

## REVIEW ARTICLE

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## Parieto-frontal coding of reaching: an integrated framework

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**Abstract** In the last few years, anatomical and physiological studies have provided new insights into the organization of the parieto-frontal network underlying visually guided arm-reaching movements in at least three domains. (1) Network architecture. It has been shown that the different classes of neurons encoding information relevant to reaching are not confined within individual cortical areas, but are common to different areas, which are generally linked by reciprocal association connections. (2) Representation of information. There is evidence suggesting that reach-related populations of neurons do not encode relevant parameters within pure sensory or motor “reference frames”, but rather combine them within hybrid dimensions. (3) Visuomotor transformation. It has been proposed that the computation of motor commands for reaching occurs as a simultaneous recruitment of discrete populations of neurons sharing similar properties in different cortical areas, rather than as a serial process from vision to movement, engaging different areas at different times. The goal of this paper was to link experimental (neurophysiological and neuroanatomical) and computational aspects within an integrated framework to illustrate how different neuronal populations in the parieto-frontal network operate a collective and distributed computation for reaching. In this framework, all dynamic (tuning, combinatorial, computational) properties of units are determined by their location

relative to three main functional axes of the network, the visual-to-somatic, position-direction, and sensory-motor axis. The visual-to-somatic axis is defined by gradients of activity symmetrical to the central sulcus and distributed over both frontal and parietal cortices. At least four sets of reach-related signals (retinal, gaze, arm position/movement direction, muscle output) are represented along this axis. This architecture defines informational domains where neurons combine different inputs. The position-direction axis is identified by the regular distribution of information over large populations of neurons processing both positional and directional signals (concerning the arm, gaze, visual stimuli, etc.) Therefore, the activity of gaze- and arm-related neurons can represent virtual three-dimensional (3D) pathways for gaze shifts or hand movement. Virtual 3D pathways are thus defined by a combination of directional and positional information. The sensory-motor axis is defined by neurons displaying different temporal relationships with the different reach-related signals, such as target presentation, preparation for intended arm movement, onset of movements, etc. These properties reflect the computation performed by local networks, which are formed by two types of processing units: matching and condition units. Matching units relate different neural representations of virtual 3D pathways for gaze or hand, and can predict motor commands and their sensory consequences. Depending on the units involved, different matching operations can be learned in the network, resulting in the acquisition of different visuo-motor transformations, such as those underlying reaching to foveated targets, reaching to extrafoveal targets, and visual tracking of hand movement trajectory. Condition units link these matching operations to reinforcement contingencies and therefore can shape the collective neural recruitment along the three axes of the network. This will result in a progressive match of retinal, gaze, arm, and muscle signals suitable for moving the hand toward the target.

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## Introduction

Architecture of the network: uniqueness of neuronal functional properties within individual areas?

Studies from different neuroscience disciplines have shown the crucial role of some parietal and frontal areas in visually guided reaching. These studies have illustrated both the specialization of the parietal lobe for spatial representations and action (for recent review see Mountcastle 1995; Caminiti et al. 1996, 1998; Andersen et al. 1997; Kalaska et al. 1997; Wise et al. 1997; Colby 1998; Lacquaniti and Caminiti 1998) and its functional parcellation: a posterior parietal region is predominantly involved in visual information processing, selective visual attention, and oculomotor control; an anterior parietal region is more concerned with somatic information processing and arm motor control; an intermediate parietal region seems to be important for correlating visual, somatic, and motor information.

Experimental results on reaching indicate that the view of a strict functional specialization of cortical areas is not tenable anymore, for at least two reasons: (1) there is no cortical area uniquely responsible for reaching and (2) the different types of reach-related signals are not segregated into individual cortical areas. On the contrary, they can be found in different parietal and frontal areas (Johnson et al. 1996; for reviews see Caminiti et al. 1996, 1998; Wise et al. 1997; Battaglia-Mayer et al. 1998), where their distribution gradually changes along the tangential cortical domain, defining a visual-to-somatic gradient. This spatial arrangement is coherent to and probably imposed by the gradients of cortico-cortical association connections between parietal and frontal cortices (Caminiti et al. 1996, 1998; Johnson et al. 1996).

Representation of information: reference frames?

Motor behavioral studies have shown that information relevant to reaching can be represented in preferred reference frames, this preference depending on task demand (Soechting and Flanders 1992; Gordon et al. 1994; McIntyre et al. 1997, 1998).

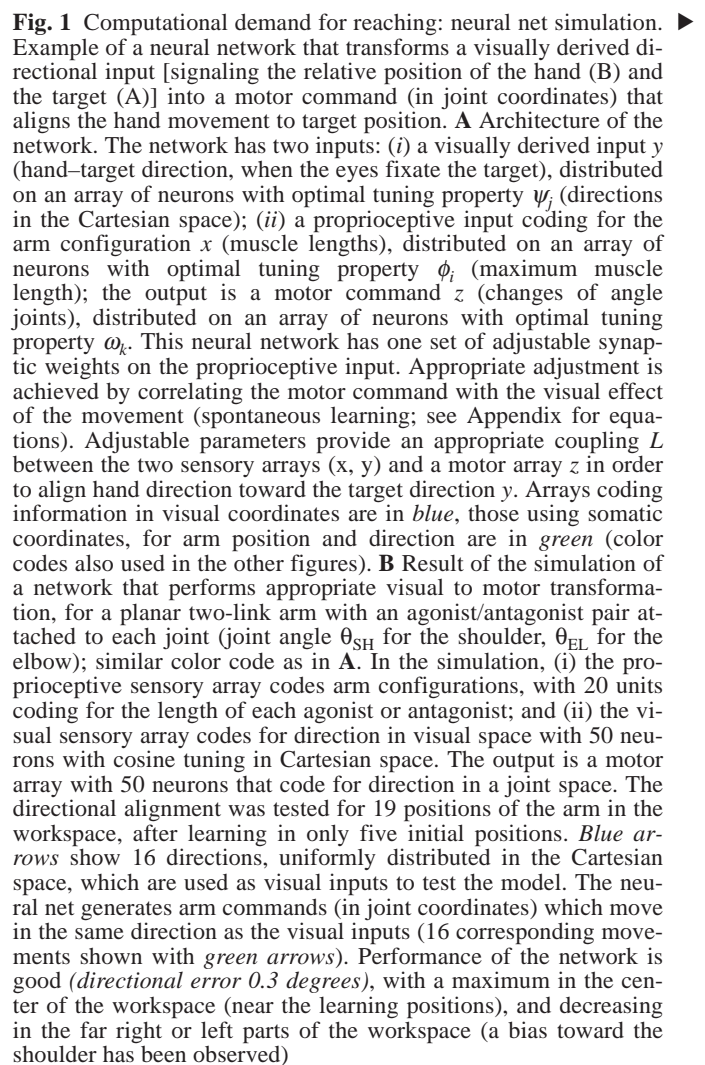
Neurophysiological studies do not reveal unequivocal relationships of neural activity to a certain reference frame in any given cortical area (see Colby 1998). For instance, information relevant to coding arm movement in the motor cortex can be represented either in terms of vector coding in external three-dimensional (3D) space or in terms of body-centered reference frames (Georgopoulos et al. 1982, 1988; Caminiti et al. 1990, 1991; Kalaska et al. 1990; Scott and Kalaska 1997). Similar considerations apply to the coding of reaching in the superior parietal lobule (Kalaska et al. 1983; Lacquaniti et al. 1995). Furthermore, in all parietal and frontal areas, more than one signal influences the activity of individual reach neurons (for reviews see Caminiti et al. 1996, 1998; Wise et al. 1997).

It seems therefore that the concept of combinatorial domains matching different sources of signals explains the biological underpinning of sensory-motor transformations more adequately than the concept of reference frames.

Computation: computational steps?

Neurophysiological studies do not support a hierarchy of computational steps that lead from vision to movement, with each step performed solely by a given parietal or frontal area. Recruitment of different reaching-related activity types in the parieto-frontal network is largely simultaneous, even if there are time lags at the peak of neuronal activation (Johnson et al. 1996; Kalaska et al. 1997) in the frontal and parietal segments of the network. This implies that sensory and motor signals relevant for reaching are processed in a parallel fashion.

In this paper, we offer a unified framework that relates the neuronal properties observed in different parts of the parieto-frontal network with the computational de-

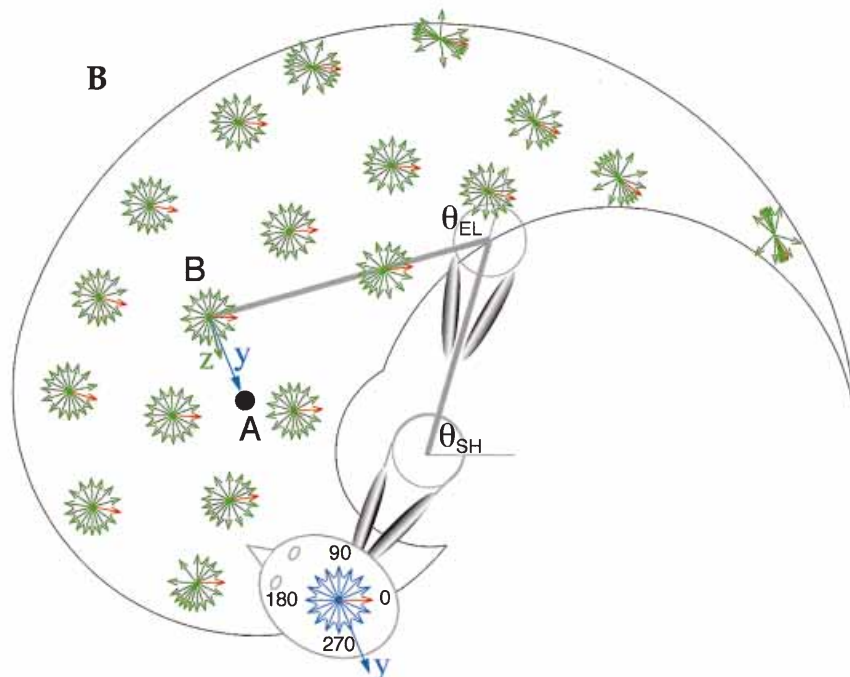
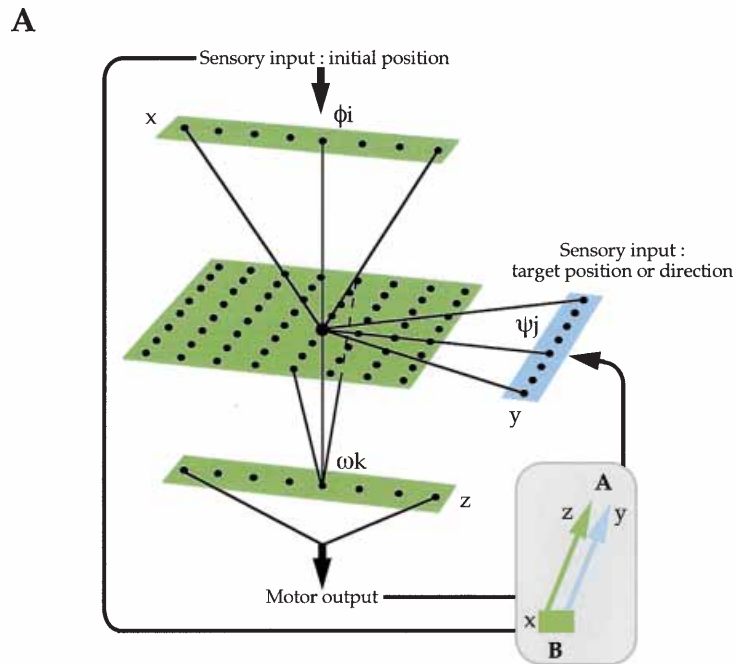
**Fig. 1** Computational demand for reaching: neural net simulation.  Example of a neural network that transforms a visually derived directional input [signaling the relative position of the hand (B) and the target (A)] into a motor command (in joint coordinates) that aligns the hand movement to target position. **A** Architecture of the network. The network has two inputs: (i) a visually derived input  $y$  (hand-target direction, when the eyes fixate the target), distributed on an array of neurons with optimal tuning property  $\psi_j$  (directions in the Cartesian space); (ii) a proprioceptive input coding for the arm configuration  $x$  (muscle lengths), distributed on an array of neurons with optimal tuning property  $\phi_i$  (maximum muscle length); the output is a motor command  $z$  (changes of angle joints), distributed on an array of neurons with optimal tuning property  $\omega_k$ . This neural network has one set of adjustable synaptic weights on the proprioceptive input. Appropriate adjustment is achieved by correlating the motor command with the visual effect of the movement (spontaneous learning; see Appendix for equations). Adjustable parameters provide an appropriate coupling  $L$  between the two sensory arrays ( $x$ ,  $y$ ) and a motor array  $z$  in order to align hand direction toward the target direction  $y$ . Arrays coding information in visual coordinates are in *blue*, those using somatic coordinates, for arm position and direction are in *green* (color codes also used in the other figures). **B** Result of the simulation of a network that performs appropriate visual to motor transformation, for a planar two-link arm with an agonist/antagonist pair attached to each joint (joint angle  $\theta_{SH}$  for the shoulder,  $\theta_{EL}$  for the elbow); similar color code as in **A**. In the simulation, (i) the proprioceptive sensory array codes arm configurations, with 20 units coding for the length of each agonist or antagonist; and (ii) the visual sensory array codes for direction in visual space with 50 neurons with cosine tuning in Cartesian space. The output is a motor array with 50 neurons that code for direction in a joint space. The directional alignment was tested for 19 positions of the arm in the workspace, after learning in only five initial positions. *Blue arrows* show 16 directions, uniformly distributed in the Cartesian space, which are used as visual inputs to test the model. The neural net generates arm commands (in joint coordinates) which move in the same direction as the visual inputs (16 corresponding movements shown with *green arrows*). Performance of the network is good (*directional error 0.3 degrees*), with a maximum in the center of the workspace (near the learning positions), and decreasing in the far right or left parts of the workspace (a bias toward the shoulder has been observed)

