Grasping objects: the cortical mechanisms of visuomotor transformation

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Grasping requires coding of the object's intrinsic properties (size and shape), and the transformation of these properties into a pattern of distal (finger and wrist) movements. Computational models address this behavior through the interaction of perceptual and motor schemas. In monkeys, the transformation of an object's intrinsic properties into specific grips takes place in a circuit that is formed by the inferior parietal lobule and the inferior premotor area (area F5). Neurons in both these areas code size, shape and orientation of objects, and specific types of grip that are necessary to grasp them. Grasping movements are coded more globally in the inferior parietal lobule, whereas they are more segmented in area F5. In humans, neuropsychological studies of patients with lesions to the parietal lobule confirm that primitive shape characteristics of an object for grasping are analyzed in the parietal lobe, and also demonstrate that this 'pragmatic' analysis of objects is separated from the 'semantic' analysis performed in the temporal lobe.

Trends Neurosci. (1995) 18, 314–320

IN OUR EVERYDAY life, we interact continually with objects. We reach for them, we grasp them, we manipulate them. All these actions are apparently very simple. Yet, this is not so. The mechanisms that underlie them are complex, and require multiple visuomotor transformations. This article examines one of these object-oriented actions, grasping.

The hand as a grasping apparatus

On the basis of the specialization of the hand and its neural apparatus in primates and man, grasping is a highly evolved type of behavior. Precision grip with true opposition of the pulpar surfaces of the thumb and index finger is considered as the hallmark of dextrous hands. Film and motion analysis of grasping shows that the motor configuration that is formed by the hand in contact with the object represents the end result of a motor sequence that begins well ahead of the action of grasping itself. The fingers begin to shape during transport of the hand. This process of preshaping first involves a progressive opening of the grip with straightening of the fingers, followed by a closure of the grip until it matches object size[1] (Fig. 1). The point in time where grip size is the largest (maximum grip size) is a clearly identifiable landmark that occurs well before the fingers come into contact with the object[1–5] (Fig. 1D). The question of why grip aperture is larger than that required by object size is still a matter of debate. The critical point is that the amplitude of maximum grip size covaries linearly with object size[6]. Monkeys also perform a similar preshaping with extra-opening and anticipatory closure of the fingers (M. Gentilucci, L. Fogassi, V. Gallese and G. Rizzolatti, unpublished observations).

Arbib and his colleagues[7,8] proposed an approach in which control programs combine perceptual and motor schemas to determine the interactions between the hand and the environment (see Box 1 for the basic notions of schema theory). For the purpose of prehension, schemas such as 'preshape', 'enclose' and 'orient', are postulated. These schemas are carried out by specific grasping units (the 'virtual fingers'). For example, in a precision grip with pad opposition[9], the thumb is one virtual finger (VF1), the finger(s) that oppose the thumb is another one (VF2), and the unused finger(s) a third one (VF3). In grasping a small object, VF2 will be composed of the index finger only. In whole-hand prehension with palm opposition, VF1 will be the palm and VF2 will (usually) include the four fingers other than the thumb.

The role of vision in grasping is not only to activate the proper schemas and specify the composition of the virtual fingers but also to determine the relative positions of the hand and the object to be grasped, so that the forces during the lift of the object can be applied in exactly opposite directions. Accurate positioning of the fingerpads on the object surface is a prerequisite for subsequent handling and manipulation. This requires defining an 'opposition space', corresponding to the grasp axis embedded in the object[10]. Then, the hand will be transported (the 'approach' schema) and the wrist will rotate it (the 'rotate' schema) in order to approximate the correct position. The formation of the grasp before contact with the object is thus the critical factor that governs the movements of the other segments of the upper limb during the reach. Although reach and grasp can be described as separate subsystems[11], studies of reaching in isolation from grasping ignore many of the key aspects of its control. The kinematic redundancy of the whole limb, and not only its distal segments, is exploited in building the appropriate opposition space[12].

Coactivation of reach and grasp raises the question of how schemas that are actuated by different

