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Neural network models of cortical functions based on the computational properties of the cerebral cortex

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Summary — We describe a biologically plausible modelling framework based on the architectural and processing characteristics of the cerebral cortex. Its key feature is a multicellular processing unit (*cortical column*) reflecting the modular nature of cortical organization and function. In this framework, we describe a neural network model of the neuronal circuits of the cerebral cortex that learn different functions associated with different parts of the cortex: 1) visual integration for invariant pattern recognition, performed by a cooperation between temporal and parietal areas; 2) visual-to-motor transformation for 3D arm reaching movements, performed by parietal and motor areas; and 3) temporal integration and storage of sensorimotor programs, performed by networks linking the prefrontal cortex to associative sensory and motor areas. The architecture of the network is inspired from the features of the architecture of cortical pathways involved in these functions. We propose two rules which describe neural processing and plasticity in the network. The first rule (*adaptive tuning if gating*) is an analog of operant conditioning and permits to learn to anticipate an action. The second rule (*adaptive timing*) is based on a bistable state of activity and permits to learn temporally separate events forming a behavioral sequence.

neural modelling / cerebral cortex / cortical column / learning / sensorimotor programs

Introduction

When facing a complex system, a valuable approach is to attempt to approximate its organization and its function by a model. In recent years, numerous information-processing models have attempted to address issues on brain functions. A classical approach in brain modelling is to study the computational problems that must be solved, independently of underlying biological constraints (Marr, 1982). Emphasis is on representation of information, algorithms, symbolic description. For example, Artificial Intelligence models assume that brain circuits manipulate symbolic information according to production rules (Pylyshyn, 1984).

Churchland and Sejnowski (1988) have stressed the limitation of Marr's approach for understanding complex information processing systems (in particular brain systems). Dissociation between hardware and software may be misleading since neurobiological data provide essential constraints on computational theories.

Connectionist models provide implementation of biological functions in terms of synaptic interactions (McCulloch and Pitts, 1943; Hebb, 1949) and are thus likely to solve the software/hardware dissociation. Furthermore, they are susceptible to learn through the modification of synaptic efficacy. This property has greatly contributed to the popularity of these models. Recently, Rumelhart and McClelland (1986) have described techniques to build connectionist models, including a powerful algorithm to train neural networks (back-propagation of error). Subsequently, back-propagation-based models were shown to capture biological (Zipser and Andersen, 1988) as well as psychological (Cohen and Servan-Schreiber, 1992) features of information processing in the brain.

Great care has been taken to justify the validity of models based on the back-propagation algorithm, and to assess their predictive value (Rumelhart and McClelland, 1986). However, Crick (1989) has stressed that these models can merely be considered as demonstrations (models demonstrate that it is not impossible to find a neural network which performs a given function. However, they do not prove that brain circuits performing the same function have a similar structure or similar internal mechanisms) since they result from an optimization-based training process which is not likely to be implemented in brain circuits.

At least four properties should characterize a reasonable model of how brain circuits learn and execute a given task (Reeke and Sporns, 1993). First, the model must rely on simple and plausible neural architectures and mechanisms, which are consistent with experimental data. Second, learning must occur through natural interactions, corresponding either to a conditioning protocol or to a developmental stage. Third, outcomes of the model must be consistent with experimental results available at the level(s) of representation used in the model (neuronal activity, behavior). Fourth, the model must make testable predictions.