mands of visually guided reaching. In the first part, we show that each sensory-to-motor transformation can be solved by a neural nets with distributed positional and directional codes similar to those of neurons experimentally studied; in the second part, we show how several neural nets of this type can cooperate, thanks to the functional architecture of the parieto-frontal network, in order to adapt the computational operations to different sensory-motor contexts and task constraints.

### Cortical computation for reaching: a unified framework

*The computational demand for reaching is met by the operations of neural nets that align distributed sensory and motor representations*

During visuomotor tasks, information about target location must be transformed into a motor command through the interplay of different populations of neurons (Salinas and Abbott 1995).



Representation of target location is distributed over populations of neurons encoding sensory information about position of visual stimuli on the retina and/or eye position in the orbit. Similarly, the control of movement is distributed over populations of neurons which encode movement-related information. The neural network has to transform the sensory information into a form that is appropriate for use by the motor system. As illustrated in Fig. 1A, different sensory and motor neural representations should align properly, so that the activity of neurons encoding target location (in an arbitrary position A) evokes activity of neurons related to the command for movement (from another arbitrary initial position B) toward the target in A. Correct alignment of the sensory and motor representations occurs when the target location and movement goal location coincide or when the direction of movement is parallel to the direction identified by initial hand position and target position. To obtain a correct solution, the network must combine the sensory input on target location with a second input concerning arm and/or eye position (Burnod et al. 1992; Bullock et al. 1993; Salinas and Abott 1995).

In computational terms, distributed sensory and motor codes can be represented by arrays (Salinas and Abott 1995): a sensory array of processing units represents a distributed code  $x$  for arm position, a second sensory array represents a distributed code  $y$  for target position, and a motor array represents a distributed code  $z$  for the motor command (Fig. 1). The neural network should therefore provide an appropriate coupling,  $L$ , between the two sensory arrays and the motor array in order to align hand and target position, or direction (see Appendix, Sect. 1):

$$z=L(x,y) \quad (1)$$

such that  $z$  is aligned with  $y$  for initial position  $x$ .

In a neural net solution, this computational demand is satisfied by adjustable parameters (sets of “synaptic weights”) that couple sensory and motor arrays. Synaptic weights satisfying this condition (Eq. 1) should arise from an unsupervised, self-organizing learning principle based on the alignment of the motor command to the visual feedback generated by the movement.

General solutions for sensorimotor transformations have been proposed (Salinas and Abott 1995) when operation  $L$  relates sensory and motor codes for positions. For instance, if the sensory arrays code for retinal position  $x$  and gaze direction  $y$  in the motor array, the network can generate a code of target position  $x$  in a body-centered reference frame (see Appendix, Sect. 1a). If the relationship between positional codes is non-linear, the relationship between sensory and motor directions (directional transformations) has the advantage of a linear approximation in each part of space. This facilitates learning and simplifies the handling of redundancy (Mel 1991; Kawato et al. 1992; Bullock et al. 1993; Frolov et al. 1994). For example, if a sensory array codes for a desired visually derived direction  $y$ , the network can generate the code for the effective direction of movement,  $z$ , in motor coordinates; this directional transformation,  $L$ ,

depends on the second sensory input that codes for limb configuration,  $x$  (see Appendix, Sect. 1b).

Comparison of these network operations with neuronal mechanisms requires that: (1) the codes for the positional inputs (limb position) should be comparable with the representations observed in the parieto-frontal network and (2) the network should learn an accurate transformation from a small number of examples.

Figure 1B illustrates a simulation of a network which transforms distributed, visually derived information into a distributed motor command for joint rotations and which satisfies the following constraints (Baraduc et al. 1999): (1) distributed codes for positions are derived from proprioceptive inputs on muscle lengths and (2) a good accuracy is obtained, even if learning is performed with only five initial positions of the arm (see Appendix, Sect. 1b).

The solutions provided by these neural networks in order to align position and/or directions with different sensory and motor codes are quite general: they relate sensory and motor information congruent in the 3D space.

To compare the operations of this model with those of neuronal populations, a specification is necessary. The parieto-frontal network implements reaching code with a different combination of inputs across different neuronal populations and can perform a variety of alignments between hand, gaze and visual signals. It is merely a “network of networks”, i.e., a network of computational nodes, where each node is a population of neurons which can perform a neural operation similar to that described in Fig. 1.

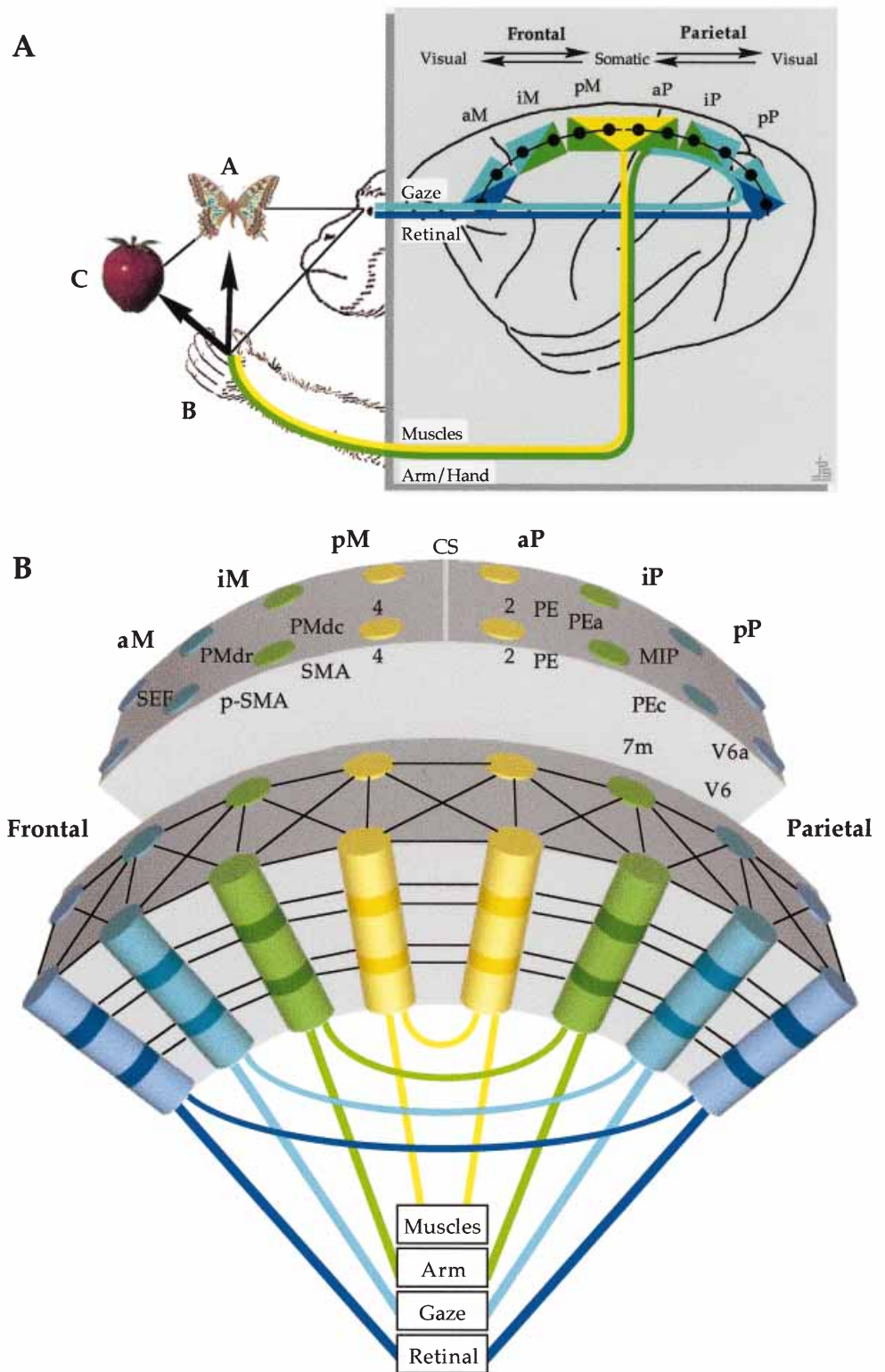
What remains to be done is to specify fully the architecture and coding parameters of this network of networks and also to provide a computer simulation, as shown in Fig. 1B for a single computational node. However, the number of unknown parameters increases with the number of nodes, and additional knowledge and constraints are required to obtain an entire model working in a computer simulation. Therefore, what we have done, as detailed below, is delineate a few basic principles of the architecture of the parieto-frontal network: (1) we represent the architecture of this network as a 3D grid of computational nodes; (2) we show that each computational node on this grid is similar to the network previously detailed (illustrated in Fig. 1); (3) we show that the different computational nodes can progressively learn different visuomotor transformations depending on their locations on the three axes of the network; (4) we illustrate how these nodes, after learning, can cooperate in a given reaching task, with a progressive recruitment of groups of neurons along the three connective axes of the network; and (5) we show that this functional architecture, even if not fully simulated on a computer model, allows predictions about the properties of neurons in the different parts of the parieto-frontal network.

#### *The cortical control of reaching is distributed on a visual-to-somatic gradient*

As shown in Fig. 2A, hand reaching can be described first by the directional change of the hand position from its ini-

**Fig. 2** Reaching, sensory-motor information flow, and combinatorial domains in the cortex.

**A. Left part:** monkey's behavior. The eyes fixate a point (*butterfly*) in A, the hand is in B and an object (*apple*) is in C. Depending on the task demands, the hand moves (*black arrows*) from B toward the fixation point (A), or toward point C, which is not foveated. Four sets of sensory-motor events processed in the cortex are schematized by different colors throughout the figures: retinal (*dark blue*) indicates retinal information about object location and hand position in the visual field. Gaze (*light blue*) indicates position and direction of gaze. Arm/hand (*green*) refers to arm and hand position and relative movement direction. Muscles (*yellow*) refers to proprioceptive activity and muscle commands. The visuomotor transformation requires the combination of retinal, gaze, hand, and muscle signals to move the hand toward the target. **Right part:** visually guided reaching involves different areas in the parietal and frontal cortex, which can be grouped, to a first approximation, in three parietal regions (anterior, *aP*; intermediate, *iP*; posterior, *pP*) and in three frontal motor regions (anterior, *aM*; intermediate, *iM*; posterior, *pM*), which are reciprocally connected. **B Architecture** of the cortical network underlying reaching. The local processing by neuronal circuits across cortical layers are schematized as "cortical columns"; *aP* includes area 2 and PE; *iP* includes areas MIP, PEa and 7m; *pP* includes areas V6 and V6a; *pM* includes M1; *iM* includes PMdc; *aM* includes PMdr and SEF. The layout of the parieto-frontal connections among these regions and the tangential distribution of functional properties of neurons define a gradient-like architecture, where regions of functional overlap identify combinatorial domains. Four sets of sensory-motor signals involved in reaching are treated: retinal (*dark blue*), gaze (*light blue*), arm (*green*), muscles (*yellow*)



tial location (B) to a foveated target (butterfly in A) or to a non-foveated target (apple in C). In these two forms of visuomotor behavior, the process of target localization requires *retinal* and *gaze* positional information. This visually derived information about target location needs to be combined with information about initial *arm* configuration

and position to compute a motor command for the *muscles* that will move the hand toward the target. Neurophysiological results indicate that these different sets of directional and positional information are distributed over large populations of neurons across different parietal and frontal areas (see Wise et al. 1997, Caminiti et al. 1998 for reviews).