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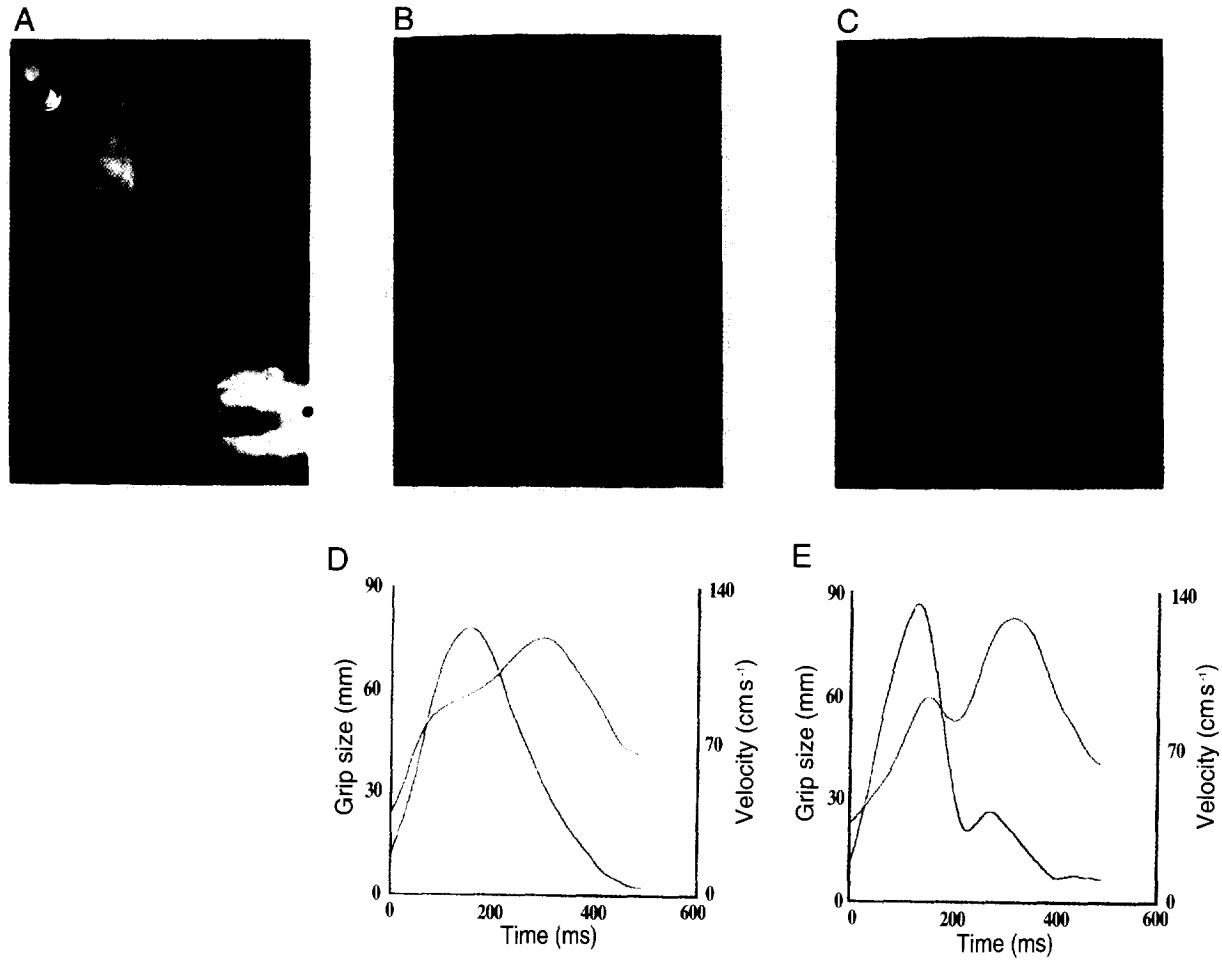

Fig. 1. ***Kinematics of grasping.*** **(A)** *The hand preshapes during transport to the target object (superimposed views of a single movement at a rate of 5 Hz).* **(B)** *Averaged two-dimensional recording of spatial paths of wrist (green), tip of thumb (red) and tip of index finger (blue) during ten reach-to-grasp movements.* **(C)** *Averaged spatial paths when a perturbation occurred (the object was displaced briskly rightward at onset of movement). Small horizontal and vertical bars on tracings represent the values of one standard deviation from mean trajectory.* **(D and E)** *Time plots of wrist velocity (green line) and grip size (red line) during one of the trials represented in* B *and* C*, respectively.* Data taken from Ref. 2.

limb segments are co-ordinated temporally by the program. The first co-ordinated control program for reach and grasp[7] postulated that completion of the activity for grasping an object involved two motor schemas: one for the slow phase of the reach and the second for the enclose phase of the hand movement. However, subsequent experiments showed this model to be inadequate. Paulignan and colleagues[2] suddenly displaced the target object at the onset of a reach-to-grasp movement. In this condition, the untrained subject is able to correct for this visual 'perturbation' and to grasp accurately the displaced object. However, this correction results in prolonging the duration of the reach by about 100 ms. Meanwhile, the opening of the grip is interrupted, grip size decreases and increases until it reaches its peak aperture at a later time, when the hand gets close to the displaced object (Fig. 1C and E). To address these data, Hoff and Arbib[13] proposed a model that included a two-way interaction between the transport and grasp schemas. They postulated the existence of an additional, co-ordinating schema that receives from each of the constituent schemas an estimate of the time that it needs to move from its current state to the desired final state. Whichever schema is going to take longer (in this case, the reach) is given the full time it needs, while the others will be slowed down (Fig. 2). The time that is needed by each schema is regulated by optimality criteria that are embedded in feedback controllers that respond to disturbances with some latency.

