of joint movement (i.e., joint positions, velocities, etc.). Interestingly, 5% of area 5 cells were termed “arm-projection neurons” by Mountcastle et al. (1975), firing only before and during reaching movements toward objects of motivational interest within immediate extrapersonal space, and not for arbitrary, non-goal-directed arm motion. Roland, Skinhøj, Lassen, and Larsen (1980) have also demonstrated in regional cerebral blood flow (rCBF) studies that area 5 is activated only during voluntary movements in extrapersonal (as opposed to *intrapersonal*) space, i.e., for movements that require that the body and limbs be “lined up” with objects in the external environment.

#### Area 7m: A Possible Focus for Type-1 Limb Control

A major outflow from area 5 in the rhesus monkey proceeds caudally and medially, culminating on the medial surface of the hemisphere in area 7m (Pandya & Seltzer, 1982; Cavada & Goldman-Rakic, 1989a,b). No physiological data are yet available for this medial parietal area, but its anatomical connections are highly suggestive of a central role in visually guided limb movements. In addition to its joint-related input from area 5, area 7m also receives projections from the upper limb, neck, and head regions of the supplementary sensory area (SSA) (Cavada & Goldman-Rakic, 1989a,b), which could provide additional somatosensory state relevant to direction-of-gaze (i.e., orientation of the head). Area 7m is also reciprocally interconnected with areas 7a (Pandya & Seltzer, 1982; Cavada & Goldman-Rakic, 1989a,b) and 7ip (Cavada & Goldman-Rakic, 1989a,b), hereafter grouped as *lateral area 7*, which, as we have seen above, are capable of providing eye-position variables and a visual signal representing movement toward the point of fixation (such as would be produced by a reach toward a fixated visual target). As with lateral area 7, area 7m is reciprocally interconnected with several areas in the upper bank of the superior temporal sulcus (STS), including areas TPO (Seltzer & Pandya, 1978, 1984) and STP (Cavada & Goldman-Rakic, 1989a,b), which contain cells selective for complex visual stimuli that *could* include hands (whether they actually do is not known).

In sum, area 7m apparently lies at an ideal juncture of joint state information from area 5 and the SSA, direction-of-gaze information from lateral area 7 (eyes) and the SSA (head), and visual pattern information from the STS that could in principle provide selectivity for the image of the hand. (Further connections of area 7m that suggest involvement in type-2 reaching are discussed in the next section.) This circuit is shown in Figure 10A, with the proviso that all of the connections shown are actually reciprocal. Note that within this picture, both modes of type-1 control are superimposed within the same complex of cortical areas. Thus, area 7m is assumed to contain representation of both joint *posture*  $\Theta_j$  and



**Figure 10.** (A) Cortical areas putatively involved in the control of sensory-driven reaching (type-1). According to this model, area 7m on the medial surface of the hemisphere receives joint state input  $\Theta_j$  from area 5, direction-of-gaze input  $\Theta_G$  from lateral area 7 (eye position) and the SSA (head position), as well as visual-motion and pattern inputs relevant to the presence and trajectory of the hand through the visual field from lateral area 7 and the upper bank of the STS. Both modes of type-1 inverse control may be learned and encoded at the synaptic inputs to area 7m. Motor output of area 7m is via the dorsal premotor area and projections to the pontine nuclei (not shown). (B) Cortical areas putatively involved in the planning of forelimb movements (type-2). In addition to those areas described in A, area 7m is driven by the SMA both directly and via area 5 during motion planning. A modifiable synaptic projection to several topographically mapped extrastriate visual areas, including V2 and PO, is the proposed locus of the forward kinematic map. Thus, internally simulated joint states on area 7m drive visual mental images of the arm on these latter visual areas.

*movement*  $d\Theta_j$  command variables, the outputs of the inverse and inverse-differential maps, respectively. The functional dependence on sensory variables  $\Theta_j$  and  $\Theta_G$ , would of course be different for each. Within this scenario, this is what happens during a type-1 reaching trial:

1. A target is fixated, determining gaze variables  $\Theta_G$  in the SSA and lateral area 7.

2. According to the learned inverse kinematic relation, these gaze variables generate a motor command image specifying final joint angles  $\Theta_j$  in a subpopulation of area 7m neurons.