We describe a biologically plausible modelling framework based on the architectural and processing characteristics of the cerebral cortex (Burnod, 1988). Its key feature is a multicellular processing unit (*cortical column*) reflecting the modular nature of cortical organization and function. In this framework, we describe a neural network model of the neuronal circuits of the cerebral cortex that learn different functions associated with different parts of the cortex: 1) visual integration for invariant pattern recognition, performed by a cooperation between temporal and parietal areas (Otto *et al, 1992);* 2) visual-to-motor transformation for 3D arm reaching movements, performed by parietal and motor areas (Burnod *et al,* 1992); and 3) temporal integration and storage of sensorimotor programs, performed by networks linking the prefrontal cortex to associative sensory and motor areas (Guigon *et al,* in press). The architecture of the network is inspired from the features of the architecture of cortical pathways involved in these functions (Ungerleider and Mishkin, 1982; Fuster, 1988; Johnson, 1992). We propose two rules which describe neural processing and plasticity in the network. The first rule (*adaptive tuning if gating*) is an analog of operant conditioning and permits to learn to anticipate an action. The second rule (*adaptive timing*) is based on a bistable state of activity and permits to learn temporally separate events forming a behavioral sequence.

Computational principles

The cerebral cortex has been subdivided into a number of functionally specific areas (Brodmann, 1909). However, in spite of this functional diversity, the cortex is made of repetitive neuronal circuits (cortical columns) which share common features in sensory, motor and associative areas (Mountcastle, 1978). This modular organization of the neocortex is now referred as an organizing principle for cortical functions (Szentágothai, 1975; Mountcastle, 1978; Eccles, 1981).

The basic columnar operation common to all cortical areas can produce a large range of behavioral adaptations, depending on: 1) the sources and terminations of connections of columns, which define the sensorimotor repertoire of cortical units; and 2) regionally specific integrative and registering properties of cortical neurons. Regional variations in anatomy have been described in relation to the nature and organization of afferent and efferent flows of information. Characteristics have been derived in terms of feedforward, feedback, or lateral information flows, of primary and secondary indices, of topographic or non-topographic mapping (Ballard, 1986). Regional variations in columnar properties are related to dendritic and somatic properties defined by the distribution of ionic channels, neurotransmitter and neuromodulator receptors (Shepherd, 1989).

The columnar organization of the cerebral cortex

The cortical maps are not made of a uniform lattice of neurons, but of local circuits with different neurons (pyramidal neurons and interneurons) arranged throughout the depth of the six cortical layers (for review see Mountcastle, 1978). These local multi-neuronal circuits form *cortical columns* which have been described as functional units in the different cortical areas (Szentágothai, 1975; Hubel and Wiesel, 1977; Mountcastle, 1978).

The cortical layers correspond to a differential distribution of neuronal types in local circuits as well as subsets of inputs and outputs. The intermediate layer IV (which contains granular cells) divides two subsets of pyramidal neurons, the upper division (supragranular cortical layers I, II and III) and the lower division (infragranular cortical layers V and VI). These divisions process different types of information. The granular layer receives the main sensory inputs, either directly from the thalamus or from columns of cortical areas involved in earlier stages of sensory processing (feedforward connections). The supragranular layers are mainly specialized in cortico-cortical connections, toward adjacent cortical zones or toward more distant cortical areas (Szentágothai, 1975; Jones, 1981). The infragranular layers project outside the cortex toward other neural structures such as the superior colliculus or control the ascending information flow, through feedback connections (van Essen and Maunsell, 1983).

Therefore, a processing unit should better model a prototypic local circuit of neurons rather than a prototypic neuron. The processing unit must have several input-output layers modelling these cortical layers, each layer corresponding to a specialized integration of subsets of inputs sharing a common origin (Burnod, 1988; Alexandre *et al,* 1991): 1) a feedforward layer receives information from a sensory channel *via* previous processing steps; 2) a lateral layer represents reciprocal connections with other units of the same map or with similar units in other maps; and 3) a feedback layer receives a copy of the output performed at a further step.