The schema hypothesis provides a framework for segmenting grasping into elementary action units, and for relating these units to the neural substrate. It also explains how grasping interacts with other functions of the upper limb, such as reaching. Ultimately, it might increase our understanding of pathological disorders of grasping.

Neural mechanisms that are involved in the control of visually guided grasping

Correct execution of grasping requires the integrity of primary motor cortex [Brodmann area 4 or field F1 (Ref. 14)]. Lesion of this area in primates, as well as damage to the pyramidal tract, produces a profound deficit in the control of individual fingers and, consequently, a disruption of normal grasping[15,16]. Direct access of visual information that is needed for hand shaping, however, is very limited in F1, where visually responsive neurons are rare and have visual properties (brisk, transient responses to abrupt stimulus presentation[17]) that do not follow those that would be expected for grip formation. The visuomotor transformations that are required for

Box 1. Schema theory and behavior

Neuroscience has a well-established terminology for levels of structural analysis (for example, brain area, layer and column) but pays little attention to the need for a functional terminology. Schema theory[a] provides a rigorous analysis of behavior that requires no prior commitment to hypotheses on neural localization. Schemas are units for this analysis. Perceptual schemas serve perceptual encoding, while motor schemas provide control units for movement. Crucially, schemas can be combined to form co-ordinated-control programs, which control the phasing-in and phasing-out of patterns of schema coactivation, and the passing of control parameters from perceptual to motor schemas. The notion of schema is recursive – a schema might later be analyzed as a co-ordinated-control program of finer schemas, and so on, until such time as a secure foundation of neural localization is attained.

The level of activity of an instance of a perceptual schema represents a 'confidence level' that the object that is represented by the schema is indeed present; while that of a motor schema might signal its 'degree of readiness' to control a part of an action. Mutually consistent schema instances are strengthened and reach high activity levels to constitute the overall solution of a problem, whereas instances that do not reach the evolving consensus lose activity, and thus are not part of this solution. A corollary to this view is that the instances that are related to a given object-oriented action are distributed. A given schema, defined functionally, might be distributed across more than one brain region; conversely, a given brain region might be involved in many schemas. Hypotheses about localization of schemas in the brain might be tested by observation of the effects of lesions or functional imaging, and a given brain region can then be modelled by seeing if its known neural circuitry can indeed be shown to implement the posited schemas. An example of this approach is given here.

In providing an account of the development (or evolution) of schemas, we find that new schemas often arise as modulators of existing schemas rather than as new systems with independent functional roles[b]. Thus, schemas for control of dextrous hand movements serve to modulate less specific schemas for reaching with an undifferentiated grasp and to adapt them to the shape or the use of an object.

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grasping movements, therefore, have to occur upstream in motor control, in areas that are connected more closely to the visual system. In this section, we present evidence for the existence of a specialized visuomotor system that encodes object primitives and generates the corresponding hand configurations. This system, which involves frontal and parietal areas, is depicted in Fig. 3.