3. Simultaneously (or instead), sensory joint-angles  $\Theta_j$  from area 5, in conjunction with  $\Theta_G$ , generate a differential motor command image  $d\Theta_j$  in a second subpopulation of area 7m neurons.

4. Through connections to premotor areas, including dorsolateral area 6 and the SMA (Petrides & Pandya, 1984; Cavada & Goldman-Rakic, 1989a,b), and to the cerebellum via the pontine nuclei (Schmahmann & Pandya, 1989), area 7m the hand to the visual target.

### **Toward a Neural Basis for Planned Reaching Movements (Type-2)**

We now examine the neural evidence relevant to the *planning* of reaching movements. To lend structure to our exploration, we review briefly the key functional components of a motion planner, using MURPHY's predictive, type-2 motion-planning subsystem as a model. The principal components are a representation of joint angles  $\Theta_j$ , projecting synaptically to a topographically organized map of the visual field  $V_R$  (Fig. 4). As previously discussed, an organism with movable head and eyes requires that additional body state variables  $\Theta_G$  encoding head and eye position be available as inputs to the kinematic maps (Fig. 2B). Finally, during all types of behavior including learning, overt motor performance, and covert motion planning, an external sequential controller drives the joint representation through sequences of states. During learning, synapses are modified from the joint to visual populations. During motion planning, internally driven sequences of imagined joint postures give rise, via the learned synaptic pathway, to the sequences of visual mental images that are used to develop motion plans.

In addition to their proposed roles in type-1 reaching, areas 5 and 7 of the posterior parietal lobe are excellent candidate components of the putative visual imagery functions underlying type-2 limb motion planning. The studies of Roland and Friberg (1985) in fact strongly implicate areas 5 and 7 in this genre of mental imagery function, having shown increases in rCBF in these areas only during a mental visual route-finding task, in contrast to an arithmetic task or a jingle recitation task. Only the route-finding task required the envisionment of action in an environmental coordinate frame. Farrah (1988) reviews further evidence that the posterior parietal lobe may be a locus of visual mental imagery, citing selective deficits in mental imagery tasks in patients with occipitoparietal lobe damage. It seems difficult to dispute, then, that the posterior parietal cortex, including both areas 5 and 7, is active selectively during actions or imagined actions carried out relative to externally specified visual

coordinate systems. This possibility is pursued below, after a discussion of a related role for the SMA.

### *The Supplementary Motor Area Projects to Area 5*

The SMA appears to be a site for the programming of sequences of motor states involved in the preparation of complex motor acts, and may play a role similar to that of the sequential planning control structure that drives MURPHY's joints through sequences of postures (Goldberg, 1985; Roland, Larsen, Lassen, & Skinhøj, 1980; Roland, Skinhøj, Lassen, & Larsen, 1980; Wise, 1985). In keeping with this notion, high levels of electrical stimulation to the SMA typically elicit stable postures, commonly elevation of the contralateral arm with abduction and external rotation of the shoulder, in contrast to the phasic and rapidly habituating muscular responses evoked with stimulation of the primary motor cortex (M1) (Humphrey, 1979). Roland, Larsen, Lassen, & Skinhøj (1980) reported that significant increases in cerebral blood flow are seen in both the SMA and in M1 during the actual execution of complex motor tasks, but that when subjects were told to *mentally rehearse* these same motor sequences, blood flow was seen to significantly increase in the SMA alone. Suggestive of its role in motion planning, extensive premotor ablation including the SMA (but also extending to the lateral premotor areas), impaired the ability of monkeys to adapt a trained, visually directed straight-line reaching movement to reach *around* a transparent barrier for a piece of food (Moll & Kuypers, 1977), a task that requires nontrivial trajectory planning. Likewise, damage to the SMA or other aspect of the medial control system in humans (e.g., through Parkinson's disease) has been found to produce a more severe impairment to intentional, preplanned actions than to actions that are in response to immediate environmental contingencies, such as visual or other sensory cues (Laplante, Talairach, Meininger, Bancaud, & Orgogozo, 1977).

