Chapter 2: Biological Background

In this chapter, we present a detailed analysis of several key regions in monkey that are involved in the planning and execution of the grasping program. Neurons in the anterior intra-parietal area (AIP) are selective to a variety of object properties (including shape, size, and orientation in space), but also show significant movement-related modulation as the grasp is executed. The rostral region of the inferior premotor cortex (F5) contains cells that fire when the monkey makes specific grasping movements with his hand and/or mouth. Cells in the caudal part of the inferior premotor cortex (F4) appear to encode the final endpoint position of reaching movements.

AIP

One area of concentration of the Sakata group has been the posterior bank of the anterior intra-parietal sulcus (Murata, et al., 1993; Sakata, Taira, Murata, & Mine, 1995; Taira, et al., 1990). This region (referred to as AIP) receives input from other areas of the posterior parietal cortex (see Figure 2.1), which provide information about the parameters of the object of interest, including location, orientation, shape, and size (Sakata, 1994). In addition, this region has very significant recurrent cortico-cortical projections with area F5 of the inferior premotor cortex (Matelli, 1994; Sakata, 1994).

Figure 2.2 demonstrates the protocol used by Sakata in these recording studies. The ready signal is given by the turning on of light 1 (L1 in the figure). The monkey responds by placing

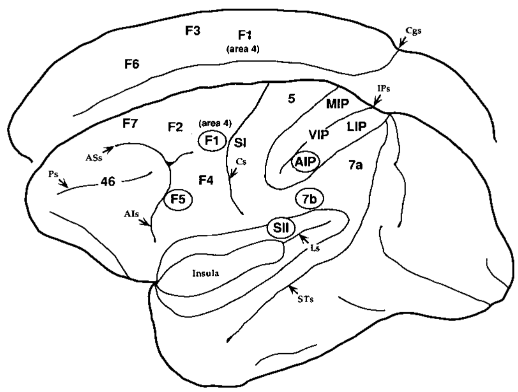

Figure 2.1: Cortical regions in the macaque involved in reaching and grasping. Figure adapted from (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995).

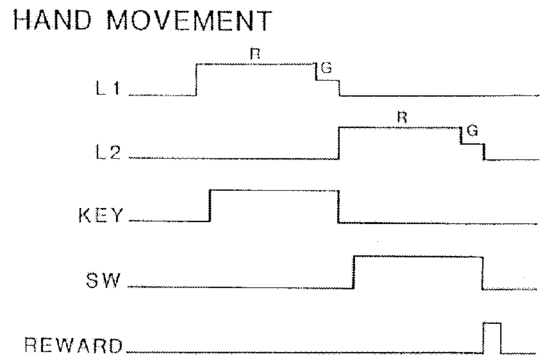

Figure 2.2: The Sakata protocol, as described in (Taira, et al., 1990). Figure from (Sakata, 1991).

his hand upon the touch pad that is located directly in front of him. Contact with the touch pad is indicated by the KEY trace. When L1 changes color (the trigger stimulus), the monkey begins the execution of the reaching movement toward the object that is located in front of him. A second light (L2) turns on as the monkey pulls away from the touch pad. The monkey grasps the object and manipulates it by pulling or pushing in the appropriate direction, as indicated by SW (also referred to as object phase). This position is held until L2 changes color (the secondary trigger stimulus), at which time the monkey releases the object and moves his hand away. If the task is performed properly, the monkey is then rewarded with a squirt of juice.

In the experiment, a variety of objects were presented to the monkey. For each object, four different conditions were used: movement in the light (to manipulate the object), movement in the dark [1], fixation of the object in the light, and fixation in the dark. The first set objects included buttons that had to be pushed, knobs to be pulled, and a joystick that had to be grasped and pushed in a particular direction (Taira, et al., 1990). A second set of objects that have been

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1 At the time dark trials are performed, the monkey has already seen the object and manipulated it in the light.

studied include various sizes of plates, cones, cubes, cylinders, spheres, and rings (Murata, et al., 1993).

Muscimol-induced lesions of AIP lead to a significant deficit in the monkey's ability to grasp objects (Sakata, 1994). The grasping movements are clumsy and uncoordinated, and as a result the monkey is unable to shape his hand or orient his wrist appropriately for objects that are presented to him. However, the monkey is still able to execute the basic sequence of the task: wait for the go signal, move the hand to the object, and then return from the object when the secondary go signal is given.

Visual versus Motor Cell Responses

Figure 2.3 shows a cell that is active primarily during conditions where the monkey makes a movement toward the object (as compared to fixation of the object). For this reason, Sakata classifies this cell as a motor-related cell. This behavior contrasts with the visual-related cell shown in Figure 2.4. Here, the cell is only active during conditions in which the monkey is able to see the object. Note, however, that the cell response in the light movement condition is modulated by the phase of movement. In addition, during this condition, we see an increase in activity at the beginning of the key phase of the task, then a suppression before the trigger stimulus. (Sakata, 1994) attributes the fluctuation during the key phase to the fact that the monkey does not continuously fixate on the object during this phase. This effect was better controlled during the second set of experiments, in which L1 and the object were superimposed upon one-another. During the fixation condition, the activity level of the cell (Figure 2.4) remains relatively constant over the entire presentation of the visual stimulus, indicating that the monkey continued to fixate on the object during the key phase.