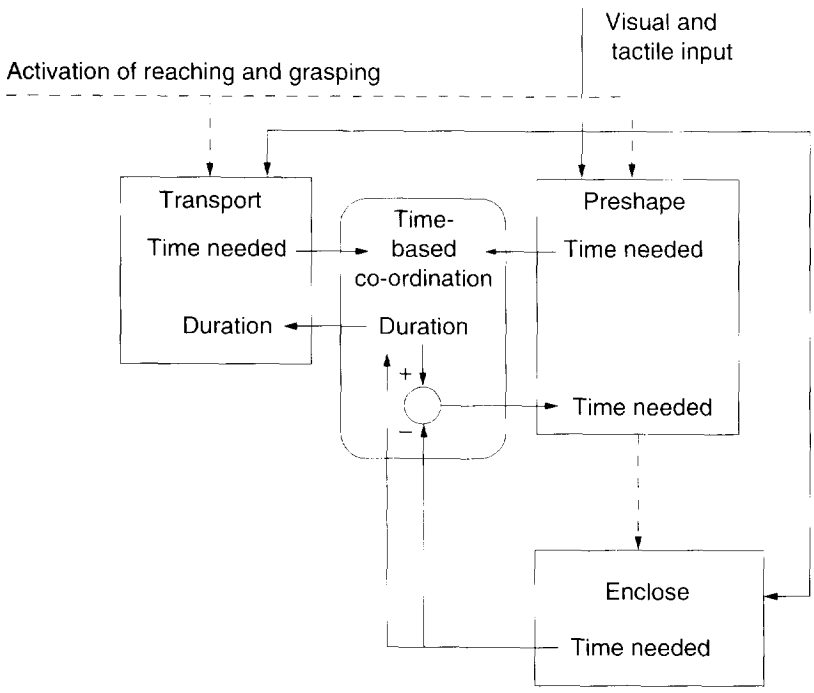

Fig. 2. ***An overview of a model of the motor schemas, and their co-ordination through timing, for reaching and grasping***[13]. *Broken lines carry activation signals to a schema, as in a computer flow diagram, while solid lines carry signals that code relevant variables, as in a block diagram for a control system. Thus, the entire diagram is an example of a schema that is defined as a co-ordinated-control program of finer schemas. The overall schema combines three motor schemas (rectangles) and one co-ordinating schema (with rounded corners). Whichever motor schema needs more time (arm: transport, or hand: preshape + enclose) sets the total duration specified by the time-based co-ordination model. The schemas then provide the optimal arm and hand trajectories for the specified duration. Parameters of the movement might be adjusted on-line (but with about 100 ms delay) in response to unexpected perturbations.*

Premotor area F5

Area F5 forms the rostral part of inferior area 6. Its connections with F1 are within the hand field of this area[18–20]. Intracortical microstimulation and single-neuron studies showed that F5 is related specifically to distal movements[21,22].

Rizzolatti and his colleagues[22,23] recorded single neurons from F5 in behaving monkeys that were tested during object-oriented motor actions. These experiments showed that most neurons that are located in the upper part of F5 (the arm field) are involved in grasping and other object-related motor actions (holding, tearing and manipulating). 'Grasping' neurons discharge in relation with finger and hand movements during the action of grasping an object. The temporal relation of this discharge with grip movements changes from neuron to neuron. Some neurons fire during the last part of grasping, that is, during finger flexion. Other neurons begin firing with finger extension, and continue during finger flexion, and others are activated in advance of finger movements, often ceasing to discharge only when the object is grasped.

An important property of most F5 neurons is their selectivity for different types of hand prehension. Eighty-five per cent of grasping neurons show selectivity for one of three basic types of grip: precision grip (the most represented type); finger prehension; and whole-hand prehension[22]. There is specificity for different finger configurations, even within the same grip type. Thus, the prehension of a sphere, which requires the opposition of all fingers, is encoded by different neurons than the prehension of a cylinder, for which a palm opposition grip is used[23] (Fig. 4A and B).

The schema approach can be used here to conceptualize these physiological data. In F5, the schemas are represented by populations of neurons that code different motor acts. Various types of schemas can be distinguished. Some define general categories of action, for example, grasp, hold and tear. Others indicate how the objects are to be grasped, for example, held and torn. In this case, each schema specifies the effectors that are appropriate for the action; for example, index finger and thumb (precision grip), all fingers (manipulation), all fingers but the thumb (palm opposition). Finally, a third group of schemas would be concerned with the temporal segmentation of the actions (the co-ordinating schemas). Thus, the motor schemas in F5 form a basic 'vocabulary'[24] from which many dextrous movements can be constructed as co-ordinated-control programs.