Having posited a tentative analogy between the SMA and MURPHY's sequential planning element, we next seek evidence for a joint representation on which the SMA could act, and which in turn projects to a topographic visual representation. Conveniently, the SMA is heavily interconnected with area 5, which, as reviewed above, contains a large proportion of neurons with both postural and movement-related joint responses. On this basis, and in analogy with MURPHY's joint-angle population, it may be concluded (see Mountcastle et al., 1975) that (1) area 5 is driven in part by the SMA, an area implicated in the planning and initiation of complex motor sequences, and (2) at least part of the function of area 5 is to represent body and limb posture information in the formation of movement plans relative to external, environmentally specified coordinates. Reiterating that area 7m receives a major outflow from area 5, in addition to its direct connections with the SMA (Petrides & Pandya,

1984; Cavada & Goldman-Rakic, 1989a,b), the further inference may be made that area 7m, in addition to area 5, is a plausible site for the representation of “mental” joint states used for limb motion planning.

### *Area 7m: Yet Another Proposed Role in Reaching*

The crucial additional feature of area 7m that invites suggestion of a role in type-2 reaching, following the model of MURPHY, is its significant connections with portions of several topographically mapped extrastriate visual areas (Cavada & Goldman-Rakic, 1989a,b), including V2, parietooccipital area PO in the parietooccipital sulcus (Gattass, Sousa, & Covey, 1985), and a region dorsal to it that is visually responsive as well (Colby, Gattass, Olson, & Gross, 1988). Thus, in addition to lying at a “hub” where all of the body-state variables needed for the visual control of reaching, including joint position and direction-of-gaze neurons, are anatomically convergent, area 7m projects to several topographically mapped visual areas.

### *A Cortical Model for Type-2 Reaching*

It is eminently clear that no simple one-to-one correspondence holds between MURPHY’s monofunctional areas and those of the cerebral cortex involved in the control of reaching. The evidence reviewed, however, suggests grounds for a functional analogy between MURPHY’s forward-kinematic planning subsystem and the “extended internally dependent, predictive or *projectional* action system of the cerebral cortex” (Goldberg, 1985), including the SMA, areas 5 and 7 of the posterior parietal cortex, and a handful of associated, topographically mapped extrastriate visual areas. Primary features of correspondence are summarized below (Fig. 10B):

1. The SMA is active during motor behavior and imagined motor behavior, in possible analogy to MURPHY’s sequential controller.
2. The SMA projects to area 5, a body representation that is rich in units encoding primarily kinematic (as opposed to dynamic) joint parameters, in analogy with MURPHY’s joint-angle population. Area 5, like the SMA, is active during both real and imagined motor behavior, *but only when the action is relative to coordinates of the external environment*. A major outflow of area 5 leads to area 7m, an area for which no physiological data are available. However, area 7m receives input as well from the SMA and from the head, neck, and forelimb regions of the SSA, making it highly likely that a subset of neurons within area 7m is devoted to kinematic forelimb joint parameters. Also, area 7m receives input from areas 7a and 7ip, which contain a subset of neurons that carry an eye-position component of direction-of-gaze (Andersen, 1989; Andersen & Zipser, 1988).
3. In the crucial step in the kinematic transformation,

area 7m projects to several topographically mapped extrastriate visual areas, including V2 and PO. This efferent synaptic projection carrying joint and gaze state information from area 7m to the complex of extrastriate visual areas could be associatively modified during learning to become the locus of the forward-kinematic model, and hence also the site of visual mental imagery generated during forelimb motion planning. These same visual areas are connected as well to area 7a, and thus may directly receive eye-position variables through this route, in addition to that which may be provided by 7m. No joint-related responses have yet been reported in these “visual” areas, though it is unlikely they have been explicitly sought, and given the complex stimulus requirements (possibly including specific active movements of the limbs), could have been overlooked.

Within this simplified picture, the SMA is continuously active during motion planning, driving the body representation in area 5 and hence 7m through a sequence of imagined postures. Activity in area 7m in turn drives a corresponding sequence of mental images within its associated extrastriate visual areas that encode the *visual* consequences of these joint postures. Throughout the process, these visual mental images are continually monitored and evaluated by unspecified “higher” centers in the prefrontal, temporal lobe, and/or limbic sites to which these visual areas project.