Many cells exhibit both visual and motor properties. This class appears to represent a continuum between the visual and motor response types. In Figure 2.5, the cell responds more heavily to the motor condition, but shows significant activity during the visual fixation case.

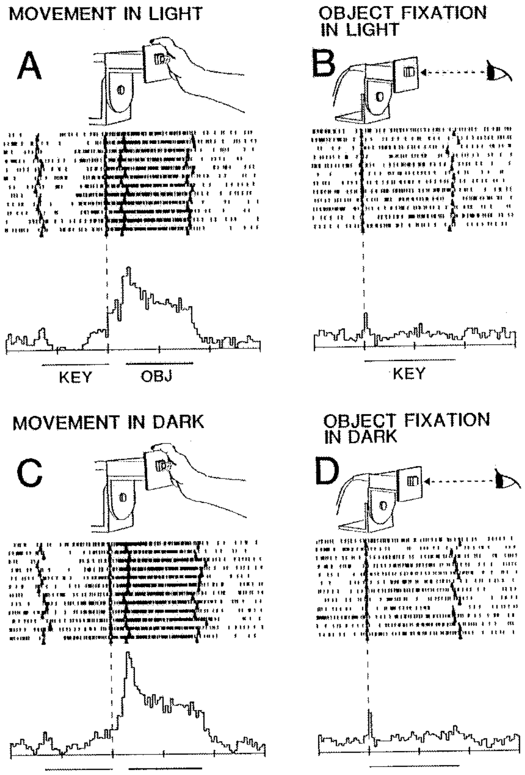

Figure 2.3: Behavior of a motor-type cell under different conditions: light / dark and fixation/manipulation. *Key* indicates the period during which the monkey has his hand on the touch pad. *Obj* indicates manipulation of the object. From (Sakata, 1991).

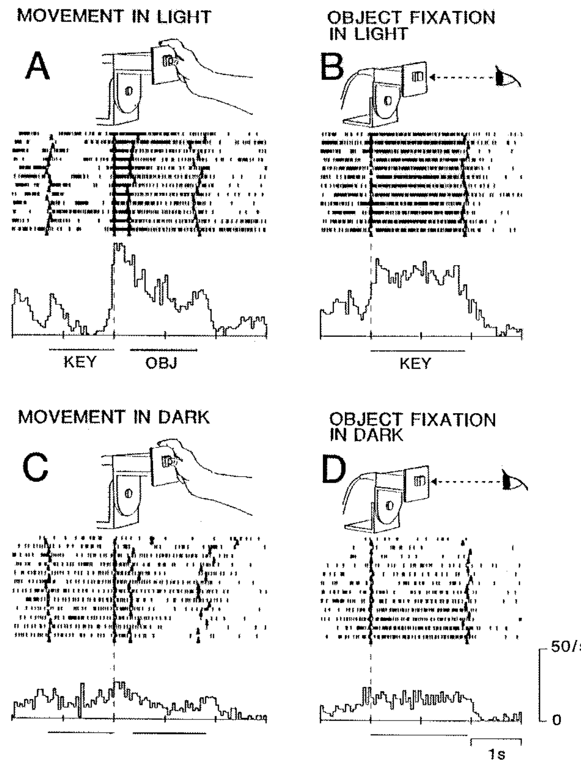

Figure 2.4: Cell that is active during lighted conditions. From (Sakata, 1991).

Within the data presented by Sakata, there are also cells that respond more favorably to the visual condition.

The cell shown in Figure 2.6 demonstrates an enhancement in activity for the movement in the dark condition (as compared to movement in the light). The cell is apparently inhibited (either directly or indirectly) by some visual features belonging to the joystick. This illustrates an important point about distributed representations of motor programs: the behavior of individual cells does not necessarily correspond in a logical manner to the computation that is performed by the network as a whole. However, what is important is that for any particular

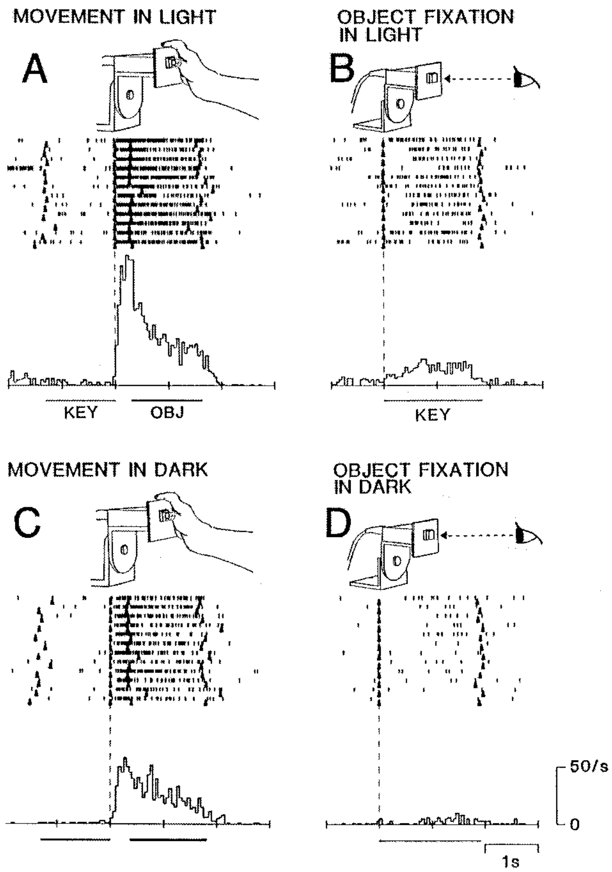

Figure 2.5: Visual/Motor cell. From (Sakata, 1991).