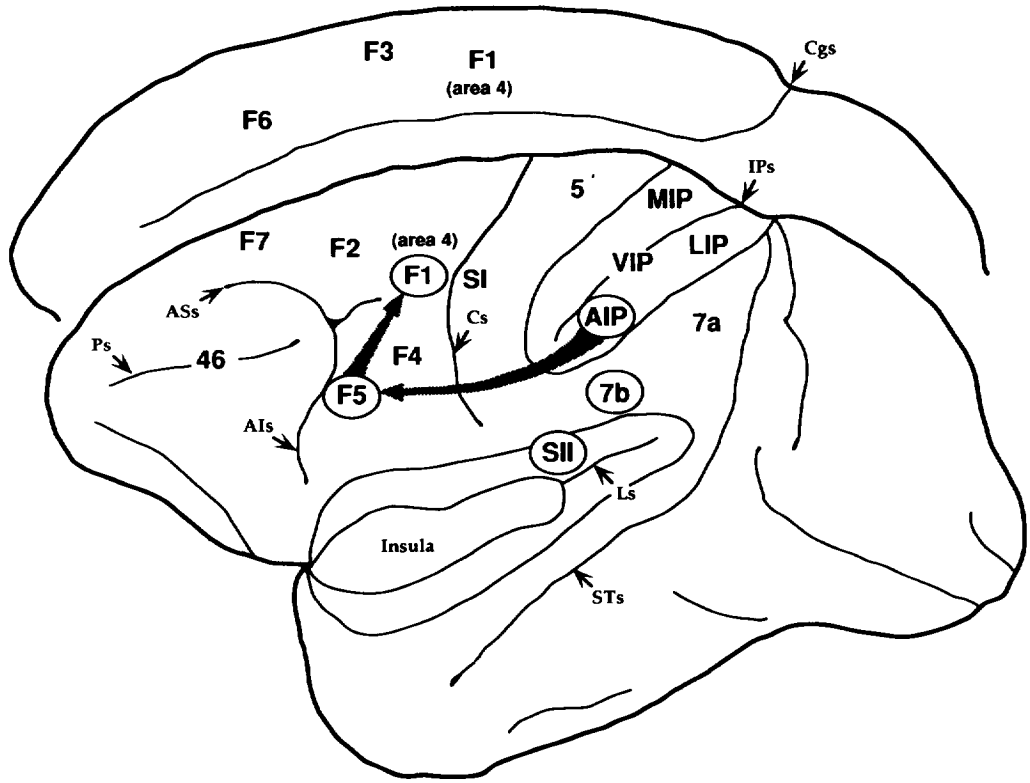

Fig. 3. ***Lateral and mesial views of monkey cerebral cortex.*** *The visuomotor stream for grasping is indicated by large arrows. F5 also receives somatosensory input from area SII, and somatosensory and visual input from area 7b (circled areas). Frontal agranular cortical areas are classified according to Matelli and colleagues[14]. Cortical areas that control grasping are connected with basal ganglia and cerebellar circuits. These circuits, although involved in grasping, are not shown in the figure. Abbreviations: AIP, anterior intraparietal area; AIs, inferior arcuate sulcus; ASs, superior arcuate sulcus; Cs, central sulcus; Cgs, cingulate sulcus; IPs, intraparietal sulcus; LIP, lateral intraparietal area; Ls, lateral sulcus; MIP, medial intraparietal area; Ps, principal sulcus; STs, superior temporal sulcus; and VIP, ventral intraparietal area. Note that IPs and Ls have been opened to show hidden areas.*

The presence in F5 of this vocabulary has some important implications. First, since information is concentrated in relatively few elements, the number of variables to be controlled is much less than if the movements were described in terms of motoneurons or muscles. This solution for reducing the high number of degrees of freedom of hand movements comes close to that proposed theoretically with the virtual fingers. Second, the retrieval of the appropriate movement is simplified. Both for internally generated actions and for those that are emitted in response to an external stimulus, only one schema or a small ensemble of schemas have to be selected or co-ordinated. In particular, the retrieval of a movement in response to a visual object is reduced to the task of matching its size and orientation with the appropriate schema. Third, the presence of a vocabulary of motor schemas should facilitate greatly the learning of associations, including arbitrary associations between stimuli and schemas (for example, if red, grasp; if green, don't). Lesion studies showed that motor association learning is impaired markedly after damage to rostral premotor areas F5 and F7 (Ref. 25).

How is the motor vocabulary of F5 addressed by external stimuli? The simplest way to examine this issue is to present different types of visual stimuli, and to establish whether the neuron will fire in the absence of movements and, if yes, in response to which stimuli. By using this approach, visual responses were observed in ~20–30% of F5 neurons. Two types of response can be distinguished. Neurons of the first type respond to presentation of graspable objects. Often, there is a relation between the type of prehension that is coded by the cell, and the size of the stimulus that is effective in triggering the neurons. This is particularly clear for the precision-grip neurons, which are activated only by small visual objects. Neurons of the second type ('mirror neurons') respond when the monkey sees movements, similar to those that are coded by the neuron but that are executed by the experimenter or another monkey. For example, many mirror neurons fire when the monkey grasps a piece of food, and also when the experimenter or the other monkey does so. However, they do not fire when the experimenter makes a grasping movement without food, or when the food is grasped with a tool[26] (Fig. 4C). Thus, the vocabulary of F5 can be addressed in two ways: by objects and by events. In both cases, the eliciting stimuli address specifically the F5 neurons that code the grip congruent with them.

Parietal areas

Parietal cortex is known to be concerned with the visual control of hand movement from the effects of posterior-parietal lesions in man (see below) and animals. Monkeys with lesions in the inferior parietal lobule typically present misreaching with the contralesional arm[27]. In addition, their contralesional hand fails to shape, and makes awkward grasps[28].

Neurons that are involved in active arm movements were first recorded in the inferior parietal lobe by Mountcastle and colleagues. They classified those neurons into two classes: 'arm projection' and 'hand manipulation' neurons[29]. More recently, neurons that are involved in hand movement were found to be concentrated in a small zone within the rostral part of the posterior bank of intraparietal sulcus,