### **Predictions of the Two Models**

The models of Figure 10A,B are speculative. As they are grounded on incomplete physiological and anatomical information, they are likely to be incorrect in at least some of their details. They are nevertheless specific enough to generate several testable predictions:

1. Area 7m must be active during both type-1 and type-2 reaching. Similarly, functional removal of area 7m alone should result in severe deficits in all types of reaching behavior.
2. A relatively large proportion of area 7m neurons should exhibit complex joint receptive fields, modulated by position of both head and eyes. Foveally directed visual motion, particularly by the hand, should also either be an effective stimulus by itself, or at least act as a subthreshold facilitatory input. Electrical stimulation of area 7m should result in joint movement.
3. Functional removal of the SMA alone (and not the entire premotor cortex) should abolish type-2 reaching behavior, such as in a task involving reaching for a target amid obstacles that are reconfigured on each trial. Functional removal of the extrastriate visual areas V2 and PO should also abolish type-2 reaching behavior, but should leave other complex nonvisually mediated motor programming functions intact.
4. Neurons in those portions of PO and V2 that receive input from area 7m should have visual receptive fields,

but be maximally driven by a combination of a visual stimulus, and any joint posture or movement that moves the arm into or through the unit's visual receptive field. Unlike the conjoint visual-joint neurons seen in other parts of area 7, visual receptive fields should be unilateral, of moderate size, and topographically organized. These visual areas should be activated during limb motion planning.

5. Conjoint visual-joint neuron responses, if observed in these extrastriate visual areas, should be selectively and profoundly disturbed in animals raised without view off their forelimbs but with otherwise normal vision. Further, in analogy to the ability of human subjects to adapt their visually guided reaching behavior when wearing prisms that systematically alter the locations of objects in the visual field (Held, 1965), these visual-joint neuron responses should be rapidly modifiable during a period of practice reaching under prism-induced visual-field perturbation.

## DISCUSSION

### Scope of the Approach

The goal of this work has been to bring formal concepts concerning the vision-based planning and control of limb movements to bear on the problem of discovering the neural basis for this ecologically important behavior. One vehicle for this conceptual transfer has been a simple, neurally inspired connectionist system for the planning and control of robot arm movements, crudely based on the style of architecture and representations of sensorimotor areas of cerebral cortex. The system, called MURPHY, has provided a concrete implementation that demonstrates how areas of cerebral cortex *could* interact to carry out an interesting and difficult systems-level visual-motor control function. At the "psychological" level, MURPHY-type learning mechanisms offer a crude, first-order model for the extended process of active physical practice with the forelimb in view needed for the proper development of the biological mechanisms for visually guided reaching. In addition, it is demonstrated how analogical sequences of visual mental images might arise in the brain as "corollary discharges" from outgoing motor-command centers, and how they could play a role in the vision-based planning of limb movements.

Moreover, the available mass of relevant neurobiological data is now at a sufficient level to permit informed guesses as to the mappings between cortical areas known to be involved in the control of visually guided reaching and the variables known to be needed for the underlying kinematic computations. These ideas are summarized in high-level cortical models of type-1 and type-2 reaching (Fig. 10). Even if all the details of these models are shown to be wrong, they provide a useful conceptual foothold that does not currently exist.

Beyond the specific physiological predictions detailed

in the previous section, at least two points have emerged from this modeling approach that are of direct relevance to the further experimental study of the neural basis of visual limb control. First, as is exemplified by the kinematic models of Figure 2B,D,F, an explicit body-centered visual representation is not needed to plan or control limb movements with vision, as has been recently suggested (Andersen, 1989, p. 392). It is only necessary that head- and eye-position variables be available as inputs to any forward and inverse kinematic computations that are performed. Neurophysiologists should therefore not be frustrated if they do not find such representations in the posterior parietal lobe. Second, the neuronal responses observed within a cortical "association" area may be due to afferents of at least three different abstract types, including conditioned inputs, unconditioned inputs, and learn-enable inputs (explicitly specifying when a desired relation holds between conditioned and unconditioned inputs) in addition to modulatory inputs that have been ignored here. [Common patterns of laminar termination of afferents in cerebral cortex (Van Essen & Maunsell, 1983) may be relevant to this distinction (Mel, 1990b).] Knowledge of this afferent-type distinction may help to interpret the significance of what are usually called simply "multimodal" response properties: Areas that contain complex, multimodal receptive fields may be the loci of specific maps between input and output variables, such as the kinematic maps discussed in this paper.