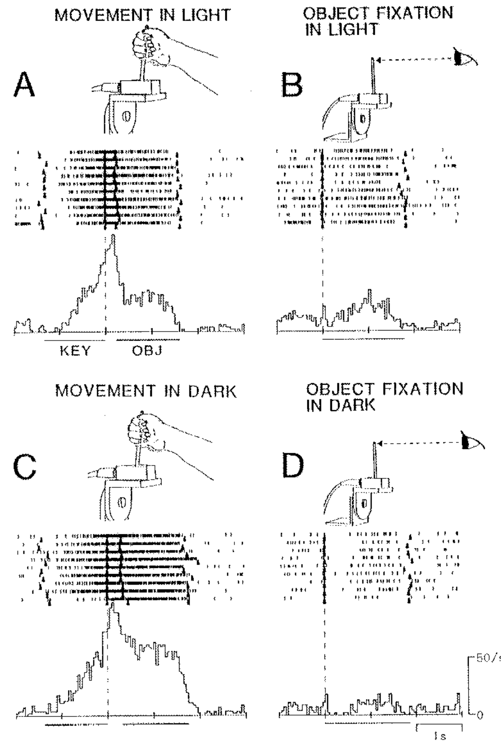

Figure 2.6: Dark enhancement cell. From (Sakata, 1991).

situation, enough cells agree about the output that is to be generated. Then, through a process of cooperation and competition, the correct output is generated while conflicting outputs are shunted.

Object Specific Activity

Many cells in this area of the posterior parietal cortex also demonstrate object-specific activity. However, it is important to note that some cells actually respond to several different objects, with varied activity levels. The cell depicted in Figure 2.7 responds heavily to a pull-knob that is recessed into a box, and partially responds to a normal pull-knob and a push-button. In addition, Figure 2.8 demonstrates a cell that has been labeled as an *angular selective cell* by

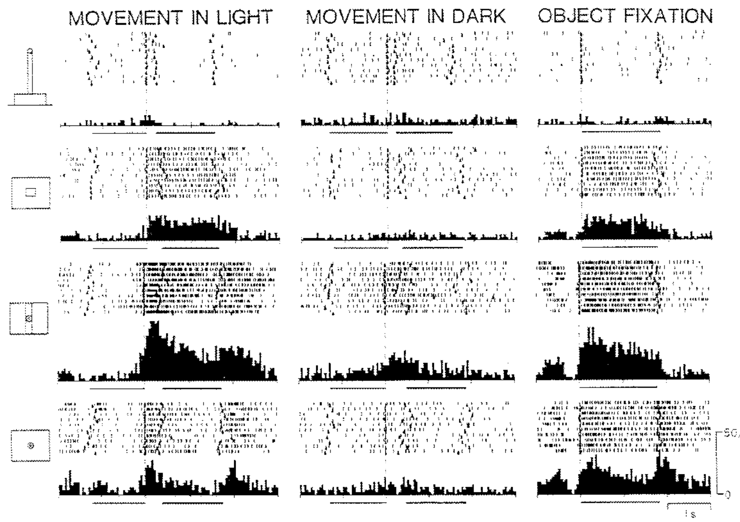

Figure 2.7: Object-specific activity From (Sakata, 1994).

Sakata (Sakata, 1994). Note that in all cases where the cell is active, a side opposition is involved in the grasp of the object.

In general we hypothesize that the more similar two objects are, the more their representations will overlap. However, the term *similar* is a difficult one. In this particular area, similar can mean a couple of things: similar in visual pattern, or similar in the required hand configuration. Most likely we will see both types of constraints reflected: we want to classify objects as easily as possible (i.e. using features that are easy to discriminate), but we must separate objects that require different motor programs. From this, we would expect two objects that are very distinct visually and require different hand configurations to use different sets of cells in AIP, and two objects that are very similar and require the same motor program to use a large number of overlapping cells. But how does the system deal with convergent and divergent mappings? At this time, the data does not give us a clear view due to the fact that very little has been done to compare similar objects. These issues will be addressed from the perspective of the model in Chapter 6.

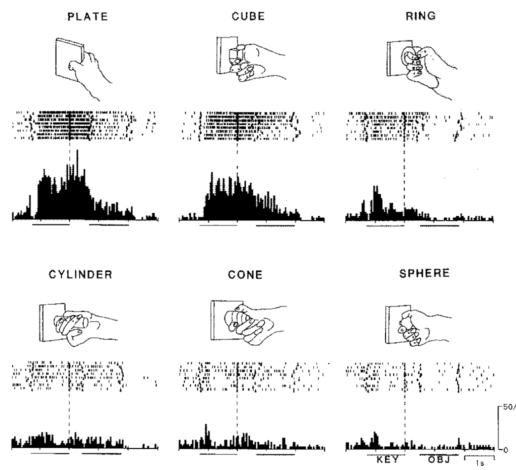

Figure 2.8: A cell that is selective for 'flat' objects. From (Sakata, 1994).

Size Selectivity

A number of AIP cells demonstrated selectivity toward the size of the presented object. Figure 2.9 shows one such cell, which is selective for small objects, but shows some independence in regards to the type of object. On the other hand, some cells demonstrated independence from the size of the object (Figure 2.10).