In the parietal cortex, this network (Fig. 2B) includes the parieto-occipital (PO) area (Covey et al. 1982; Gattass 1985; Colby et al. 1988), now divided into V6A and V6 (Galletti et al. 1996), medial intraparietal (MIP) area (Colby et al. 1988; Colby and Duhamel 1991; Johnson et al. 1993, 1996; Snyder et al. 1998), area 7 mesial (7m) (Johnson et al. 1993, 1996; Ferraina et al. 1997a, 1997b), the cortex of both the exposed part of area 5 (labelled PE) and of the medial bank (labelled PEa) of the intraparietal sulcus (IPS) (Pandya and Seltzer 1982), and area 2. Parietal area 7m projects mainly to dorsorostral premotor cortex (PMdr, F7) and to its border with dorsocaudal premotor cortex (PMdc, F2); MIP projects mainly to PMdc (F2) and to its border with primary motor cortex, M1 (labeled as area 4 in Fig. 2B). Area PE, in contrast, projects preferentially to the PMdc/M1 border and to M1 (F1). A connection of V6A with PMdr and part of PMdc (Tanné et al. 1995; Matelli et al. 1998; Shipp et al. 1998; Caminiti et al. 1999) has also been described, although the area of termination of this projection in PMdr remains to be characterized physiologically. These connections are reciprocal.

The architecture of the fronto-parietal network involved in reaching can, therefore, be schematized as being formed by three parietal and three frontal regions, reciprocally connected and symmetrical with respect to the central sulcus (Fig. 2A, brain figurine): (1) a posterior parietal region (*pP*) including V6 and V6a, is mainly connected, through V6A, to an anterior frontal region (*aM*), formed by PMdr; (2) an intermediate parietal region (*iP*), including areas 7m, MIP and PEa, is mainly connected to an intermediate frontal zone (*iM*), coextensive with part of PMdr (7m), the border PMdr/PMdc (7m, MIP), PMdc (MIP, PEa); (3) an anterior parietal region (*aP*), which encompasses areas PE and 2, is connected to a posterior frontal lobe region (*pM*), represented by M1.

As shown in Fig. 2, each parietal and frontal region processes different signals related to reaching. These different signals are not confined within intra-area borders, but distributed in the parieto-frontal network, as illustrated in Fig. 3A: (1) neurons with dominant arm movement-related activity, probably linked to muscle output mechanisms, predominate in cortical regions flanking the central sulcus (Johnson et al. 1996), mainly in its rostral bank; these neurons also receive somatosensory inputs; (2) neurons tuned to arm position extend more rostrally in the frontal lobe and, symmetrically, more caudally in the superior parietal lobule (SPL) (Johnson et al. 1996; Ferraina et al. 1997a, 1997b; Caminiti et al. 1999); they can be found, however, along the entire parieto-frontal network; (3) eye-movement-related neurons signaling the position or direction of gaze are distributed more caudally in the SPL (Galletti et al. 1996; Ferraina et al. 1997a; Caminiti et al. 1999) and rostrally in the frontal lobe (Boussaoud et al. 1995, 1998; Preuss et al. 1996), including the supplementary eye fields (SEF); and (4) neurons signaling for target location in retinal and/or extra-retinal coordinates predominate in the SPL at the more caudal (V6A, V6) (Galletti et al. 1993, 1996; Caminiti et al. 1999) and intermediate (MIP) (Johnson et

al. 1996) levels, and in the more rostral part of the frontal lobe (Weinrich and Wise 1982; Weinrich et al. 1984; Tanné et al. 1995; Johnson et al. 1996).

The functional properties of parietal and frontal reaching-related neurons within this network change gradually, such that we can define a visual-to-somatic gradient (Fig. 3A) with spatial arrangement matching that of cortico-cortical association connections (Johnson et al. 1996; Caminiti et al. 1996, 1998, 1999). In fact, regions with similar properties tend to be preferentially linked by cortico-cortical connections (Johnson et al. 1996; for reviews see Caminiti et al. 1996, 1998; Wise et al. 1997).

This gradual change of properties results in regions of functional overlap, which define combinatorial domains where the four sets of reach-related signals (retinal, gaze, arm position, and muscle output) can be matched. In these areas, individual neurons are mostly tuned to more than one of the sensory-motor signals relevant to reaching and process both positional and directional informa-

**Fig. 3** Network architecture and visuomotor transformations. **A** Parieto-frontal network, architecture, and combinatorial properties of neurons. The four sets of sensory-motor signals (retinal, gaze, arm/hand, muscles) involved in reaching are represented over large populations of cortical neurons. The tangential distribution of these neurons changes gradually in the cortex, as illustrated by the proportional variation in shape of the *colored regions* along the visual-to-somatic gradient. These rather continuous neural representations result in large regions of overlap within each cortical area, defining at least three combinatorial domains in the parietal cortex (*aP*, *iP*, *pP*) and three in the frontal cortex (*pM*, *iM*, *aM*). The different *gray levels* on the vertical dimension of the figure indicate the different distribution of *sensory*, *match*, *set (condition)* and *motor* neurons in parietal and frontal cortices, as defined in the text. **B** Functional axes of the parieto-frontal network. A processing unit is shown by a *colored circle*: it models a group of neurons (within a column) with similar connections on the parieto-frontal network. The properties of each processing unit depend on its location with respect to the three axes of the network: (i) the visual-to-somatic axis displays four sets of sensory-motor information, both positional and directional, with a similar color code as in Fig. 2: muscles, arm/hand, gaze, retina. Units that model corresponding parietal and frontal populations are aligned vertically on the same locations on the visual-to-somatic axis (*aP* aligned with *pM*, *iP* with *iM* and *pP* with *aM*), and *vertical lines* represent reciprocal frontal-parietal connections along processing units with similar sensory-motor combinatorial properties; (ii) the sensory-motor axis contains four types of processing units (sensory, match, condition, motor), distributed in both parietal and frontal regions; (iii) the position-direction axis contains units tuned for different combinations of positions and directions (virtual 3D pathways); in this figure, we show four virtual 3D pathways for hand (*left*) and gaze (*right*) with two initial positions (AB) and two directions for each position (AC, AB, BA, BC), and active on the sensory-motor context, as illustrated in Fig. 2. Units coding for equivalent 3D pathways are aligned horizontally. *Thin black lines* indicate pre-existing anatomical connections among units, *orthogonal lines* show relationships between processing units with similar properties ( $OT_{\perp}$ ) on one axis, *diagonal lines* relationships between units with properties congruent in 3D space. *Double curved lines* identify examples of reinforced connections of matching units (after learning), which can transfer visual to motor information for reaching: the reinforced connections illustrate two processing routes that can guide the hand to foveated targets (between 3D pathways AB and BA), and two that can guide the hand to a non-foveated target (between 3D pathways AC and BC). The *thick lines* represent the specific processing routes that are activated for reaching to foveated targets in the behavioral situation shown in Fig. 2

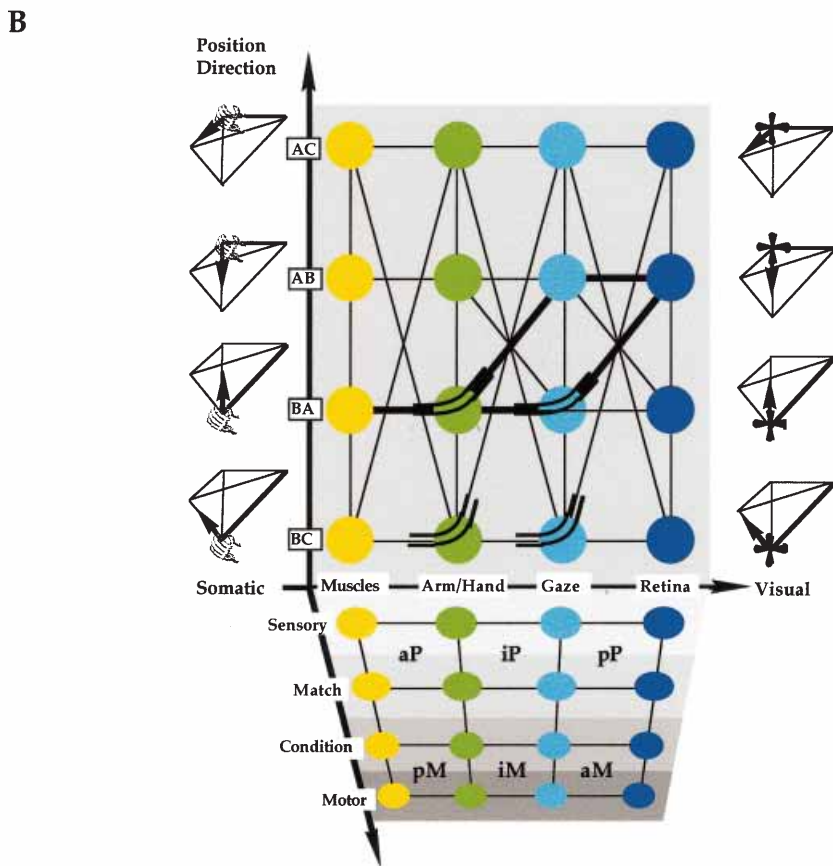
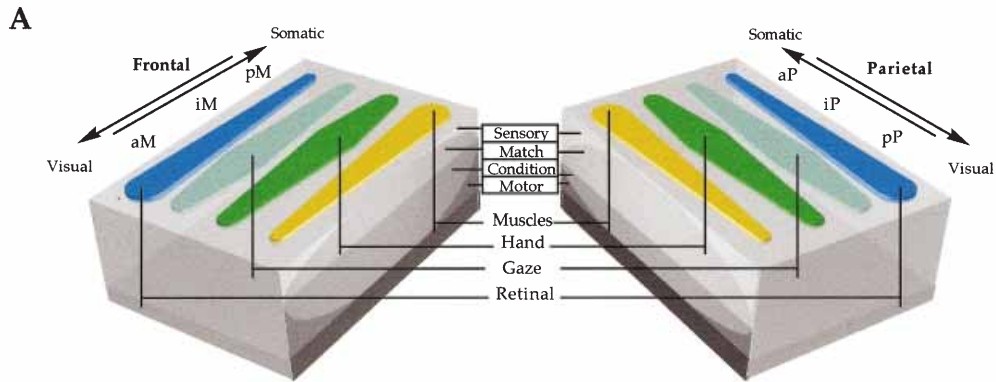
tion. This convergence of inputs confers to these neurons their specific combinatorial properties. Thus, the crucial features of this parieto-frontal network are the gradient-like architecture and its combinatorial domains.

*Functional properties of neurons are defined by their location on three axes of the connective architecture of the parieto-frontal network*

The distribution of neuronal tuning properties along the visual-to-somatic gradient, as shown in Fig. 3A, is crucial for the understanding of the neural computation for visually guided reaching performed by the underlying neural circuitry. A large set of experimental results has suggested

that the cerebral cortex is organized in “cortical columns”. A cortical column is a neural assembly (for discussion, see Mountcastle 1979, 1997) which is composed, across layers, by several cell types sharing certain properties and forming a local network which relates different sets of inputs and outputs, both extrinsic and intrinsic. Functional properties of neurons in the parieto-frontal network directly depend on these different input–output relationships.

A processing unit of the network models a neural assembly within a column where neurons share the same input–output connectivity. We can thus differentiate, within columns, subsets of neurons more related to the periphery (modeled by sensory or motor units) and subsets more dependent on cortico-cortical relationships (modeled by matching or condition units).