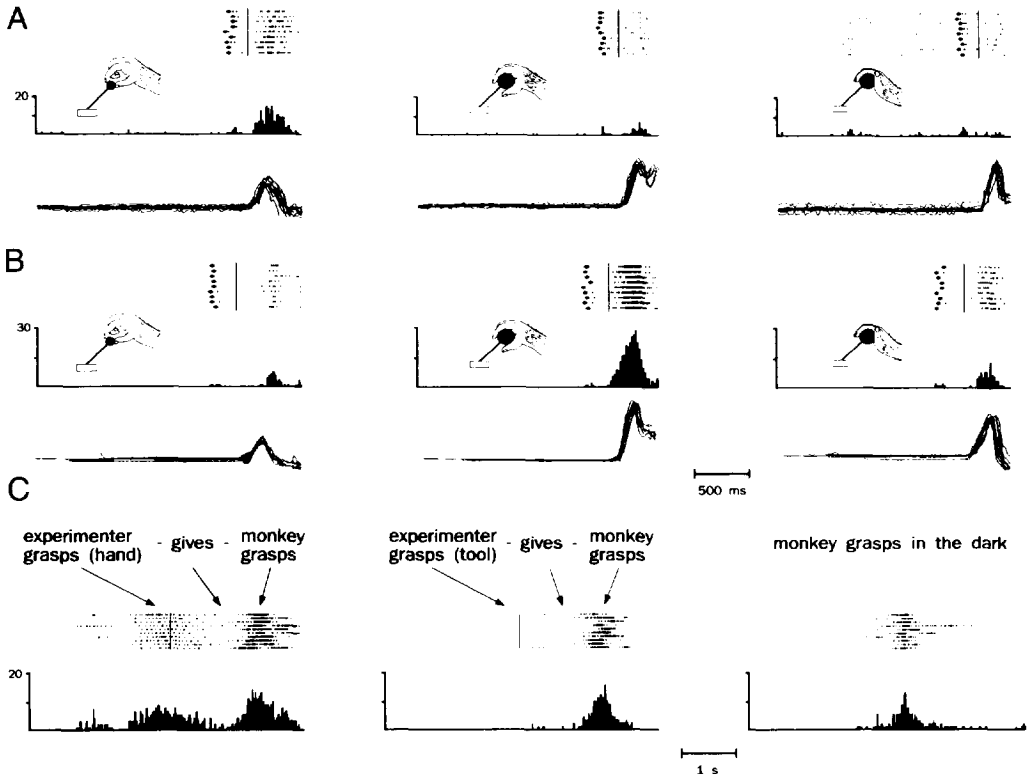

Fig. 4. *Examples of F5 neurons.* (A and B) *Grasping neurons. The monkey is seated in front of a dark box. The trial started when the monkey pressed a bar. The box was then illuminated and a geometric solid, located inside it, became visible. After a variable time interval, the door of the box opened automatically, and the monkey was allowed to release the bar, and reach for the object. Time plots of neuronal discharge (rasters and histograms), and the distance between the thumb and index finger (recorded with a computerized movement analyzer) are shown. The traces are aligned with the onset of hand movement (vertical bar). Black marks indicate the moment when the door opened. The presented objects were (from left to right) a small sphere, a large sphere, and a horizontally positioned cylinder. Ordinates: spikes bin^{-1}; binwidth, 20 ms.* **(C)** *Grasping neuron with mirror properties. First two panels: an experimenter grasps a raisin in front of the monkey (first discharge), moves it towards the monkey (no discharge), the monkey grasps it (second discharge). Note the difference between hand and tool grasping (pliers). Right panel: same neuron. Monkey grasps an object in the dark.*

corresponding to an area [anterior intraparietal area (AIP)] that is connected closely with area F5 of the premotor cortex[30] (Fig. 3). Neurons from this area were recorded in monkeys that had been trained to manipulate various types of switches (some are shown in Fig. 5) that elicited from the animal different motor configurations. Most of these neurons were activated selectively during grasping one or two of these objects among the four routinely used configurations of the hand. The activity of the neurons was not influenced by changing the position of the object in space, showing that the activity was related to distal hand and finger movements rather than to proximal movements of the arm.

In order to determine the role of visual factors in activating these neurons, Sakata and his colleagues let the monkey perform the same task in the dark, guided only by a small spot of light on the object[31,32]. Thus, the task-related neurons were classified into three groups, according to the difference between the activity in the light and in the dark: 'motor dominant' neurons (Fig. 5A) did not show any significant difference in activity between these two conditions; 'visual and motor' neurons (Fig. 5B and C) were less active in the dark; and 'visual-dominant' neurons (Fig. 5D) were active exclusively in the light.

Many of these visually responsive neurons were activated by the sight of objects during fixation without grasping ('object' type, Fig. 5B and D). In most visual and motor neurons, the visually effective object and the type of grip coded (assessed in the dark) coincided. Another type of neuron was not activated during the fixation of objects ('non-object' type, Fig. 5C) but seemed to require other visual stimuli, such as the view of the moving hand, to be activated. Responses of the non-object type of neuron were usually elicited after the initiation of the hand movement, and were likely to be concerned with the interaction of the hand with the object. Finally, using a broader variety of graspable objects, including primitive shapes such as spheres, cubes, cones, cylinders, rings and plates of different sizes, Sakata and colleagues[32] found many neurons in the rostral intraparietal-sulcus (IPS) posterior bank (area AIP) that were activated selectively during grasping or fixation of one or two of these objects. Some of them were also sensitive to the size or the orientation of the objects.