Position Selectivity

A very small number of cells exhibit activity modulation as a function of the position or orientation of the object (e.g. Figure 2.11). This information may be made available to F4 as a mechanism for modulating the position of the wrist as a function of the grasp type that is used.

Temporal Characteristics

In addition to the various selectivity classes, the neurons in AIP also show striking temporal behavior that is related to the ongoing movement. The identifiable phases are: set (*key phase* in the figures), preshape, enclose, hold (*obj* phase), and ungrasp.

Figure 2.12 depicts a cell that shows a small increase of activity slightly before the key phase and maintains the same level through the duration of this phase. This indicates that

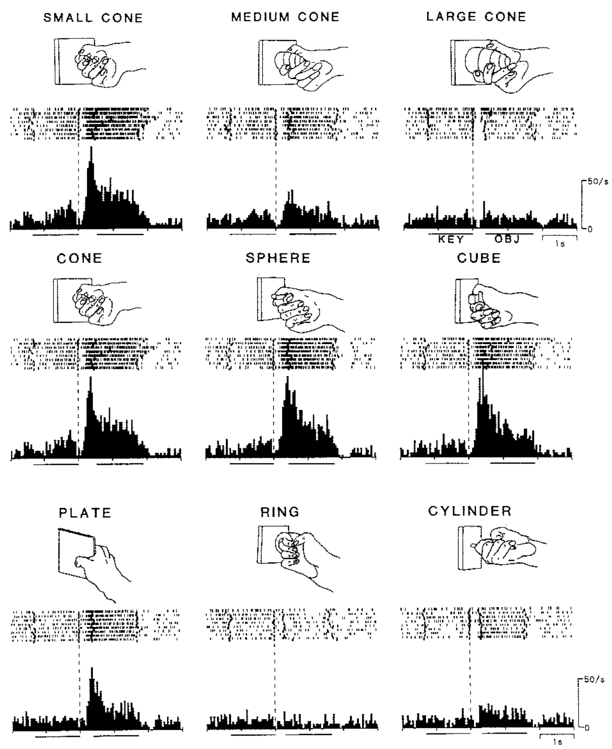

Figure 2.9: Selective toward small objects, somewhat independent of object type. From (Sakata, 1994).

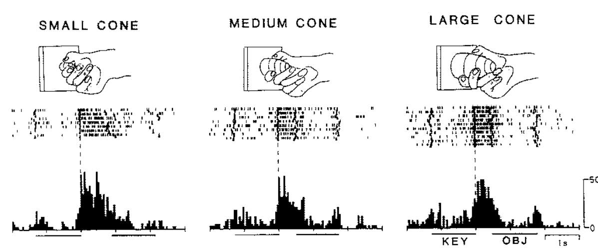

Figure 2.10: Activity independent of object size. From (Sakata, 1994).

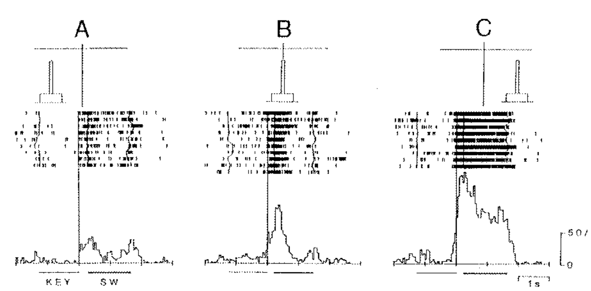

Figure 2.11: Modulation of activity as object position changes. From (Sakata, 1991).

the monkey is fixating on the object before his hand reaches the touch pad. Compare this behavior to the cell's activity during movement in the dark (Figure 2.13). In this case, we only see a small increase in activity at the end of the key phase. Note also that this cell shows very high activity during the preshape and enclose phases and moderate activity during the hold phase of the motor program.

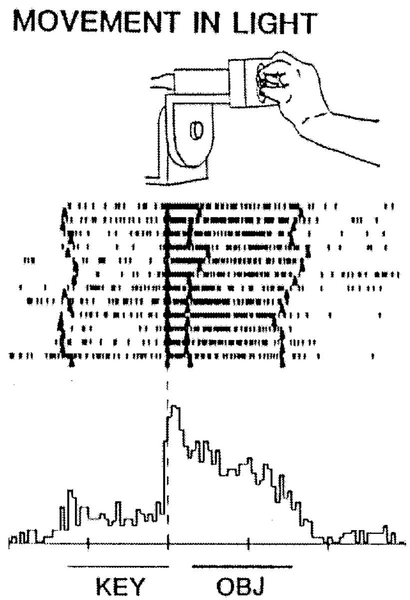

Figure 2.12: Small increase during key phase, with high activity during movement and hold phases. From (Sakata, 1991).

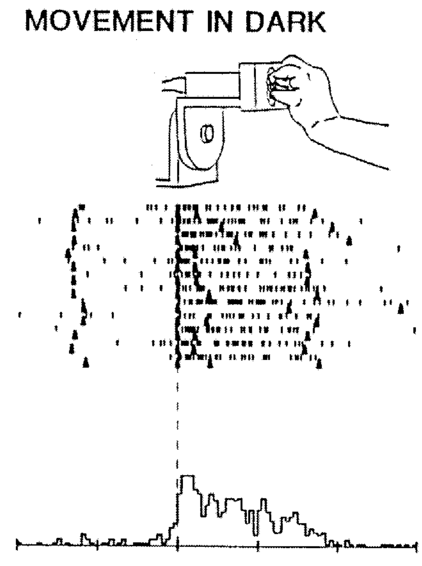

Figure 2.13: Same neuron as in Figure 2.12, except during movement in the dark condition. From (Sakata, 1991).