We propose to relate the distribution of functional and computational properties to the connective architecture of the cortical network. Tuning and combinatorial properties of neurons, as well as computational properties of processing units, are determined by their location relative to three main axes of this network (Fig. 3B, Appendix, Sect. 1).

The combinatorial properties of neurons are differentiated along a *visual-to-somatic axis* (Fig. 3B), both in the parietal and in the frontal lobe. This reciprocal visual-to-somatic processing pathway is defined by its extrinsic connections with sensory and motor systems, as well as by its intrinsic feed-forward and re-entrant connections. Information within the same combinatorial domain is distributed within large populations of neurons tuned for different positions and directions (of arm, gaze, etc.). Functional properties are further differentiated along a *position-direction axis* (Fig. 3B); here, both excitatory and inhibitory lateral connections shape the collective representation of positional and directional information in neuronal assemblies. Finally, neuronal properties are further differentiated along a sensory-motor axis: different anticipatory properties, functionally mediating between sensory inputs and motor outputs, are shaped by reciprocal connections between the parietal cortex and the frontal cortex.

*Visual-to-somatic axis.* As suggested by the experimental results along the visual-to-somatic gradient (Fig. 2 and Fig. 3), neurons have combinatorial properties that depend on at least four sets of sensory-motor signals: retinal, gaze, arm position/movement direction, and muscle output. We assume that these properties reflect the underlying computation performed by processing units. (1) In the anterior parietal (aP) and posterior frontal motor region (pM), processing units relate two sets of information: positional and directional signals on the arm and information on muscle dynamics. (2) In the intermediate parietal (iP) and frontal premotor areas (iM), they relate arm and gaze positional signals with information about movement direction. (3) In the posterior parietal (pP) areas, they relate positional and directional information of gaze and arm with visual inputs on the retina. Processing units in related anterior premotor areas (aM) form similar combinations, probably with more elaborate and complex signals. This may depend on their relationship with the dorsolateral prefrontal cortex and, therefore, with spatial memory processes (see Goldman-Rakic 1995).

Gaze and arm position signals play a unifying role within the entire parieto-frontal network. In most cortical areas of the network, neurons are modulated by at least one of these two inputs. These properties reflect the underlying computation: a subset of processing units is pre-selected, depending on gaze and arm position, and then can learn and compute stable relationships between visually derived and somatomotor signals.

*Position-direction axis.* Within each combinatorial domain, processing units are tuned to both position (state)

and direction (change of state). A combination of position and direction of gaze or arm can be viewed as representing *3D pathways* for gaze or hand (Fig. 3B). The advantage of this simplified view is that virtual 3D pathways for hand and gaze can be directly compared and related in the 3D space, regardless of the combinatorial domain.

Positional and directional information are encoded in a parallel fashion in the activity of cortical neurons which share the same combinatorial domain. Populations of arm-movement-related cortical neurons in areas 4 and 6 display a uniform distribution of directional tuning properties in 3D space (Georgopoulos et al. 1988; Caminiti et al. 1990, 1991). In part of area 5 (PE and PEa), hand position and movement direction tuning properties related to the azimuth, elevation, and distance of the hand in space are symmetrically distributed relative to the origin of the coordinate system (Lacquaniti et al. 1995). In both cases, these regular distributions (either uniform or symmetrically arranged) result in simple population coding of hand position and movement direction and facilitate a parallel computation of the motor command (Burnod et al. 1992).

*Sensory-motor axis.* Neurons sharing the same combinatorial domain and similar positional and directional tuning properties may have different temporal relationships with the signals relevant to reaching. At least four sets of neuronal properties can be experimentally observed and can be interpreted as reflecting four types of computation on the sensory-motor axis (Fig. 3B):

1. Neurons in the somatic and visual poles of the parietal network are time-locked to sensory signals. Processing units in the visual pole are *sensory units* which process retinal information about target location and hand movement in the visual field; in the somatic pole, they are sensory units that process somatic information about arm position and movement direction.
2. Neurons in the somatic pole of the frontal network are time-locked to motor events. Processing units in these regions are *motor units* concerned with shaping the output motor command for the arm. *Motor units* in the visual pole can process the output motor command for eye movements.
3. Neurons in the intermediate parietal and frontal regions have intermediate associative properties. A first class of neurons anticipate the motor command thanks to multimodal sensory inputs. This property reflects the underlying computation; processing units in these intermediate regions can store correlations between different sensory and motor signals, induced by arm or gaze movements. After learning, these *matching units* will be tuned to different sensory and motor signals congruent in the 3D space, such as signals about hand movement toward the fixation point (see next section and Appendix, Sect. 2). In this way, they can generate anticipatory activities about the sensory consequences of motor commands for hand or gaze. As



illustrated in Fig. 3A, matching units are differentially distributed along a parietal-to-frontal gradient and are mostly represented in the parietal lobe, where they are influenced by somatic and visual signals. The properties of matching units directly depend on their combinatorial domain along the visual-to-somatic gradient.

4. *Set-related* reaching neurons along the visual-to-somatic gradient display a second type of associative property (Johnson et al. 1996). These neurons can be activated by a sensory event (such as target presentation) and, when a delay occurs or is imposed, their activity selectively anticipates the upcoming motor command in relation to the task demand and, therefore, on the basis of expected reinforcement signals. This property reflects the operation of processing units, called *condition units* (see Appendix, Sect. 3), which store correlations between sensory-motor signals and reinforcement contingencies. The activity of condition units reflects not only positional and directional information, but also the arbitrary relationships imposed by the task demand in order to obtain a reinforcement. As shown in Fig. 3A, condition units are differentially distributed along a parietal-to-frontal gradient and are mostly represented in the frontal lobe, which is more influenced by reinforcement-related signals. The properties of condition units also depend on their combinatorial domain along the visual-to-somatic gradient.

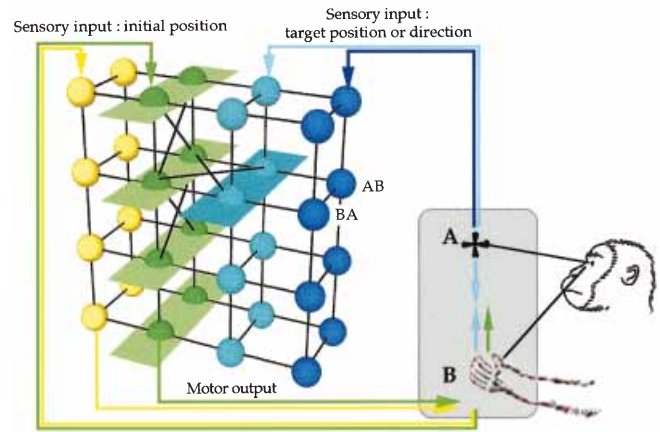
*Matching units select the motor command signals appropriate to match the different sets of sensory information on the parieto-frontal flow*

Repeated co-activation by two different inputs can induce changes in the strength of the functional relationships between units. Such learning, based on Hebbian activity-dependent changes of synaptic strength, is suggested by experimental observations of associative potentiations in different parts of the visual-to-somatic gradient, including the visual (Frégnac et al. 1988; Artola et al. 1990), somatomotor (Baranyi and Féher 1981), and frontal cortical regions (Hirsch and Crépel 1990).

*Learning situation* Figure 4 illustrates learning in matching units in combinatorial domain iP. On the sensory-motor axis, they are connected to condition and motor units that control the direction of hand movement. When the hand moves (3D pathway of the hand from B in direction BA), these matching units are activated both by the proprioceptive input about initial arm configuration and by the efferent copy of the motor command. On the visual-to-somatic axis, these matching units are also connected to processing units sensitive to visual stimuli and gaze shift (3D pathway for gaze).

Hand movement produces strong co-activations in iP matching units in at least two situations:

1. When the hand is in the fovea – in this case, the reafferent visual input produced by the hand movement (BA)

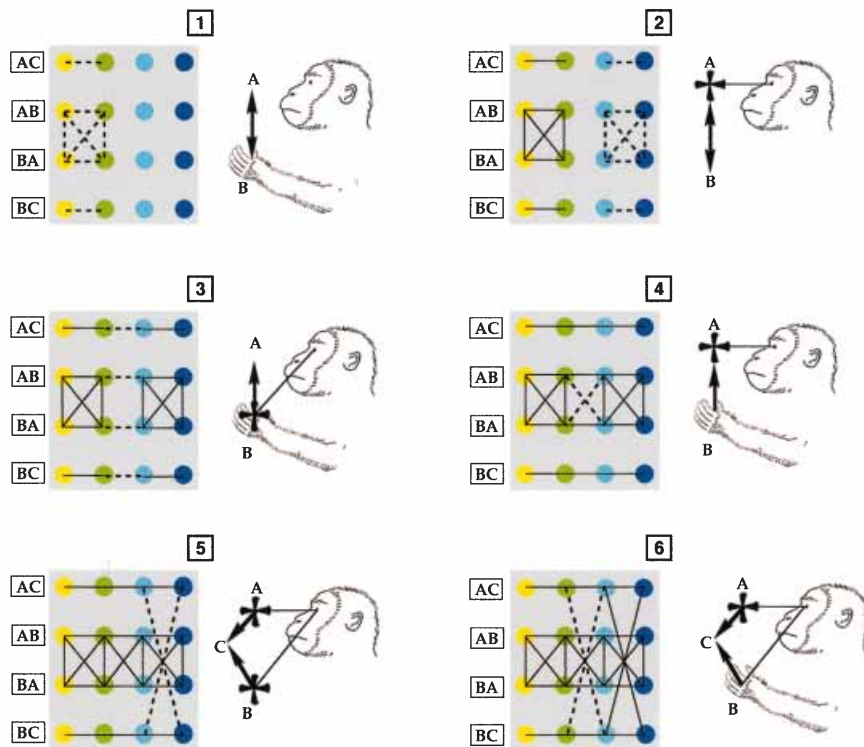


**Fig. 4** Neural operations within combinatorial domains correlating visual and somatic information; reaching to foveated targets. Sets of matching units can perform sensory-motor transformations similar to the neural net illustrated in Fig. 1, which aligns hand direction (in motor coordinate) toward the target (in visual coordinate). *Right part:* monkey's behavior. As in previous figures, the fixation point is in A, the hand is in B; the hand moves from B toward the fixation point, A. Visual and motor directional information has similar color codes as in the network (at left) and as in Fig. 1. *Left part:* the modeling of the parieto-frontal network is the same as in Fig. 3B, with the three axes, visual-to-somatic (from right to left), sensory-motor (from top to bottom), position-direction (rear–front). Only the two 3D pathways involved in a reaching movement from B to foveated targets in A are shown, BA in front plane, and AB in back plane. The color code is the same as in the previous figures, with units colored according to their main modality. We focus on the set of matching units (second horizontal plane from top on the sensory-motor axis) in iP (green, in the visuo-somatic axis) coding for different 3D pathways for the hand (in the position-direction axis). This node of the parieto-frontal network has a similar architecture as the neural network shown in Fig. 1. It combines two different sensory inputs: (1) a visually derived input (in blue) from units that are tuned for 3D pathways for gaze signaling the hand-target direction AB, and (2) a proprioceptive input coding for arm configuration in initial position of the arm B (from sensory units, in green); the outputs project to units that code for the motor command (condition and motor units, in green, can together be considered as a single output layer; they will be further differentiated by task-dependent conditions). The set of matching units in iP can learn a distributed operation (as the network shown in Fig. 1) that transforms any visually derived sensory input on hand-target direction (3D pathways for gaze) in a directional motor command that aligns the hand to the target position (3D pathway for hand aligned with the gaze pathway). See text for detailed explanation

activates a virtual 3D pathway outward from the fovea and parallel with hand movement in the 3D space (visual inputs tuned for 3D gaze pathway BA are active).

2. When the hand moves toward the fovea (the direction of the hand movement points to the fixation point) – in this case, the reafferent visual input activates a virtual 3D pathway inward to the fovea and antiparallel with hand movement in the 3D space (visual inputs tuned for 3D gaze pathway AB are active).