Neuronal processing

Tuning properties

Neuronal activities in the cerebral cortex can be described by their optimal tuning (vector of synaptic weight). It corresponds to the tuning of the sensitivity of neurons to a particular combination of afferent signals that depicts a stimulus attribute not specifically encoded by any single set of primary afferent fibers, but which is reconstructed from combinations. These operations have been well characterized in thalamic-receiving neurons in sensory areas (visual, somatosensory, auditory). Typical examples are orientation columns in V1 (Hubel and Wiesel, 1977), axis of motion columns in the middle temporal area (Albright *et al,* 1984). Studies on neuronal activity within the motor cortex (Georgopoulos *et al,* 1986) have shown that the activity of individual arm-related neurons is broadly tuned to a preferred direction of arm movement in the 3D space.

Gating properties

A major property of cortical neurons is that they are tuned for more than one sensory or motor modality. For example, retinal (*eg* disparity) and extra-retinal (*eg* vergence) signals are combined in neuronal responses in the primary visual cortex (Trotter *et al,* 1992). When two different sets of inputs converge on a cortical circuit, tuning curves in response to the first type of inputs are modulated by the second type as a gain factor. Multiplicative combinations have been observed between eye position and retinal position in the primary visual cortex (Trotter *et al,* 1992) and in the posterior parietal cortex (Andersen *et al,* 1985), between vision and memory in the inferotemporal cortex (Eskandar *et al,* 1992a,b), between arm position and visual trajectory in the motor and premotor cortex (Caminiti *et al,* 1991; Burnod *et al,* 1992).

The biological basis for neuronal multiplication may be related to: i) the integrative properties of dendritic trees which generate non-linear dendritic operations (Shepherd and Koch, 1989; Mel, 1993); ii) the voltage properties of NMDA receptors which provide a multiplicative gain control mechanism (Nowak *et al,* 1984); and iii) the suppression of inhibition which may enhance neuronal activity by revealing subthreshold excitatory inputs.

Timing properties

Neuronal responses are generally described as transient variations of membrane potential, with a time scale of milliseconds, reflecting selective response to some event. There is now strong evidence for a complementary process, acting over the time scale of seconds, involved in performing tasks requiring temporary storage and manipulation of information to guide appropriate actions (Goldman-Rakic, 1987; Fuster, 1988; Baddeley, 1992). Neural correlates of this process are long-lasting activities recorded during delayed tasks in many parts of the cerebral cortex: prefrontal cortex (Fuster, 1973), premotor cortex (di Pellegrino and Wise, 1991), parietal cortex (Andersen *et al,* 1990) and inferotemporal cortex (Miyashita, 1993). These activities have been shown to reflect short-term memorization of instruction cues, expectation of forthcoming signals and preparation of a behavioral reaction.

The origin of these sustained activities is a major question. Recurrent circuits of excitatory and inhibitory neurons are likely to produce a sustained activity (recurrent excitatory pathways) and to stop it (inhibitory pathways) (Dehaene and Changeux, 1991). Zipser *et al* (1993) provided direct evidence for bistability of cortical neurons in a recurrent neural network trained to mimic the input-output characteristics of an active memory module. Such circuits are likely to exist in the brain. Reciprocal connections between the dorsolateral prefrontal cortex and the mediodorsal nucleus of the thalamus are a possible pathway (Fuster, 1988), as well as the multiple cortico-basal ganglia loops (Alexander *et al,* 1986).

Alternatively, sustained activity may be controlled at the single cell level, *via* the properties of specific ionic channels. Integration of synaptic inputs over a long time, exceeding the time span of classical temporal summation, has been demonstrated in hippocampus (Storm, 1988) and the prefrontal cortex (Hammond and Crépel, 1992). This membrane behavior is due to a slowly inactivating potassium current (I_D in the hippocampus, I_{Ks} in the prefrontal cortex). Prolonged near-threshold depolarizing stimuli activate these currents, which initially inhibit spike firing since they overwhelm inward currents. Delayed firing is then observed which can last for several seconds (Storm, 1988). Inactivation allows sodium-mediated inward currents to be unmasked and thus the discharge of the neuron. Since these currents are partly inactivated, a steady-state potential, hyperpolarizing or depolarizing the neuron, changes the availability of the channel and allows the firing mode of the neuron to be controlled (Hammond and Crépel, 1992). Repetitive long depolarizing pulses induce a progressive reduction of the delayed activation and can favor spontaneous plateau depolarization lasting for several seconds.