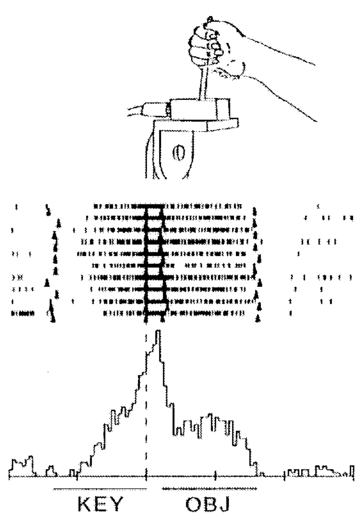

Figure 2.14: Ramp up of activity during key phase. From (Sakata, 1991).

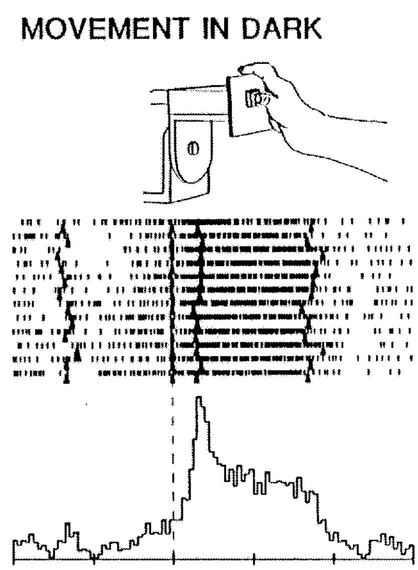

Figure 2.15: Late onset of movement-related activity. From (Sakata, 1991).

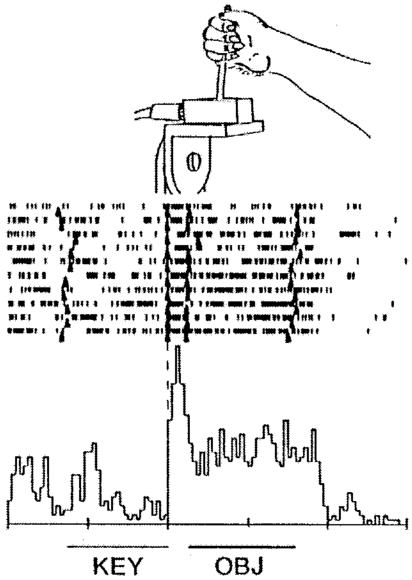

Figure 2.16: Reduction during key phase and longer extent of activity. From (Sakata, 1991).

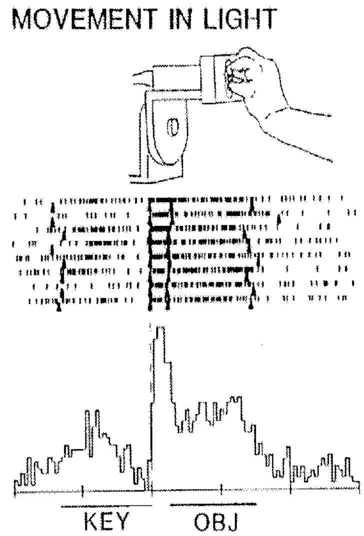

Figure 2.17: Increase, then decrease of activity during key phase. From (Sakata, 1991).

Figure 2.14 demonstrates a significant difference in reaction to the visual stimulus. Shortly into the key phase, we see a rapid increase in cell activity, peaking during the movement. This type of cell is most likely to be directly involved in configuring the motor set for the coming reach and preshape. As in the previous cell, there is also substantial activity during the hold phase of the motor program, ending when the handle is released.

Figure 2.15 depicts a cell that shows a very late onset of movement-related activity. This activity is most likely related to the enclose phase of the grasp.

The cell in Figure 2.16 exhibits a similar behavior to that shown in Figure 2.4, where the activity starts at a relatively high level, but during the key phase, this activity is suppressed until the trigger stimulus. Also note that after the object is released, this cell continues to fire at a significant level, a behavior that is unlike most other cells. This activity indicates possible participation in the ungrasp phase of movement. Similarly, the cell in Figure 2.17

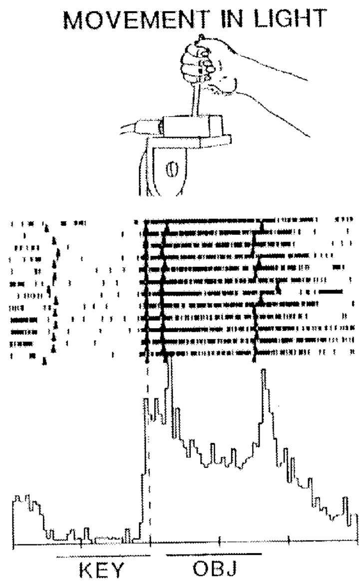

Figure 2.18: Suppression during key phase. Active during movement, hold, and release phases. From (Sakata, 1991).