These strong co-activations (Hebbian learning process) tend to increase the functional links between units tuned for virtual hand and gaze 3D pathways which are aligned, or congruent, in the 3D space. At least two alignments are



**Fig. 5** Progressive learning of visual to motor transformations for visually guided reaching. The six panels illustrate different sets of matching units specified during six successive learning stages by different sensory-motor congruences. 1: motor babbling; 2: control of gaze and attention; 3: hand tracking; 4: reaching to foveated targets; 5: visual invariance; 6: reaching to peripheral targets. See text for detailed description. Each panel shows both the learning in the parieto-frontal network (*left*) as well as the related behavior (*right*). The modeling of the network is the same as in Fig. 3B, at the level of matching units (section through the sensory-motor axis, showing the two other axes, visual-to-somatic and position-direction; processing units and color codes as in Fig. 3B). Along the position-direction axis, the same four virtual 3D pathways for hand and gaze are shown: AB and BA are antiparallel pathways, and BA and BC are convergent pathways. Anatomical connections pre-exist between the different processing units (not shown); only connections reinforced by learning are shown. Sets of matching units are characterized by reinforced connections that store sensory-motor congruences illustrated for each learning stage by an *inset* with monkey's behavior; *Dashed lines*: new reinforced connections and new processing routes formed during each learning phase. *Plain lines*: reinforced connections and processing routes formed in previous learning stages (at each stage, the plain lines are always the sum of all the connections that have changed in the previous steps, illustrating the fact that the learning process is cumulative). *Horizontal, short diagonal, and long diagonal lines* (as in panels 5 and 6) represent reinforced connections that relate parallel 3D pathways for gaze or/and 3D pathways for hand which are respectively parallel, antiparallel (as BA and AB), and convergent (as AC and BC). See text for a detailed explanation of each learning stage

possible (Fig. 4). Matching units in combinatorial domain  $iP$  can associate equivalent or parallel hand and gaze 3D pathways (same initial and final positions of hand and gaze), or antiparallel hand and gaze 3D pathways (same final position of hand and gaze). Similar co-activations also occur between convergent pathways (initial positions are different but final positions are the same).

*Computation after learning.* Retinal and gaze position inputs activate units representing a 3D pathway for gaze, which then activates (through reinforced connections) matching units, representing a 3D pathway for hand aligned with this gaze pathway. For instance, when the target is foveated, the matching units coding for hand pathway BA are activated by a visual input representing a 3D pathway for gaze in the direction of the image of the hand (AB); they generate directional information for hand movement toward the fixation point (BA).

After learning, a set of matching units that code for different positions and directions performs the same distributed neural operation as that described in Fig. 1: this population of matching units transforms a visually derived sensory input on target position into a motor command that aligns the hand on the target position (see Appendix, Sect. 2). A set of matching units that learns a visuomotor transformation is thus characterized by: (1) its location within a combinatorial domain and (2) reinforced connections (synaptic weights), which store a sensory-motor congruence within the combinatorial domain (a relation between two 3D pathways).

This model of the functional architecture of the parieto-frontal network allows us to predict the different sets of matching units which, after learning, can subserve different visuomotor transformations (as shown in Fig. 5 and detailed in Appendix, Sect. 2). We assume that different subsets are differentiated by successive learning stages. Each new set of matching units benefits from the processing routes formed in previous learning stages. Thus, the visuomotor transformation underlying reaching appears as a result of an incremental skill acquisition.

Six sets of matching units are shown in Fig. 5.

*Motor babbling (panel 1).* When the monkey moves the hand, co-activations (in combinatorial domain aP) due to the motor commands (yellow column) and the re-afferent somatosensory inputs (hand position and direction: green column) result in reinforced connections, which represent a 3D pathway for the hand (horizontal dashed lines; for example, see BA). After learning, this set of matching units can generate adequate motor commands to the muscles to produce an expected sensory effect on hand/arm position and direction. Reinforced connections during alternating movements specify a subset of matching units that can relate antiparallel pathways for the hand (diagonal dashed lines; see, for example, those between AB and BA).

*Control of gaze and attention (panel 2).* When the gaze shifts toward a stimulus, co-activations (in combinatorial domain pP) due to the gaze movement (position and direction: light blue column) and the retinal input (dark blue column) result in reinforced connections, which represent a 3D pathway for the gaze (horizontal dashed lines; see, for example, BA). This new set of matching units can shift the gaze from any point B toward any point of interest or any focus of attention. As in phase 1, reinforced connections during alternating movements specify a subset of matching units that can relate antiparallel pathways for gaze (diagonal dashed lines; see, for example, those between AB and BA).

*Hand-tracking (panel 3).* When the eyes look at the moving hand, co-activations (in combinatorial domain iP) due to the gaze movement (position and direction: light blue) and to the hand movement (position and direction: deep blue) result in reinforced connections, which relate equivalent hand and gaze 3D pathways (same initial position and direction: horizontal dashed lines; see, for example, BA). This new set of matching units can compute the position and direction of gaze, which matches the position and direction of hand movement (learning along horizontal routes BA or AB): it can thus subserve the visual tracking of the hand movement.

*Reaching to foveated targets (panel 4).* When the hand moves toward the fixation point and, therefore, toward the fovea, co-activations (in combinatorial domain iP) due to hand movement (position-direction: green column), gaze fixation, and retinal inputs (blue columns) result in reinforced connections, which relate the antiparallel 3D pathway for hand and the virtual 3D pathway for gaze (diagonal dashed lines between BA and AB). This new set of matching units can compute the direction of the hand movement toward the fixation point (routes between BA and AB) and can thus subserve reaching movements to foveated targets, even if the hand is not in the field of view.

The same set of matching units can predict the gaze pathway to hand position, thus defining the retinal error between target location and hand position in the visual field. This retinal error can be used for optimal shaping of the motor command.

*Visual invariance trajectory (panel 5).* When the gaze moves to different positions, co-activations (in combinatorial domain pP) due to successive gaze (light blue columns) and retinal signals (dark blue columns) result in reinforced connections, which relate convergent 3D pathways (same final position, for example BC and AC, connected by long diagonal dashed lines). This subset of matching units can predict the consequences of saccades on eye position as well as the next retinal position of a visual stimulus after a saccade (position of stimulus B after saccade AC).

*Reaching to non-foveated targets (panel 6).* The set of matching units specified in the previous stage (5) can transform any retinal input into a prediction of gaze position, and matching units in iP (stage 4) can compute a prediction of a motor command that moves the arm toward this predicted gaze position. These two sets together can compute hand movement toward non-foveated targets. When the hand moves toward non-foveated targets (defined in space by a combination of gaze and retinal information AC), i.e., outward from the fovea, co-activations (in combinatorial domain iP) due to hand movement (position-direction: green column), gaze fixation, and retinal inputs (blue columns) result in reinforced connections between convergent hand and gaze 3D pathways (long diagonal dashed lines, see for example those between AC and BC). After learning, this set can directly compute the direction of reaching movement to non-foveated targets.

*Condition units selectively amplify matching operations compatible with the task demand on the fronto-parietal flow*

Hand movement in different directions can be performed using the same set of visually derived information, i.e., movements toward the fixation point or toward a non-foveated target. At any given time, the selection of a target depends on the task (in behaving monkey experiments, on the training protocol and, thus, on the reinforcement contingencies). This process can be controlled on the sensory-to-motor axis by condition units. The activity of condition units reflects both a sensory-motor relationship and a task-related component (see Appendix, Sect. 3).

The distributed representation of the task requirements (for example, those of an instructed delay reaching task) can be learned by a set of processing units that model prefrontal neurons (Guigon et al. 1995). Through sensory-motor experiences, these “prefrontal” processing units can acquire tuning and timing properties similar to the properties of neurons recorded in the prefrontal cortex in such task. Units modeling prefrontal neurons have two properties: (1) they can switch between two stable states of activity in response to synaptic inputs, as suggested by the intrinsic properties of pyramidal neurons (Delord et al. 1996) and (2) they can modify their synaptic weights by reinforcement-dependent learning (Sutton

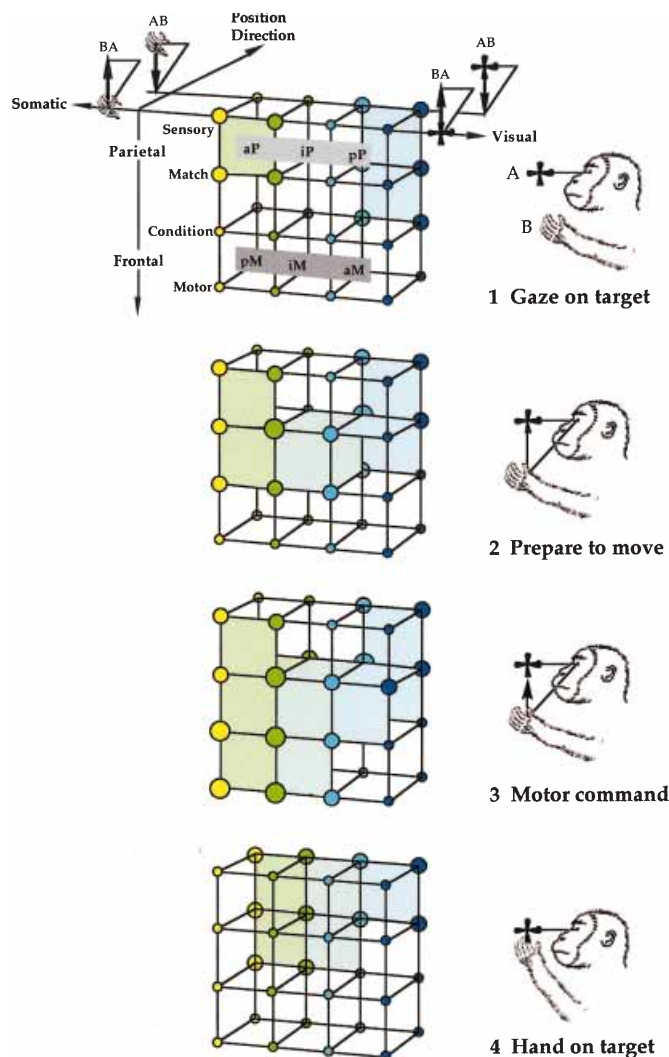
and Barto 1981; Barto et al. 1989). Computer simulations (Guigon et al. 1995) have shown that, after learning, the task demand is distributed over a population of “prefrontal” processing units that can activate other sensory-motor units at the appropriate time and in the appropriate order. After learning, these “prefrontal” units display sustained selective activities between two successive task events: the sustained activity represents a temporal link between two sensory or motor events, with both the selective memorization of a past event and the selective anticipation of a future event (for example, instruction stimulus/go signal with an intervening delay activity; go signal/movement). This is a general property of neurons in the frontal cortex.

The transfer of information from matching to condition units is thus gated by task-related inputs from “prefrontal units” that have learned the task-constraints. Condition units are similar to matching units in terms of sensory-motor tuning properties, but differ in their modulation by task requirements.

The concept of condition units allows us to discuss three sets of experimental results:

1. Condition units are closely related to those matching units whose combinatorial domain and tuning properties are similar on the visual-to-somatic axis, as shown in Fig. 3B; they can control any aspect of the visual-to-motor process. Experimental results show that “set-related neurons” are also distributed along the visual-to-somatic gradient, with specific directional and positional tuning properties (Johnson et al. 1996). The model predicts different types of set-related neurons in various experimental conditions, as, for example, when a peripheral visual stimulus serves as a target or as a trigger stimulus (di Pellegrino and Wise 1993).
2. In contrast to matching units, which store congruences in the 3D space, condition units are sensitive to reinforcement contingencies. This property is consistent with experimental results showing that set-related neuronal activity can be both selectively tuned to an arbitrary visual stimulus (signal-related activity) and can predict a future movement direction (instructed-delay related activity) in relation to the task constraints (Johnson et al. 1996).
3. Condition units have sustained activities that predict a possible motor command, even if the visual positional and directional signals are not available anymore. This property is consistent with observations of sustained activities during delays that predict the next motor command (Smyrnis et al. 1992 ; Kalaska and Crammond 1995; Johnson et al. 1996).