Adaptive properties

There is now a great deal of evidence that neocortical neurons can express long lasting modifications of synaptic transmission such as long-term potentiation (LTP) and long-term depression (LTD) (Tsumoto, 1992). These phenomena have been observed in the visual cortex (Artola *et al,* 1990), in the motor cortex (Baranyi and Féher, 1981) and in the prefrontal cortex (Hirsch and Crépel, 1990).

An hypothesis about the mechanism of plasticity is that experience-dependent synaptic changes depend on correlations between pre- and post-synaptic activity (Hebbian rule; for review see Brown *et al,* 1990). However, all forms of plasticity may not actually follow the same rule. For example, Artola *et al* (1990) have observed that induction of LTP and LTD in the visual cortex depends on different voltage-dependent thresholds. Stimulations occurring at different levels of postsynaptic depolarization are likely to have different actions (LTP or LTD).

Furthermore, theoretical studies have stressed that the Hebbian paradigm may not be appropriate for all adaptations. Sutton and Barto (1981) have shown that computational capabilities provided by a plasticity rule based on temporal contiguity should not extend beyond spatial correlations. As a consequence, a network of Hebbian adaptive elements is not likely to learn problems including temporal dependencies. Bienenstock *et al* (1982) have shown in a model that Hebbian modifications combined with a time-varying threshold between increase and decrease produce a temporal competition rather than a spatial one. This theoretical prediction has received support from recent experimental studies which have shown that the direction of synaptic modification can be controlled in the temporal domain (Huang *et al,* 1992).

Architecture: processing pathways and processing steps

Neuronal operations performed by different populations of neurons are integrated together by a set of cortico-cortical connections between temporal, parietal and frontal regions relating the different sensory, motor and internal reference frames with processing pathways. Following anatomical connections, cortical networks can be schematically described by a circular representation (Burnod, 1988; Morel and Bullier, 1990; Young, 1992). Figure 1 provides a view of the circular network, with four input-output poles and reference frames. Functionally important branches are shown: 1) a parietal branch which relates the retinal frame (primary visual area) to the somatomotor frame (primary motor and somesthetic areas; Johnson, 1992); 2) a temporal branch which relates the retinal frame to regions which can store knowledge in an object-centered reference frame (Ungerleider and Mishkin, 1982); and 3) a frontal branch which can relate somatomotor and object reference frames by taking into account internal signals on reinforcement contingencies (Goldman-Rakic, 1987). Each branch can be further divided in several sub-branches (for example, the MT-MST-FST pathway for motion processing).

Within each processing pathway, neurons are connected through feedforward and feedback connections, and show a gradient of properties along the pathway (Johnson *et al,* 1993; Tanaka, 1993). For example, in the temporal branch, cortical neurons are selective (Tanaka, 1993): i) to simple features like oriented edges, color, direction of movement of moving patterns in the first steps; ii) to complex patterns (or prototypes) in the highest steps (and not to their component features); and iii) to both in intermediate associative levels. In the frontal and parietal branch, a gradient of