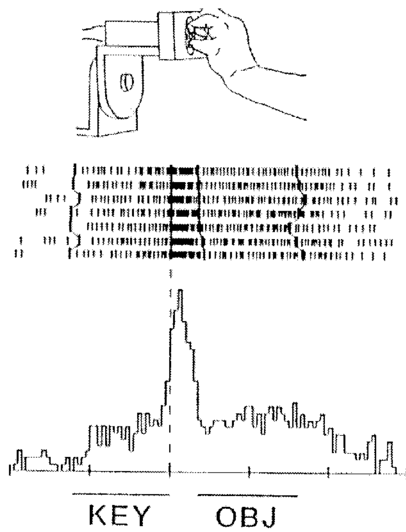

Figure 2.19: Primarily a movement-related neuron. From (Sakata, 1991).

demonstrates an initial increase in activity at the onset of the ready signal, which decreases to almost zero activity at the end of the key phase, and then shows a significant increase when the movement begins. Unlike the previous cell, the activity level drops off as the monkey releases the object.

The cell of Figure 2.18 shows significant activity as the object is being released, which tapers off slowly. This compares with many cells that have very abrupt drops in activity when the object is released. The second activity peak is possibly due to the fact that the monkey occasionally regrasps the object after it is released (Sakata, 1994).

Finally, Figure 2.19 demonstrates activity that is related primarily to preshape and enclose, and with only slight activation during key, hold, and return phases.

Summary of AIP Responses Properties

To summarize, the key features of the AIP responses are:

- A few cells (21% in one study (Taira, et al., 1990)) respond to simply fixating an object (visual-related), others (37%) are active only when a movement is being made to manipulate the object (motor-related). However, many cells (37%) fall somewhere between these two extremes.
- Many cells within this area are selective for the type of object that is presented. Most often, cells are actually selective to varying degrees for several objects. Typically, these objects share some common characteristics.
- Some cells demonstrate specificity toward the size of the object to be grasped, but show a certain degree of independence from the type of object.
- A small number of cells show modulation based upon the object's position and/or orientation in space.
- Most cells demonstrate phasic activity related to the motor behavior. The identifiable phases include: the "key" (set activity), preshape, enclose, and hold. Cells participate in varying degrees during different phases of the movement, but are usually most highly active during the preshape and enclose phases of movement. Very importantly, once a cell becomes active, it typically remains active until the object is released.

Inferior Premotor Cortex

The macaque inferior premotor cortex (located ventral from the spur of the arcuate sulcus) has been identified as being involved in reaching and grasping movements (Rizzolatti, 1987). This region has been further partitioned into two sub-regions: F5 (rostral region, located along the arcuate) and F4 (caudal region). The neurons in F4 appear to be primarily involved in the

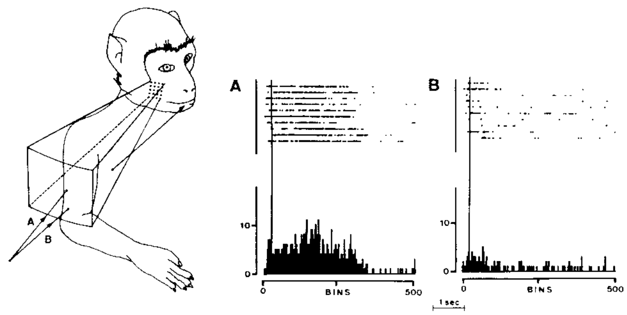

Figure 2.20: Visual and somatosensory receptive fields of an F4 neuron. The two traces demonstrate the neuron's responses to an object moving along two separate trajectories that share the same starting location. The neuron is also responsive to tactile stimulation on the marked area of the face. From fig. 10 of (Gentilucci, et al., 1988).

control of proximal movements (Gentilucci, Fogassi, Luppino, Matelli, Camarda, & Rizzolatti, 1988), whereas the neurons of F5 are involved in distal control (Rizzolatti, et al., 1988).

Many F4 neurons demonstrate responsiveness to both visual and somatosensory stimuli. The somatosensory map is topological and covers both the face and the upper body. Visual responses can be elicited by (among other things) the movement of objects toward the monkey. These visual responses are also topologically mapped according to the moving object's projected point of contact with the face or upper body of the monkey, as shown in Figure 2.20. It is important to note that these two topological maps coincide with one another. In the figure, the cell is responsive to trajectories that terminate on the marked area of the monkey's face (such as trajectory A). This is precisely the same region in which the cell is responsive to tactile stimuli. Even though trajectory B initiates at the same location as A, its point of contact with the monkey's face is significantly different and thus the cell does not respond.

In addition to the passive properties of these F4 neurons, recordings were also taken during the active generation of arm and hand movements. Three primary groups of neurons were observed: movement-towards-the-mouth, movement-towards-an-object, and facial movement. The movement-towards-the-mouth neurons appeared to be involved in any movement that brought the monkey's hand toward the mouth, despite the location of the arm prior to