The functional architecture of the parieto-frontal network with its three axes allows one to predict the information flow in this network if two sets of inputs are known, the sensory context (inputs to matching units), and the task-dependent requirements (inputs to the condition and motor units). For example, Fig. 6 illustrates the information flow in the parieto-frontal network in a prototypic task used to analyze neuronal activities in behaving monkeys,



**Fig. 6** Progressive recruitment of units in the network. Reaching to foveated targets. Information flows in the parieto-frontal network during an instructed-delay reaching task. An instruction signal (I1) provides information about target location and, therefore, direction of next arm movement. This is performed, after an intervening delay time, when a GO-signal (I2) is presented. The four panels, from top to bottom, decompose the task into four phases, showing both the activation of the network (*left*) and the related behavior (*right*): (1) at the time of the instruction stimulus (I1), when the monkey looks at the target; (2) during the delay period; (3) at the time of the GO stimulus (I2), when the monkey decides to move; and (4) at the end of the movement. The modeling of the parieto-frontal network is the same as in Fig. 3B, with its three axes: visual-to-somatic, position-direction, and sensory-motor. Along the position-direction axis, only the two 3D pathways involved in a reaching movement from B (initial position of the arm) to A (foveated target) are shown: the front plane represents units that code for position B and for movement direction BA, and the back plane represents units that code for position A and for direction AB. The *size of the circles* indicates the level of activation of units, the smallest size corresponding to background activity. The *colored surfaces* between circles indicate groups of units recruited at each time, in order to illustrate the propagation on the three axes of the network. Information flows among units depending on the conjunction of available sensory information (activation of sensory and matching units by visual and somatic inputs) and the task-related signals (activation of condition and motor units by I1 and I2). Propagation of activity also depends on the previously reinforced connections which relate 3D pathways for hand and gaze (as shown in Fig. 5, between antiparallel pathways AB and BA). See text for a detailed explanation of each panel

the instructed delay reaching task. This allows a dissociation in time between the signal about target location for the next arm movement (instruction stimulus: I1) from the signal for movement execution (GO stimulus: I2), through a variable delay time between the two stimuli (see Appendix, Sect. 3).

The four panels from top to bottom decompose this reaching task into four phases (panels 1 and 2 after I1, and panels 3 and 4 after I2), showing both the information flow on the three axes of the network (left) and the related behavior (right).

*Panel 1 (Gaze on the target).* When the instruction stimulus (I1) is presented, the visual pole of the network (pP-aM) is activated by two types of input: (1) retinal and gaze-related inputs activate sensory and matching units (in pP, in position A); and (2) task-related signal I1 (time locked to instruction stimulus, with a sustained activity) activates condition units (in aM). The integration of these two inputs results in a propagation of information on the sensory-motor axis (in pP-aM and position A, on the two other axes). The interplay between matching and condition units on the sensory-motor axis can control *foveation and attention to the target in A*. The somatic pole of the network is also active (units in aP coding for initial arm position B), but the lack of integration with task-related inputs prevents propagation of activity on the sensory-motor axis and, therefore, in arm movements.

*Panel 2 (Prepare to move).* Units in the intermediate part of the network (iP-iM) are then activated by the integration of two independent inputs originating (1) from units in the somatic pole (in aP coding for arm position B) and (2) from units in the visual pole (units in pP coding for target position A). The integration of these two inputs results in propagation of information both on the visual-to-somatic axis (in iP-iM) and on the position-direction axis (between units coding for A, and units coding for B and BA). Matching units in iP are activated by both inputs and can predict the direction of the arm movement (3D pathway for hand BA) that matches the gaze position and the retinal input (propagation of information in the visual-to-somatic direction); matching units can also predict the position and the future direction of the hand on the retina (propagation of activity on the reverse somatic-to-visual direction). There is also propagation of information on the sensory-motor axis, in the intermediate part of the network (iP-iM), where the interplay between matching and condition units (activated by I1, as shown in panel 1) can maintain, during the delay, the prediction of the direction of the next arm movement (BA).

*Panel 3 (Motor command).* When the GO stimulus appears, motor units in the anterior part of the network (pM) trigger the motor command, since they are activated by the integration of two inputs: (1) sustained activity from condition units in iM (coding for 3D pathway BA, as shown in panel 2), and (2) signal I2 (GO signal).

There is a propagation of activity on the sensory-motor axis in the somatic pole (initial motor command), followed by a new bidirectional propagation on the visual-to-somatic axis (during the movement). In fact, matching units (in iP) are reactivated by both the efferent copy of the motor command and the re-afferent signals of a somatosensory nature (from aP), as well as by retinal inputs (from pP). These matching units can monitor the direction of movement of the image of the hand on the retina (propagation in the somatic-to-visual direction) and can then improve the directional control of the movement toward the target (propagation of information in the visual-to-somatic direction).

*Panel 4 (Hand on the target).* The movement ends when the hand enters the fovea and reaches the target, thus activating the matching units which correlate arm and gaze position in A.

In the view illustrated above, the cortical processing for reaching is not simply a chain of computational steps from visual to motor areas; it rather appears as a recruitment of neuronal populations performing a *progressive match* between the available sensory-motor (visual, somatic, motor) and task-related signals on the three axes of the parieto-frontal network: propagation of information along the visual-to-somatic axis relates the sensory-motor somatic and visual contexts and results in predictions on the sensory-motor events (gaze and hand 3D pathways) in both modalities; propagation on the position-direction axis extends the predictions from parallel to antiparallel or convergent 3D pathways, and shapes the population activity toward a common and coherent output, regardless of the initial set of inputs which could convey contradictory and ambiguous information; propagation along the sensory-motor axis maintains and/or amplifies those sensory-motor predictions that are compatible with task-related conditions.

Such a progressive recruitment, with a timing of activation that strongly overlaps in different groups of units, is consistent with experimental results comparing activation of reach-related neurons in premotor, motor and related parietal areas after the presentation of a signal that instructs the animal about the direction of the next arm movement that is triggered by a GO signal (Johnson et al. 1996; Kalaska et al. 1997).

*The progressive match framework relates the neuronal tuning properties in the parietal, motor, and premotor areas to the underlying computation*

The proposed mechanism of interplay between virtual 3D pathways for hand and gaze in the posterior and intermediate parts of the parietal network is consistent with functional properties of neurons in areas V6, V6A, and 7 m.

A first set of matching units computes the 3D pathway for target location using retinal and gaze signals (as in Fig. 3B, position-direction AB in pP). This computation describes the properties of a class of neurons in the

posterior part (pP) of the SPL that is both activated by visual stimuli on the retina and modulated by gaze position. These neurons have been experimentally observed in areas V6 and V6A (Galletti et al. 1993; 1996; Caminiti et al. 1999).

A second set of matching units computes the virtual 3D pathway for arm reaching to the target by combining somatic information about arm position and movement direction with visual information concerning the retinal image of the hand (as in Fig. 3B, position-direction BA in pP). This implies the existence of a class of neurons in the posterior part (pP) of SPL which (1) is modulated by the direction of arm-movement before the onset of movement, (2) has similar directional properties before and during arm movement, (3) is active during reaching, even in absence of retinal inputs about hand trajectory toward the target, i.e., in total darkness, and (4) is tuned to hand position in space. Recent results (Johnson et al. 1997; for a review see Battaglia-Mayer et al. 1998; Caminiti et al. 1998; Lacquaniti and Caminiti 1998; Caminiti et al. 1999) show that in area V6A, there are reach-related neurons matching these four properties, since they (1) are directionally tuned during both reaction- and movement-time, (2) have similar directional properties during both epochs, (3) are activated even when the movement is performed in darkness, and (4) show different modulation when the hand is held in different spatial positions. Furthermore, it has recently been shown that neurons in area 7m are tuned to eye position and saccadic movement and, at the same time, to arm position and movement direction (Ferraina et al. 1997a, 1997b); these neurons, therefore, combine hand and gaze signals relevant to reaching.

This model also predicts that some neurons combining target and hand information do not have the same directional tuning before and after onset of the movement: they should invert their preferred direction from reaction- to movement-time. This would correspond to a shift between two possible control modes of reaching: before movement onset, the control is mainly proprioceptive (with information flowing from the somatic to the visual domain) and given by eye and arm position signals; when hand movement begins, the control is mainly given by the retinal image of the hand moving toward the target, and, therefore, toward the fovea.

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## Discussion

This study models the parieto-frontal network involved in reaching by focusing on the nature and spatial distribution of different neuronal properties relevant to reaching.

The main feature of this network consists of its gradient architecture. This is determined by the tangential distribution of neurons, which defines trends of functional properties. They form a visual-to-somatic gradient along the parieto-frontal network.

The second crucial feature of this network is that the distribution of neurons with different types of reach-

related activity in both the parietal and the frontal cortex is characterized by zones of functional overlap, where individual reach-related neurons are tuned to more than one signal and where, at the same time, different reach-related neuronal types coexist. These zones are, therefore, *combinatorial domains*. In these domains, different signals are combined, probably thanks to local intra-area connections. Combinatorial domains with similar properties in frontal and parietal cortices are linked through inter-area association connections.

The rich pattern of intrinsic and association connections between the parietal and frontal lobes can subserve a process of parallel computation within and among the different cortical areas underlying visual reaching. This process may lead not only to the composition of motor commands but, through re-entrant signaling, it can also allow the visual monitoring of hand movement trajectory necessary for a fine tuning between hand movement planning and execution.

The computational units of the network mimic the operations performed by neuronal assemblies within cortical columns. The tuning properties of these units depend on their location relative to the three main axes of the network. The unit position in the visual-to-somatic axis defines the nature of the combinatorial process which is subserved. The position in the sensory-motor axis will assign different temporal relationships to the network units depending on the combination of reach-related sensory-motor and task-related signals. The location in the position-direction axis will determine the positional and directional tuning properties of computational units.

## Correlations performed by network units

Matching units correlate different sensory and motor signals which are congruent in 3D space. During learning, these units can compute three sets of visual-to-motor transformations, those underlying reaching to foveal targets, reaching to non-foveal targets, and eye-hand tracking movement. This depends on their capacity to match different sets of positional and directional reach-related sensory and motor signals.

Condition units store the relationships between sensory-motor signals and reinforcement contingencies, and, at any time, select the potential processing stream defined by matching units. Thus, condition units select an appropriate motor command not only on the basis of the signals available, but also on the basis of arbitrary contingencies dependent on task demands.

These two hypothesized operations result in two specific predictions about the properties of neurons in the parieto-frontal network: neurons (or pairs of neurons) modeled by matching units should have combinatorial tuning properties congruent in 3D space and reflecting the underlying neural process. An example is offered by neurons tuned for arm and gaze position and for the direction of the arm movement toward the gaze position, such as neurons in 7 m (Ferraina et al. 1997a, 1997b).

This congruence between arm- and gaze-position information may be apparent only when reaching movements are made in a limited part of space. Neurons modeled by condition units should also have combinatorial tuning properties, but these properties are amplified by reinforcement contingencies. Learning in those combinatorial domains where reinforcement-related signals are critical should highlight the role of set-related neurons. Furthermore, set-related neurons in the combinatorial domain of the motor command should have long-lasting anticipatory activities instructed by the task-related signals. Neurons with such characteristics have been observed in the parieto-frontal network (Johnson et al. 1996).

### Progressive match framework and reference frames

The computational demands of a visually guided reaching movement have been decomposed into sets of interactions (Jeannerod 1988): (1) extract the 3D position of the target in space from retinal and extra-retinal signals and direct the gaze toward this target; (2) command a coordinated elbow and shoulder movement that drives the hand toward the target; (3) pre-shape the hand according to the 3D local characteristics of the target; and (4) adjust the position and configuration of the hand near the target under control of foveal vision. Each step can then be analyzed as a sensory-motor transformation between appropriate sensory inputs and motor command outputs in different reference frames: retinal, head-centered, etc., representing perceptual and motor information (for discussion, see Paillard 1991).

A major question remaining to be answered is the “correspondence” between these reference frames, inferred by psychophysical experiments and related models, and the neuronal properties in the different areas of the parieto-frontal network underlying reaching.

In the progressive match framework presented in this paper, there is no segregation of different reference frames in different cortical areas, but instead a gradual shift between different combinatorial domains along a visual-to-somatic gradient. This allows a smooth transition between information coded in different dimensions.

The main property of the network does not rely on a specific reference frame, but on the local interactions in the different combinatorial domains. These interactions represent sets of predictions on the correlations between sensory-motor activities in the 3D space. A good example is offered by two sets of neurons in the posterior parietal cortex, one modulated by arm position and movement direction (virtual hand pathway) and the other by gaze and retinal signals (virtual gaze pathway). An important property of the combinatorial domains is to induce stable correlations between signals, such that a combination of retinal and gaze position information can be directly related to a combination of arm position and direction.