Visual and motor and visual-dominant neurons in this region are likely to be interconnected. In addition, a group of neurons that are sensitive to the three-dimensional (3D) orientation of the longitudinal axis of visual stimuli were found recently in the caudal part of the IPS posterior bank[33]. Therefore, it is likely that the 3D characteristics of the object are processed outside AIP, and that the output of such processing is sent to AIP. Thus, the parietal visual neurons encode the 3D features of objects in a way that is suitable to guide the movements for grasping them. They might be regarded as a neural implementation of perceptual schemas.

If the properties of parietal neurons are compared with those of F5, striking similarities, but also important differences, emerge. Visual responses to 3D objects are found more frequently in parietal cortex than in F5. By contrast, mirror neurons, responding to the view of hand action of other individuals, were not found in AIP. As for the motor properties, parietal motor-dominant neurons also code elementary motor acts, such as precision grip, whole-hand prehension and wrist rotation. However, most of the parietal neurons appear to represent the entire action, since they start to discharge with the hand shaping, and continue to fire while the monkey is holding the object. This property contrasts with those of F5 neurons, which were related commonly to a particular segment of the action. Indeed, in primary motor cortex, on which F5 projects heavily, neurons code even more fragmental movements[34].

Transient inactivation of AIP, by injecting a GABA-receptor agonist (muscimol) into the rostral IPS posterior bank, produces a subtle change in the