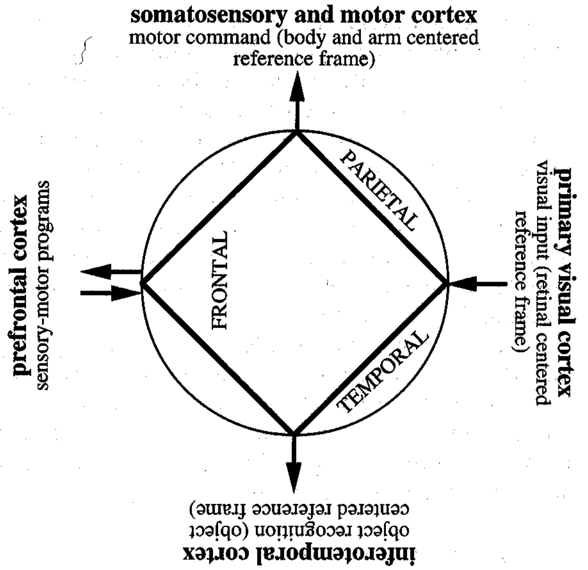

Fig 1. Circular multilayered network for sensorimotor transformations with reference frames and corresponding cortical areas. Four input-output poles are shown: (right) external sensory inputs such as visual inputs in a retinal centered reference frame; (top) sensory interoceptive inputs and motor commands: for example, this input represents the position of the arm in a body-centered reference frame; (bottom) information relative to the objects, stored in an object centered reference frame, with an input specifying their significance; (left) internal coding of sensorimotor programs.

properties is also observed during visually-guided reaching movements with neurons more related to the signal in the rostral part of premotor cortex, and neurons more related to movement in the caudal part of the motor cortex, with similar distributions in the parietal region, symmetrical with respect to the central sulcus (Johnson *et al*, 1993).

A unit for cortical processing

We have stressed that cortical columns are multicellular circuits organized around a small set of pyramidal cells and local-circuit interneurons. Several circuits have been proposed as a model of the cortical column (Szentágothai, 1975; Eccles, 1981). These models provide a description of the intrinsic organization of the column in relation to cell types. We focus here on the functional aspect of columnar operations (Burnod, 1988). The main components of a plausible column-like unit must be the following: i) a layered organization corresponding to the selective processing of different types of inputs; ii) a set of intra-laminar interactions corresponding to the filtering operation performed on columnar inputs; iii) a set of inter-laminar interactions corresponding to the vertical integrative role of pyramidal cells within a column; and iv) a set of registration coefficients defining the adaptive properties of the column.

These components are summarized in figure 2. The laminar organization of the column is represented by a set of input/output layers. A layer receives a subset of inputs sharing a common origin or a common modality. Each layer provides a specific output, computed from the contribution of each layer, to a particular target. Adaptive properties are provided by a set a modifiable columnar registration coefficients, both within a layer and between layers.

According to the architecture of the column (fig 2), processing is performed in two steps, first within each layer (feature extraction), and then between layers (vertical integration). The mathematical description is given in the *Appendix*.

Feature extraction within a layer

This operation reflects the properties of cortical neurons receiving thalamic inputs. Distributed incoming signals are integrated through a weighted convolution-like operation (equation 1 in the *Appendix*). Note that the processing within a layer is similar to that of neural units in most neural network models. The set of coefficients is defined

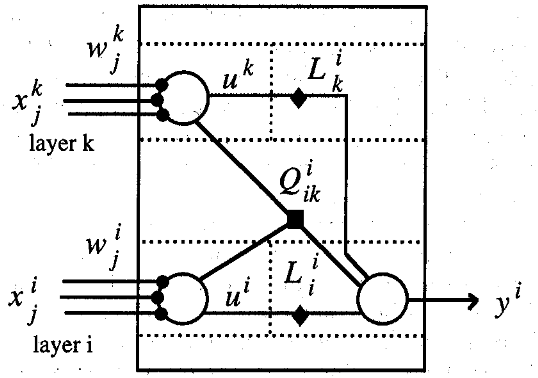

Fig 2. The column-like processing unit. The unit is made up of several input/output layers (separated by horizontal hatched lines). Each layer has two parts separated by the vertical hatched line. It corresponds to the two processing steps of the unit: 1) each layer receives a subset of inputs (x), which are integrated independently, and provides a global layer input (u); 2) the second step is a vertical integration of global layer inputs. It produces an output per layer (y). Each symbol refers to a particular type of coefficient (•, *intra-layer*; ◆, *layer*; ■, *inter-layer*).

as *intra-layer* coefficients and corresponds to the receptive field of the layer.