Another set of important properties, not fully accounted for by the reference frame concept, is the intricate

link between representation of information and computation, such as the one revealed by anticipatory signals predicting the sensory effect of a motor command. Such a predictive visual effect of saccadic eye movement has been observed in the posterior parietal cortex (Duhamel et al. 1991). The link between these reference frames and neuronal activity can be viewed in terms of dynamics of neuronal populations which, of course, cannot be confined within any anatomical border. In this respect, the progressive match framework allows us to relate several results of the physiological, psychophysical, and modeling literature:

1. It has been proposed that the posterior parietal cortex computes an invariant representation of visual targets in head-centered coordinates, by combining the visual input on the retina and the position of the eye in the orbit (Kuperstein 1988;; Zipser and Andersen 1988; Mazzoni et al. 1991). The combination of inputs underlying this hypothesized computation has been experimentally observed in neurons recorded in both the inferior (Andersen and Mountcastle 1983; Andersen et al. 1985, 1990) and superior parietal lobule (Galletti et al. 1993). Furthermore, coding mechanisms based on neuronal populations that are tuned to the absolute spatial location of the target and are independent of retinal and eye-position information (Galletti et al. 1993; Duhamel et al. 1997) have been proposed.

In the progressive match framework, these observed combinations can be used to define the direction of the hand movement toward a foveated target, as it seems to occur in area V6A (Johnson et al. 1997; Battaglia-Mayer et al. 1998; Caminiti et al. 1998, 1999; Lacquaniti and Caminiti 1998) and 7m (Ferraina et al. 1997a, 1997b). The progressive transfer from visual input to control of arm movement can be widely distributed in the activity of different population of posterior parietal neurons. Thus, “visual fixation” and “visual tracking” neurons (Sakata et al. 1995) could participate in a control mechanism used to map eye position signals into expected arm position. “Projection” and “hand manipulation” neurons (Mountcastle et al. 1975; Taira et al. 1990; Sakata et al. 1995) could be critical to gate both somatomotor and visually derived information, as matching units in iP. Posterior parietal neurons sensitive to visual stimuli moving inward to the fovea or outward from the fovea could subserve the visual monitoring of hand trajectory in space (Motter and Mountcastle 1981; Mountcastle 1995; Caminiti et al. 1999).

2. It has been suggested that the initial motor planning of arm movement occurs in the external coordinates of the physical world, encoding for the hand trajectory in space (Morasso 1981; Hogan 1985; Hollerbach and Atkeson 1987; Hogan and Atkeson 1988). In the progressive match framework, the combinatorial properties of condition units in aM could be the appropriate neural substratum to represent such plan-

- ning, even if there is no explicit neural representation of the external coordinates of the physical world.
3. Psychophysical experiments have revealed that in the transformation of information about target location and arm position into a motor command, the endpoint of movement can be represented either in shoulder-centered (Soechting and Flanders 1989a, 1989b; Flanders et al. 1992) or in hand-centered (Flanders et al. 1992; Gordon et al. 1994) reference frames. Recent data (McIntyre et al. 1997) show that when reaching is directed to a memorized target in 3D space, the brain uses a viewer-centered frame of reference. In the progressive match framework, somatomotor signals are mainly combined with arm-position signals, and retinal signals with gaze position, both combinations favoring a direct correspondence of information. Experimental results suggest that this can occur in iP, for example. Such combinations can be viewed as a projection on an intermediate reference frame, where both types of information can be correlated. Here, again, representation and computation are intrinsically linked and do not necessitate an invariant representation of target location in a given reference frame at the neuronal level.
  4. In the progressive match framework, the entire network computes the motor command as a progressive combination of visually derived information about target location and somatic information about arm position, which is equivalent to projecting the visual information on the arm. This allows specific predictions of the tuning properties of neurons along the visual-to-somatic gradient. Any tuning property measured in the visual space or the external 3D space will depend on the initial position of the arm (Caminiti et al. 1990; 1991). This dependence will increase along the visual-to-somatic gradient. This prediction is consistent with the results showing that, during arm movement, the orientation of the preferred directions of cells in PMd, M1, and area 5 (Caminiti et al. 1990; 1991; Ferraina and Bianchi 1994) depends on the initial arm position, and also with the recent observation that reach-related neurons in V6A (Johnson et al. 1997; Battaglia-Mayer et al. 1998; Caminiti et al. 1998; 1999) and 7m (Ferraina et al. 1997a, 1997b) are not only modulated by direction of movement but also by the position of the arm. A similar result has also been observed in PMv, where the visual tuning of PMv neurons changes with the arm position (Graziano et al. 1994).
  5. The progressive match framework also sheds some light on the controversy about the reference frames represented in PMd and M1: representation in terms of Cartesian 3D space, muscle commands, joint angles, etc. The combinatorial properties of neurons allow both processing of visually derived signals as well as generation of appropriate motor commands to muscle synergies. There is no invariant representation of the Cartesian 3D space at the single cell level. Instead, populations of neurons form a “tangential approxima-

tion” of the 3D space for each arm position and the regular distribution of their tuning properties allows the population to establish a simple correspondence with the 3D Cartesian axes. This Cartesian-like representation can be seen as a simplified view of the relationships of premotor and motor cortices with other brain regions that are more remote from the peripheral motor apparatus and more closely related to vision. At the population level, this construct of space represents movement trajectories, even if individual cells project to spinal motoneurons commanding muscle activity. This correspondence between internal and external constructs of space, may be a way of reconciling apparently conflicting views on the functions of the motor cortex, which are based either on a representation in terms of command of muscle activities (movement dynamics) or on a representation in terms of movement trajectories in 3D space (movement kinematics).

#### Corticocortical and subcortical relationships

The functional architecture of the cortical networks proposed in this paper does not explicitly take into account the processing performed by subcortical structures, which are important for reaching, such as the cerebellum and the basal ganglia.

These subcortical processing systems should also be included in the model to provide a more complete description of cortical operations. The cortical architecture (as in Fig. 3B) is non-hierarchical and every processing unit in the network can have subcortical inputs (and outputs) that can gate or shape cortical activation.

Two subcortical systems important for reaching, the cerebellum and the basal ganglia, are known to project on the motor and premotor areas and are organized on a gradient on the caudo-rostral axis of the frontal cortex. The basal ganglia, along with their connected cortical and thalamic areas, can be viewed as components of a family of “basal ganglia-thalamo-cortical” circuits that are organized in a parallel manner and remain largely segregated from one another, both structurally and functionally (Alexander et al. 1986; 1990): the “motor circuit” is focused on the precentral motor fields; the “oculomotor circuit” on the frontal eye field; the “prefrontal circuits” on the dorsolateral prefrontal cortex; and the “limbic circuit” on the anterior cingulate and medial orbitofrontal cortex. Two important functional roles have been hypothesized: (1) the initiation of voluntary movements by a gating mechanism of focused disinhibition (Chevalier and Deniau 1990; Alexander et al. 1990; modeled in Contreras-Vidal and Stelmach 1995); (2) the initiation of sustained discharge (working memory) when situations are either too complex to be automated or are relatively novel (Houk and Wise 1995).

We could then complement the model of this paper by including the basal ganglia inputs. This is addressed, on the visual-to-somatic axis, mainly to units in iM (control of the arm) and aM (control of the eyes), and, on the sen-



sory-motor axis, mainly to condition units. The basal ganglia could provide the cortex with signals very similar to the task-related inputs that we have considered for the condition units. These signals can trigger the sequence of movements at the appropriate time and in the appropriate order, when several motor outputs are possible for a given task and when a decision has to be made between concurrent tasks. These gating signals toward condition units do not necessarily contain a precise description of the motor command to different joints, since this description is provided both by corticocortical connections (inputs from matching units) and cerebellar inputs (direct input to the motor units).

The input from the cerebellum is also organized along the caudo-rostral axis of the frontal cortex, with more caudal than basal ganglia input (Ito 1984). The cerebellum is more involved in the dynamic control of movement, which deals with forces and torques applied to specific joints (Schweighofer et al. 1998a). Such dynamic control is critical for reaching movements, because of the different constraints existing on moving masses, as described by the laws of dynamics. The cerebellum may increase the accuracy of multi-joint reaching movements by compensating for the interaction torques – it has been suggested that this can be achieved by learning an internal model of the motor apparatus that refines a basic inverse model in the motor cortex and the spinal cord (Schweighofer et al. 1998a). A model of the cerebellum can learn that part of the inverse dynamics of the arm not provided by the cortico-cortical nodes of the network (Schweighofer et al. 1998b).

Thus, we could complement the cortical model by a cerebellar input that activates mainly units in pM (on the somato-visual axis) and, within this population, activates mainly units that specify the motor command (motor unit on the sensory-motor axis); this cerebellar input should be important in shaping the motor command in the initial phase of the movement to increase the speed and accuracy of multi-joint reaching.

From the progressive match framework to complete neuronal net modeling

Implementation and simulation of a complete neural network which simultaneously performs all the neural operations of matching and condition units has not been solved and is beyond the scope of this paper. No existing quantitative neural net model accounts for the variety of neural operations working in parallel.

Viewing the cortex as a “network of networks”, we have, in this paper, decomposed one problem into two. In the first part, we have simulated the computation performed by an elementary network, which relates two sets of information in two different informational domains (retinal and motor). Such simulation shows how the computation can be distributed within a neuronal population. It also reveals the importance of combinatorial tuning properties within populations of neurons.

Furthermore, we propose a functional architecture of the parieto-frontal network, which relates these neural nets by functional axes. This architecture shows how the computation for reaching can be distributed within different neuronal populations and allows prediction of the properties of the neurons in the different parts of the network.

Neural operations performed by each subset of matching and condition units are in essence similar to several neural net models previously proposed. For example, matching units implement directional mappings. Several neural net solutions have been previously proposed. They differ mainly in the codes for the input and output variables: some models consider kinematic variables (e.g. angular positions, velocities and accelerations) directly coded into neuronal firing rates (Kawato et al. 1992; Frolov et al. 1994), while others use coarse-grained tabular representations [for example, with radial basis functions (Mel 1991) or a finely-grained tabular representation (Bullock et al. 1993)]. In the simulation shown in Fig. 1B, we use a coarse tuning (Lacquaniti et al. 1995). This coarse tuning is compensated by lateral connections between units that play a selective role during learning. Most of these models learn in a similar way, without an external teacher, by associating the visual or proprioceptive feedback with the motor command (Mel 1991; Bullock et al. 1993). Neuronal net solutions proposed for directional mappings facilitate learning and simplify the handling of redundancy (Kawato et al. 1990; Mel 1991; Bullock et al. 1993).

Several neuronal net models have also proposed solutions to store task-related constraints. These also differ mainly in the codes for the input and output variables and their granularity. Some models directly implement “rule coding units” (Dehaene and Changeux 1989; Cohen and Servan-Schreiber 1992) or show how distributed tuning and timing properties can be learned by correlating sensory-motor experience with reinforcement (Guigon et al. 1995).

Previous work that relates the profiles of activations in these neural nets with neuronal activities recorded in specific cortical areas could be reconsidered in this framework. For example, units modeling area 7 and lateral intra-parietal (LIP) properties (Zipser and Andersen 1988; Mazzoni et al. 1991) could be viewed as matching units correlating retinal and gaze information. The neural net model, related to the composition of motor commands in motor and premotor cortices, as previously proposed (Burnod et al. 1992), is based on a similar principle of matching units that correlate somatic information concerning the orientation of the arm, visually derived information on the target location, and direction of the motor command.

The model of the functional architecture of the parieto-frontal network proposed in this paper provides, for the first time, a systematic description for the matching properties of the different populations of neurons in the parieto-frontal network.

Several improvements of the framework can be made by further work based on the proposed architecture.

These should (1) define different codes and granularities in the various parts of the network, since it is possible that, along the visual to somatic gradient, this granularity changes continuously for visual and somatic inputs; (2) provide a model of the temporal properties of reach neurons; and (3) provide a model of the interaction with the processing performed by other neural structures underlying reaching, such as the cerebellum and the basal ganglia.

## Appendix

### 1. Neural net implementation of $z=L(x,y)$ to align sensory and motor representation

During sensory-motor tasks, information about target positions or direction must be transferred from sensory arrays  $y$  of neurons to motor arrays  $z$  that generate and control movement, thanks to another sensory array that codes for arm and/or gaze position. In the following, we use notations similar to those used by Salinas and Abbott (1995).