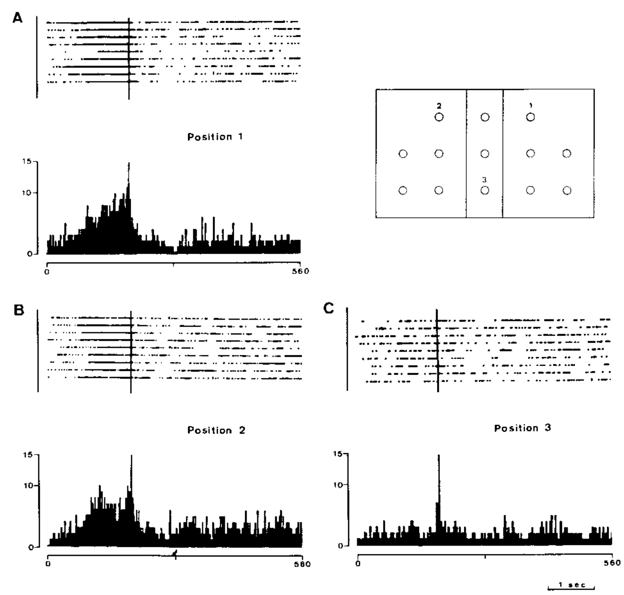

Figure 2.21: Response of a single F4 neuron modulated by the region of peripersonal space that the monkey is reaching toward. This particular cell is responsive to upper areas of the space. The histograms are aligned at the point where the hand made contact with the target object. From figure 11 of (Gentilucci, et al., 1988).

movement initiation. The movement-towards-an-object neurons, however, were selective for specific areas of the peripersonal space, as demonstrated in Figure 2.21. The receptive fields of these neurons contained very large areas of the peripersonal space. The active and passive response properties of individual neurons also show some congruence: neurons active during movement toward the upper region of space were sensitive to tactile stimulation on the face and lips. The sensory properties of these neurons (in response to visual and tactile stimuli) may be involved in either the elicitation of movements toward regions of the body in direct response to the various stimuli, or may actually be involved in the visual- and tactile-based guidance of the ongoing movement.

Recently, cells in the inferior premotor cortex (probably within F4) have been identified which have visual receptive fields in the region around the hand (Graziano, Yap, & Gross, 1994). These cells appear to encode position information of objects relative to the hand's current location. This information could be used to visually guide the hand towards the target object.

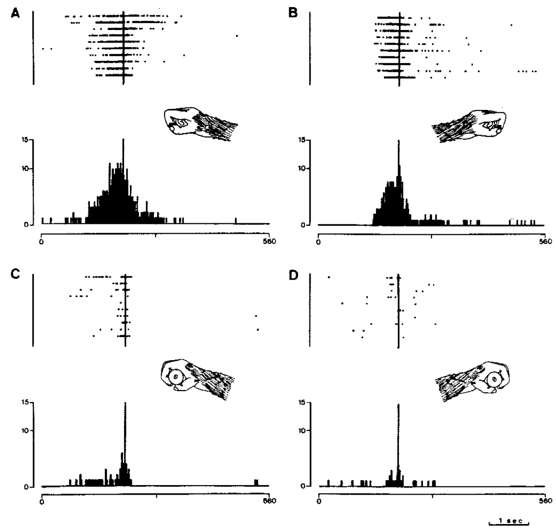

Figure 2.22: An F5 neuron that codes for precision grip in both the contralateral (A) and ipsilateral (B) hands. The neuron does not respond significantly to a palm-opposition type grasp. The histograms are centered at the point where the monkey made contact with the object. From figure 4 of (Rizzolatti, et al., 1988).

A functional distinction between F4 and dorsal premotor cortex (referred to as F2 by Rizzolatti) has also been made recently through the use of muscimol-induced lesions (Kurata & Hoffman, 1994). In a task in which the monkey had to pair an arbitrary instruction stimulus with the movement of a joystick (requiring an arm movement), a lesion in the arm area of F2 resulted in the monkey's inability to correctly match the correct movement with the stimulus. However, when the lesion was performed in the inferior premotor cortex, the direction of joystick movement was typically correct, but the executed movements were much weaker than normal.

Muscimol lesions of F5 result in a similar behavior as was observed in AIP: the monkey is only able to make clumsy grasping movements (Rizzolatti, 1995). One interesting difference, however, is that the deficit is most clear during execution of the precision grasp (as compared with lateral pinch or power grasp). Among other things, this effect might be due to the encoding of more primitive grasps in regions other than F5.

Individual neurons within F5 are responsive to somatosensory stimuli on the hands and mouth, as well as to visual stimuli (correlating with the size of the object [2]). During movement execution, many neurons code for the specific grip that is made by the monkey, but do not respond during axial or proximal movements made in the absence of distal movements. A neuron that codes for a precision grip made by either the contralateral or ipsilateral hand is shown in Figure 2.22. Other neurons were observed to be active during the formation of whole-hand grips (palm opposition) as well as lateral pinches (side opposition). Additional groups of neurons within F5 are responsive to other motor acts involving the hands. These include neurons that fire while the monkey is grasping with the hand and mouth, as well as neurons that are active while the monkey is tearing an object.

Activity of the F5 neurons correlated with the phase of the ongoing movement. The following phases were identified (Rizzolatti, et al., 1988): preparatory, finger extension, finger flexion, and holding. Cells that show activity prior to the onset of movement are labeled as preparatory cells. Note that these cells would probably have been considered *set cells* (Evarts, Shinoda, & Wise, 1984) if the protocol utilized an explicit a delay period between the viewing of the target object and the initiation of movement (we will use this term here).

Many cells are actually active during more than one phase of movement. The neuron shown in Figure 2.22 initially activates as movement is initiated, and continues to fire during the finger extension and finger flexion phases. Figure 2.23 demonstrates a cell that activates as the hand encloses on the target object, and terminates one second after contact is made. On the other hand, the neuron shown in Figure 2.24 begins to fire shortly before contact is made and continues to fire through the length of the grasp.