### Unresolved Issues

A number of important issues have not been addressed in this work. Among them, first, several relevant brain areas have not been discussed, including the lateral premotor cortex, basal ganglia, the cerebellum, and the limbic system, all of which are heavily interconnected with the cortical areas that *have* been discussed here, and all of which are themselves involved in the control of reaching (Alexander & Crutcher, 1990a,b; Godschalk, Lemon, Kuypers, & Van Der Steen, 1985; Godschalk, Lemon, Nijs, & Kuypers, 1981; Humphrey, 1979; Riehle & Requin, 1989; Wise, 1985). Second, the simple models of Figure 10 make no attempt to connect with the details of the psychophysics of reaching behavior, such as the velocity profiles of reaching movements, speed-accuracy tradeoffs, etc. (e.g., see Paillard, Jordan, & Brouchon, 1981; Atkeson & Hollerbach, 1985; Georgopoulos, 1986), all of which could help to pin down more exactly the neural representations used for the production of limb movements. Third, the closely related problems of planning and visual control of *hand* movements for grasping and manipulating objects under visual control are also left undiscussed, though it is known that the frontal and parietal areas discussed here also subservise these sensorimotor functions (e.g., Hyvärinen & Poranen, 1974; Mountcastle et al., 1975; Rizzolatti & Gentilucci, 1988). An analysis of these related problems similar to that



carried out here might provide an additional wedge into the neural basis for visual limb control.

In a different vein, the current approach is sobering in that it brings into relief a number of differences in representational and processing strategies between simple artificial models that are crudely imitative of neural architectures and algorithms, such as MURPHY [see Rumelhart, Hinton, & McClelland (1986) for introduction to PDP concepts], and the actual neurobiological substrate. Several such differences are identified below, without an attempt to explain their significance. First, whereas MURPHY's populations are homogeneous, consisting of spatially uniform groups of only a single type of unit, the cortical populations discussed in the current model, such as the lateral cortex of the posterior parietal lobe, are highly heterogeneous, consisting of mixtures of units of several different types, where the densities of individual types appear in many cases to vary as gradients across the surface of cortex (e.g., Mountcastle et al., 1975; Hyvärinen & Shelepin, 1979). Second, whereas MURPHY's synaptic connections between populations are spatially uniform, allowing any unit in a source population to, in principle, project to any unit in a destination population, projections that terminate in association areas of cerebral cortex are, in general, microscopically patchy, macroscopically fractionated (i.e., connect only parts of one area to another), partially overlapping with projections from other areas, and almost always reciprocal (Cavada & Goldman-Rakic, 1989a,b; Pandya & Seltzer, 1982; Petrides & Pandya, 1984). Third, whereas a single behaviorally relevant variable is represented by a single population within MURPHY's artificial cortex, the cortical representations of a single variable may be distributed in partially redundant fashion across several tightly linked areas, such as the representation of visual motion, scattered throughout the visually responsive cortex of the occipital, parietal, and temporal lobes, or the body-state variables needed for the control of limb movements carried in differential mixtures in areas 2, 5, 7b, 7a, 7ip, the SSA, and presumably in area 7m. Fourth, whereas MURPHY's neurons "cleanly" separate problem-state variables along standard mathematical lines, such as the distinction between static ( $\Theta_j$ ) and movement-related ( $d\Theta_j$ ) joint variables, cortical neurons commonly represent varying mixtures of tonic (e.g., position) and phasic (e.g., velocity) components of such variables through temporal modulation of their responses (Kalaska, Cohen, Prud'homme, & Hyde, 1990). Thorough consideration of these differences may suggest novel principles of neural information processing of use in future modeling efforts.

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### Notes

1. The map from joint and gaze angles to the retinal image is not strictly a function, since the retinal image is simultaneously a function of infinitely many other variables, such as the layout of objects in the workspace, the presence or absence of sunglasses, etc. However, during normal behavior, the state of the arm and direction of gaze together consistently predict that portion of retinal input that is due to the presence of the arm in the visual field.
2. A visual image in head-centered coordinates is independent of eye position, i.e., is equivalent to the image that would be observed with the eyes fixed straight ahead in their sockets. Likewise, a body-centered visual representation does not change with head or eye position.
3. The term direction-selective is used here to include responses to *actual* movement in a specific direction, as well as responses to *desired* direction of movement for a stationary hand. The use of the term is thus not equal to the common physiological designation of direction selectivity.

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