The neural network has to perform an appropriate coupling,  $L$ , between sensory ( $x, y$ ) and motor arrays ( $z$ ) to align the sensory and motor representations:

$$z=L(x,y) \quad (1)$$

$L$  such that  $z$  is aligned with  $y$ ;  $x, y$ , and  $z$  are represented in arrays of neurons with optimal tuning properties (OTs)  $\phi_i, \psi_j$ , and  $\omega_k$ , respectively.

#### Positional transformations

Equation 1, which relates positions  $x, y$ , and  $z$ , can be approximated by a linear equation (Salinas and Abbott 1995): for example,  $x$  is initial position of gaze,  $y$  is position of the stimulus on the retina, and  $z$  is the final position of gaze (or hand) on target.

The average firing rate  $R_i$  for one neuron ( $i$ ) depends on the distance between the position  $x$  being coded and the preferred position  $\phi_i$  for that neuron  $i$ :

$$R_i=R[x, \phi_i]$$

$R_i$  codes gaze position, with  $\phi_i$  OT for gaze position evoking the maximum average firing response in neuron  $i$ . Similarly, neurons  $R_j$  and  $R_k$  have OTs,  $\psi_j$  and  $\omega_k$ , respectively:  $R_j=R[y, \psi_j]$ ,  $R_j$  codes retinal position of the target;  $R_k=R[z, \omega_k]$ ,  $R_k$  codes movement goal location. Neurons  $R_{ij}$  in the associative array have combinatorial OTs ( $\phi_i, \psi_j$ ), similar to both input neurons  $R_i$  and  $R_j$ . A solution is given by adjusting the synaptic weights between  $R_{ij}$  and  $R_k$ :

$$R_k=\sum_k W_{ijk} R_{ij}$$

This simple linear transformation could be realized by adjusting the synaptic strength  $W_{ijk}$ , with either the Hebb rule or the covariance rule (Salinas and Abbott 1995).

#### Directional transformations

Equation 1, which relates two directions  $y$  and  $z$  has a linear approximation for each position of the arm (or gaze)  $x$  (Baraduc et al. 1999), with, for example,  $y$  direction of gaze (or direction of the visual stimulus of the retina),  $z$  direction of the hand movement, and  $x$  position of the hand.

On the simulation shown in Fig. 1, the activities in the three arrays of neurons are: (1)  $R_i=R[x, \phi_i]$  codes the length of each agonist or antagonist muscle, with a linear code; (2)  $R_j=R[y, \psi_j]$  codes the direction of the stimulus on the retina (or the direction of the eye movement), with a cosine tuning; (3)  $z=\sum_k R_k \omega_k$  codes the direction of the hand movement toward the target; a motor neuron  $k$  contributes to the movement by its action on a direction in joint space  $\omega_k$  (corresponding to  $\theta_{EL}$  and  $\theta_{SH}$  in Fig. 1).

Associative neurons  $R_{kj}$  have combinatorial OTs similar to both neurons  $R_k$  and  $R_j$ . A solution is given by adjusting the synaptic weights between the input array  $R_i$  and the associative array  $R_{kj}$ :

$$R_{kj}=(\sum_i W_{kji} R_i) R_j$$

$$R_k=\sum_j R_{kj}$$

The adjustable weights  $W_{kji}$  are modified according to the optimal learning rule (see Baraduc et al. 1999):

$$\Delta W_{kji}=[R_k R_j - R_{kj}] R_i$$

Lateral connections in the associative array can increase the efficacy of the network (see Baraduc et al. 1999).

### 2. Learning different visuomotor transformations in different populations of matching units

As shown in the previous sections, a neural network can perform an appropriate coupling  $L$  between sensory ( $x, y$ ) and motor arrays ( $z$ ) to align the sensory and motor representations (Eq. 1). On the somatic-to-visual axis in the parieto-frontal network, several sensory and motor informational domains coexist:

- For sensory-motor information  $x, y, z$ , and combinatorial OTs ( $\phi_i, \psi_j$ ), ( $\phi_i, \omega_k$ ), ( $\psi_j, \omega_k$ )
- For sensory-motor transformations  $L(x, y)$ , that we note  $L_q(x, y)$ , with different values of  $q$  for different populations of matching units

#### Combinatorial OTs

Sensory-motor information  $x \in \{\gamma; \alpha\}$  and  $y \in \{\rho; \rho'; \gamma; \gamma'; \alpha; \alpha'; \mu; \mu'\}$ ;  $\rho$  and  $\rho'$ , respectively, retinal position and direction;  $\gamma$  and  $\gamma'$  gaze (eye and neck) position and direction;  $\alpha$  and  $\alpha'$ , joints position and direction;  $\mu$  and  $\mu'$  position and direction of muscle commands. We note the OTs with the same symbols; for example,  $\alpha_i$  is an OT for arm position  $\alpha$ .

OTs  $\varphi_i \in \{\gamma_i, \alpha_i\}$  and  $\psi_j \in \{\rho_j, \rho'_j; \gamma_j, \gamma'_j; \alpha_j, \alpha'_j; \mu_j, \mu'_j\}$ . Units in combinatorial domains (pP-aM; iP-iM; aP-pM) have combinatorial OTs ( $\varphi_i, \psi_j$ ):

- $(\varphi_i, \psi_j) \in \{(\rho_i, \gamma_j); (\rho'_i, \gamma'_j); (\gamma'_i, \gamma_j)\}$  in pP-aM
- $(\varphi_i, \psi_j) \in \{(\gamma'_i, \gamma'_j); (\alpha_i, \gamma_j); (\alpha'_i, \alpha_j)\}$  in iP-iM
- $(\varphi_i, \psi_j) \in \{(\alpha'_i, \alpha_j); (\mu'_i, \alpha_j); (\mu_i, \alpha_j)\}$  in aP-pM

These combinatorial OTs code for 3D virtual pathways for gaze or hand. A 3D virtual pathway between two positions B and A is noted BA: BA represents an OT both for position B and for direction from B toward A in the 3D space. Similar reasoning can be applied with different sensory and motor codes in the different informational domains.

Two units increase their functional relations when they have combinatorial OTs corresponding to 3D pathways congruent in the 3D space. For example, two units in the combinatorial domain iP-iM, with combinatorial OTs, respectively  $(\gamma'_i, \gamma_j)$  and  $(\alpha'_k, \alpha_i)$ , can have three types of congruences – parallel, antiparallel, and convergent:

- The two units code *parallel pathways* BA for gaze and hand: positions  $\gamma_i$  and  $\alpha_k$  are the same (for example, position B), and directions  $\gamma'_j$  and  $\alpha'_i$  are aligned (direction from B toward A).
- The two units code *antiparallel pathways* AB for gaze and BA for hand: positions  $\gamma_i$  and  $\alpha_k$  are different (respectively, positions A and B), and directions  $\gamma'_j$  and  $\alpha'_i$  are antiparallel (respectively, directions from A toward B, and B toward A).
- The two units code *convergent pathways* AC for gaze and BC for hand: positions  $\gamma_i$  and  $\alpha_k$  are different (respectively, position A and B), and directions  $\gamma'_j$  and  $\alpha'_i$  converge on the same final position (respectively, directions from A toward C, and B toward C).

#### *Operations $L_q$ performed by a subset of matching units $q$*

An operation  $L_q$  is learned by a population of matching units  $q$ , which is specified both by a combinatorial domain and reinforced connections (synaptic weights) representing a relationship between two 3D pathways which are congruent (or aligned) in 3D space (parallel, antiparallel, or convergent). Different matching operations  $q$  can be successively learned on the different connections of the network, resulting in progressive acquisition of different visuo-motor transformations, as illustrated in Fig. 5.

#### 1. Motor babbling

Operation:  $\mu' = L_1(\alpha, \alpha')$

$L_1$  such that, if the arm position  $\alpha$  is in B, motor command on muscles  $\mu'$  produces a movement in a direction

BA aligned with a sensory movement direction of the hand  $\alpha'$  from B toward A (parallel pathways); similar relationships can be learned between reciprocal movements (antiparallel pathways AB for  $\mu'$  and BA for  $\alpha'$ ).

#### 2. Control of gaze and attention

Operation:  $\gamma' = L_2(\gamma, \rho)$

$L_2$  such that, if the gaze position  $\gamma$  is in A, the gaze direction  $\gamma'$  becomes aligned with the direction AB toward the retinal target position  $\rho$  in B (parallel pathways); similar relationships can be learned with reciprocal movements (antiparallel pathway BA for  $\gamma'$  and AB for  $\rho$ ).

#### 3. Hand tracking.

Operation:  $\gamma' = L_3(\gamma, \alpha')$

$L_3$  such that, if the gaze position  $\gamma$  and the hand position  $\alpha$  are the same (in B), gaze direction  $\gamma'$  is aligned with hand direction  $\alpha'$  (BA, from B toward A).

#### 4. Foveal reaching.

Operation:  $\alpha' = L_4(\alpha, \gamma)$

Operation:  $\alpha' = L'_4(\alpha, \gamma')$

$L_4$  such that, if the arm position  $\alpha$  is in B, and the gaze position  $\gamma$  is in A, movement direction of the hand  $\alpha'$  is aligned with the direction toward gaze (BA);  $L'_4$  such that movement direction of the hand  $\alpha'$  (direction BA) is antiparallel with the direction of gaze  $\gamma'$  toward the hand (AB) (antiparallel hand and gaze pathways).

#### 5. Visual invariance.

Operation:  $\gamma' = L_5(\gamma, \rho)$

$L_5$  such that, if a visual stimulus with retinal position  $\rho$  is in C, and the predicted position of the gaze  $\gamma$  is in B (as for example, defined by the visual image of the hand), the direction of the next gaze direction  $\gamma'$  is aligned with the direction toward the stimulus  $\rho$  (BC) (two convergent gaze pathways AC and BC).

#### 6. Peripheral reaching.

Operation:  $\alpha' = L_6(\alpha, \gamma)$

$L_6$  such that, if the arm position  $\alpha$  is in B, and the predicted position of the gaze  $\gamma$  is in C (as for example, defined by a visual stimulus  $\rho$  in C), the direction of the hand  $\alpha'$  is

aligned to the direction pointing toward this predicted gaze position (BC) (two convergent arm and gaze pathways).

### 3. Task dependent control of flow for reaching to foveated targets: condition units

Condition units control the transformation from matching units (computing sensory-motor operations  $L_q$ , as shown in the previous section) to the effective motor command, in order to amplify those predictions which are compatible with the task constraints.

On the sensory-motor axis in the parieto-frontal network, the same sensory-motor information  $z$  can thus be coded by different types of units  $u$  representing different anticipatory levels of the motor command:  $u \in \{s, m, c, a\}$ , respectively, sensory, matching, condition and motor units ( $a$  for action). For example, a motor prediction  $z$  has intermediate representations  $z_m$  in matching units,  $z_c$ , in condition units, and  $z_a$ , in motor units.

In the instructed-delay reaching task (Fig. 6), the sensory-motor predictions  $z_m$  are computed by different subsets of matching units (operations  $L_q$ ), for example predictions of gaze and arm movements  $\gamma'_m$  and  $\alpha'_m$ :

$$\gamma'_m = L_2(\gamma, \rho) \quad \alpha'_m = L_4(\alpha, \gamma'_m)$$

The input arrays  $f_c$  and  $f_a$  code the temporal structure of the task: they can activate condition and motor units at the time of the instruction stimulus ( $f_c$ ), and a GO stimulus ( $f_a$ ) (Guigon et al. 1995). The input array  $f_c$  codes for the instruction stimulus  $I_1$  at time  $t_1$  with a sustained activity. The input array  $f_a$  codes for a GO signal  $I_2$  at time  $t_2$ .

Condition units  $z_c$  receive two inputs: a sensory-motor prediction  $z_m$  (output of the matching unit) and the second task-dependent input  $f_c$ . They select sensory-motor predictions compatible with the task constraints:

$$z_c(t) = z_m(t_1) \text{ when } f_c(t) = 1 \text{ that is } t \geq t_1$$

In a similar way, the motor unit  $z_a$  receives two inputs: the sensory-motor predictions compatible with the task constraints  $z_c$  (output of the condition units) and the second task-dependent input  $f_a$ . They trigger the motor command when the task-dependent signal  $f_a$  occurs:

$$z_a(t) = z_c(t) \text{ when } f_a(t) = 1 \text{ that is } t = t_2$$

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