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[2] In these experiments, the monkeys were only presented with two basic types of objects: bars and small raisin-size objects. Thus, it is not possible to distinguish object size from object or grasp type.

The activity patterns seen in F5 contrast significantly with those of the hand area of the primary motor cortex (Rizzolatti's F1) in two significant ways. First, many of the F5 neurons fire over several phases of the movement, even though each phase activates different sets of muscles. In fact, we see some cells that begin to fire before movement is observed. Second, a large number of the F5 neurons fire during movements of both the contralateral and ipsilateral hands, which would not be the case for a muscle-related coding scheme. What we conclude from this is that F5 is involved in some higher-level specification of the distal movement to be performed. However, this is not at such a high level that an individual neuron codes for the entire motor act.

Regarding general neural coding issues, individual neurons in F5 code for only a piece of the grasp that is being executed. By *piece of a grasp*, we mean that the representation of the grasp is distributed across a set of neurons, whose collective responsibility is to produce the appropriate grasp. This distributed coding within F5 is both in time (representing different phases) and in action space (e.g. different grasps). An important point about distributed representations is that individual neurons often take on multiple roles. We see this in the temporal domain in those neurons that are active during multiple phases of movement. This has also been seen in the action domain. Some neurons have been observed in F5 that are active during two distinct motor acts: grasping with the hand and grasping with the mouth. Also, if one looks carefully at Figure 2.22, one can see some activity during the whole-hand grasp of the contralateral hand (panel C), even though this cell has been labeled as being selective to the precision grip. The key point is that despite this not so discrete coding of actions at the neural level, the system is still able to produce discrete actions as a result of the collective behavior of the neurons. At the same time, because we observe discrete classes of behaviors, this does not necessarily imply that the discreteness should be reflected down at the level of the individual neuron.

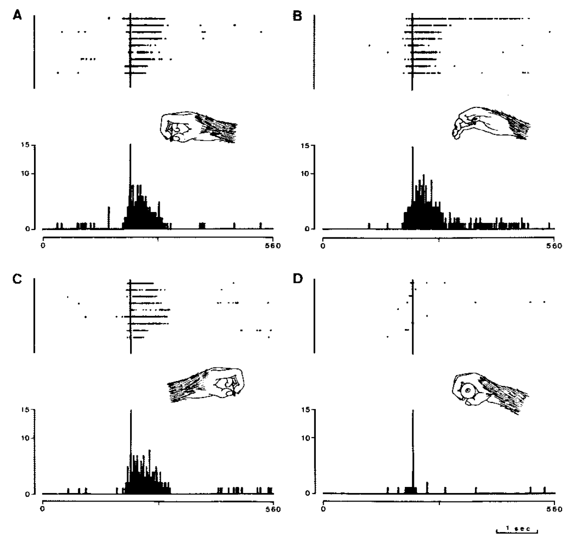

Figure 2.23: F5 neuron responsive to precision grip. Note that the activity of the neuron is not modulated by the orientation of the hand during the grasp. From figure 6 of (Rizzolatti, et al., 1988).

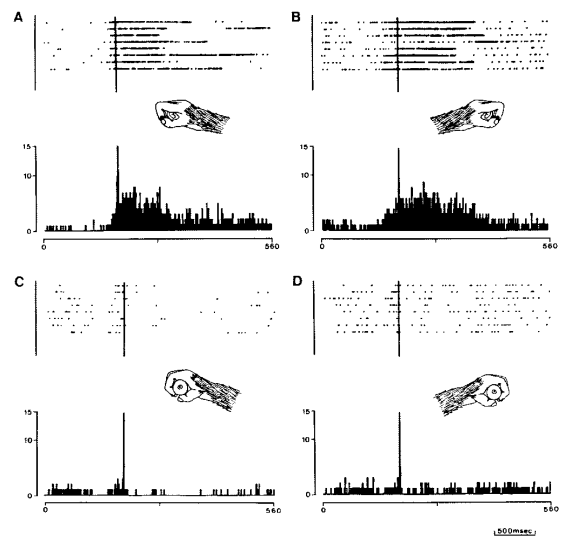

Figure 2.24: Another F5 cell that is responsive to the precision grip. This particular cell continues to fire for the duration of the grasp. From figure 7 of (Rizzolatti, et al., 1988).

Summary of F5 Responses

The most important observations made of F5's role in the execution of grasping movements are summarized as follows:

- Cells tend to be most responsive for specific grasp types made by the monkey. Cells coding for grasps that are not being executed are sometime inhibited.

- The largest number of cells are dedicated to grasps involving the thumb opposing the fingers (pad opposition or precision grasp); a moderate number of cells is involved in the coding of side opposition; and very few cells are active during power grasps. In one experiment, 39% (56/142) of cells active during the grasp were observed to code a precision grip, 30% coded a finger prehension grasp (all fingers opposing the thumb), 4% coded for palm opposition, and 27% were non-specific (Rizzolatti, et al., 1988).

- Most cells are most responsive to a particular phase of movement. The identifiable phases are: set, extension, flexion, and hold. The largest number of cells are active during the extension and flexion phases of movement. In the same experiment, 34% (35/104) of grasp-related cells were active prior to distal movements, 35% during finger extension, and 32% were active during finger flexion. These grasping units constituted 66% of observed cells; 9% of cells were active while holding the object.