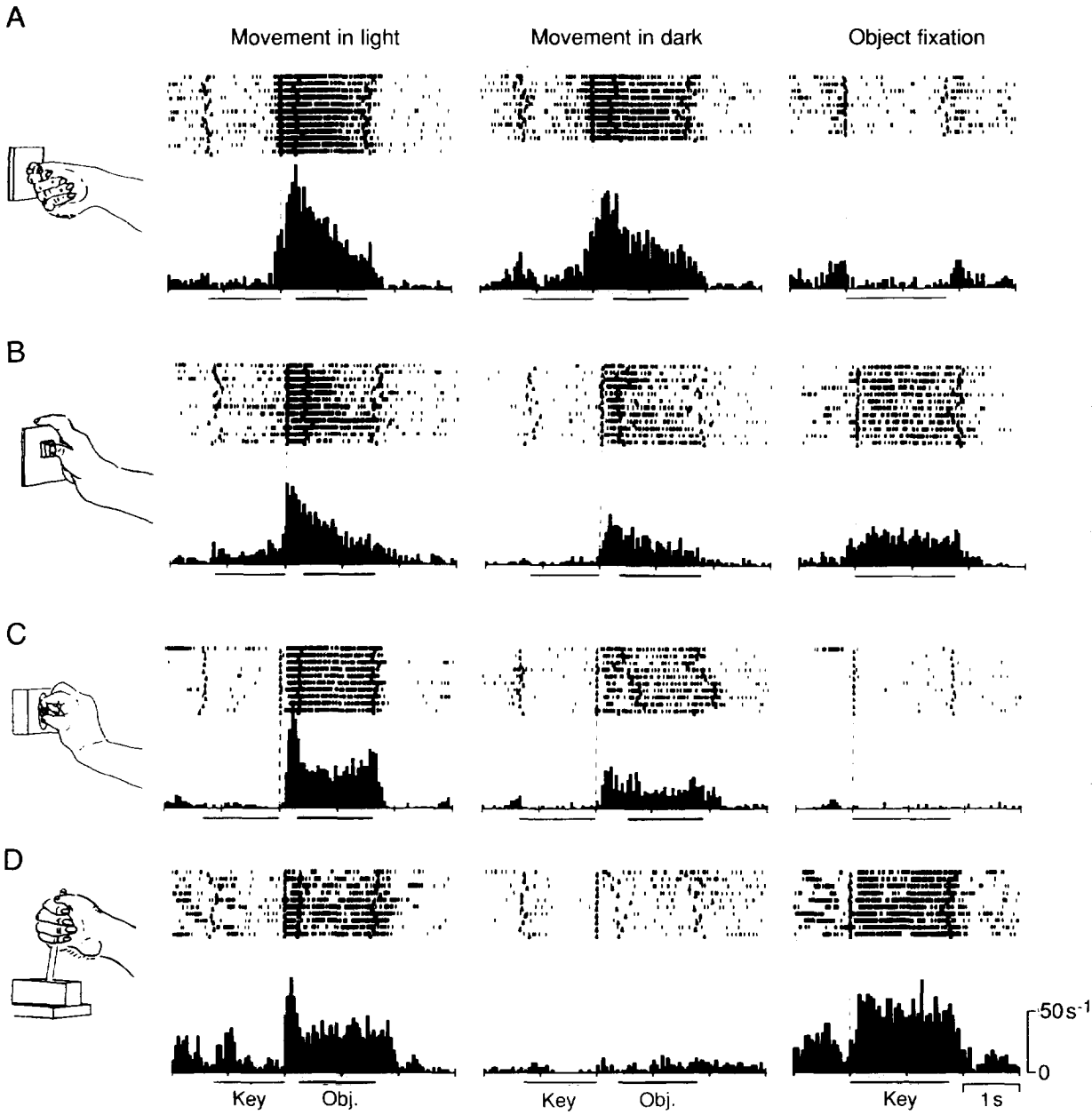

Fig. 5. ***Types of neurons in monkey anterior intraparietal area (AIP) that are involved in hand manipulation.*** *Activity of cells during hand manipulation in light and in dark, as well as during visual fixation of objects, is shown with rasters and histograms.* **(A)** *'Motor-dominant' neuron that preferred 'open pull knob'. The cell was active equally during manipulation in light and in dark but was not active during object fixation.* **(B)** *An object-type of 'visual and motor' neuron that preferred 'push button'. The cell was less active during manipulation in dark than in light, and was activated partly during object fixation.* **(C)** *A non-object type of visual and motor neuron that preferred 'pull knob in groove'. The cell was less active during manipulation in dark but was not activated during object fixation.* **(D)** *'Visual dominant' neuron that preferred 'upright pull lever'. The cell was not activated during hand movement in dark but was activated fully during fixation of the object in light. Key indicates the period of pressing the anchor key before moving to the object. Obj. indicates the period of holding the object to keep the switch on.* Data taken from Ref. 30.

performance of visually guided movements during grasping tasks. In some cases, grasping errors are observed only in difficult tasks that require a precision grip, or during sticking out the index finger to insert it in a groove. Lack of preshaping can be observed during easier tasks also, such as grasping a small cube or sphere. In addition, there is a clearcut dissociation of the effects of muscimol on grasping and reaching[35]. The alteration of preshaping is obtained consistently after injection in the rostral part of the posterior bank of the sulcus, whereas misreaching occurs after injection within its more caudal part. These results support the view that the parietal neurons that are involved in manipulation play a specific role in the visuomotor transformation that is used for grasping objects.

A neuropsychological perspective on grasping movements

The foregoing data can now be integrated within a broader framework that concerns the way that object-related visual information is processed. A highly influential conception[36] attributed different modes of visual processing to diverging corticocortical pathways. One of these pathways, the ventral route, links striate cortex to prestriate areas and inferotemporal cortex. Its interruption abolishes object discrimination without affecting perception

of spatial relationships between objects. The other pathway, the dorsal route, diverges from the previous one by linking the prestriate areas to the posterior part of the parietal lobe. Its interruption produces visual–spatial disorientation.

Recent observations, however, have prompted a reappraisal of the respective functions of the two cortical pathways. Posterior parietal cortex would be crucial for organizing object-oriented action. This role would be complementary with that of occipitotemporal structures that are specialized for object identification and recognition[37]. This view can be illustrated dramatically by two clinical cases. The first case is that of DF, a 35-year old woman, observed by Goodale and colleagues[38]. Following a bilateral lesion of occipitotemporal cortex (the ventral route), DF was unable to recognize objects. She was also unable to demonstrate with her fingers the size of visually inspected objects. By contrast, when instructed to take objects by performing prehension movements, she was quite accurate, and her maximum grip size correlated normally with object size. The second case is that of AT, also a 35-year-old woman, with a lesion of the occipitoparietal region that was likely to have interrupted the dorsal route of visual processing[39]. AT was able to recognize objects, and was also able to demonstrate their size with her fingers. By contrast, preshape of the hand during object-directed movements was incorrect. Correlation between object size and maximum grip size was lacking, with the consequence that objects could not be grasped between the fingertips; instead, the patient made awkward palmar grasps[39,40]. The schema framework offers a compelling explanation for this deficit. Because the grasp schemas were destroyed by the lesion, or disconnected from visual input, the grip aperture did not stop at the required size, grip closure was delayed and the transport was prolonged in order to remain co-ordinated with the grasp.

In agreement with the perception–action distinction in visual processing made earlier by Goodale and Milner[37], this double dissociation suggests that object attributes are processed differently according to the task in which a subject is involved. To serve object-oriented action, these attributes (spatial as well as intrinsic) are subjected to a 'pragmatic' mode of processing, the function of which is to extract parameters that are relevant to action, and to generate the corresponding motor commands. During identification, another 'semantic' mode operates, through which object attributes are bound together to produce a unique percept. Although these modes of processing correspond to widely different cognitive functions[41,42], they can be integrated, and the semantic system can influence the pragmatic system. AT cannot preshape her hand for neutral objects like plastic cylinders, yet, when faced with a familiar object whose size is a semantic property, like a lipstick, she can grasp it with reasonable accuracy[39]. This interaction reflects the role of the abundant anatomical interconnections between the two cortical systems[43].

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