Vertical integration between layers

The output activity of a layer depends upon the combination of two terms, based on the results of feature extraction within each layer: the first term expresses the influence of each layer independently, with a *layer* coefficient, and the second one expresses the non-linear interaction between pairs of layers, with an *inter-layer* coefficient. Two different processes are introduced related to *inter-layer* and *layer* coefficients, which are consistent with neuronal processing and adaptive properties of cortical circuits described above: *gating* and *timing*.

Gating and adaptive tuning if gating

Pure non-linear interactions between layers occur when *inter-layer* coefficients are non-zero and *layer* coefficients are zero. In this case, each layer acts as an adjustable gain on other layers. There are two ways to adjust this gain, either by changing directly the *inter-layer* coefficient, or by changing the *intra-layer* coefficients (receptive field) of the gating layer.

In the first case, it is possible to learn which of the gating effect (*inter-layer*) and of the simple linear influence (*layer*) is best adapted to a given behavior. For example, several models of coordinate transformations consist of a two-layer network which executes an And operation over inputs in the first layer and a Or operation in the output layer (Burnod *et al,* 1992; Groh and Spark, 1992). The processing units in these two layers should thus be able to learn the appropriate linear or non-linear operation. The rules can be found in Burnod *et al* (1992) and Guigon and Burnod (in press).

In the second case, the *inter-layer* coefficients are 1, the *layer* coefficients are zero, and the *intra-layer* coefficients are adjusted to produce the appropriate behavior. We propose a rule named *adaptive tuning if gating* (equation 3 in the *Appendix*) which enables the processing units to measure the consequence of their activations in relation to the expected goal, in order to learn to reach that goal. Equation 3 can be described intuitively in the following way. For a given state of a unit, defined by an input in one layer (relator input), the output activity of this unit (action) produces a reafferent input in a different layer, which can be viewed as the sensory consequence of the action. A 'photography' of this reafferent input is stored in the *intra-layer* coefficients of the layer. Typically, the relator input can be the position of the arm, the action a command of an arm movement, and the reafferent visual input the visual effect of the movement. The processing unit learns the consistent relationship between a position, a movement and a target. In this way, for a given arm position, an input in the visual layer corresponding to a target predicts the appropriate command to reach this target.

A neural correlate of *adaptive tuning if gating* has been described in the cat visual cortex by Frégnac *et al* (1988). They showed that the orientation selectivity of a visual cortical neuron can be modified by pairing an increase in postsynaptic activity with a new stimulus.

Timing and adaptive timing

Linear contributions within a column can be used to learn to correlate events that are not contiguous in time (Guigon *et al,* in press). Within each layer, a transient input can elicit a long-lasting activity which represents a short-term memory for this input (equation 4 in the *Appendix*). The probability of eliciting a sustained activity is defined by the *layer* coefficient. The sustained activity is stopped by a transient input in an other layer. This bistable behavior performs a 'temporal And' operation upon pairs of non-simultaneous inputs.

The probability of eliciting a sustained activity can be adjusted by learning, by relating successive inputs which form a behavioral sequence to a reinforcement signal indicating the correctness of the behavior (equation 5 in the *Appendix*). The *layer* coefficient, which controls the transition to the On state of the bistable behavior, first undergoes a decrease at the transition to the Off state, and then a greater increase after the reinforcement signal. This rule results in a global increase for reinforced sequences and a global decrease for non-reinforced sequences. Before learning, the *layer* coefficients are assumed to have low values, and thus units are unlikely to become activated (sustained activity). Repeated presentations of a reinforced sequence lead to increased weight. Thus, after learning, the unit will become activated when the first event of the sequence is presented, predicting the occurrence of a reinforcement. This rule relates the quantity of sustained activity to the predictability of reinforcement.

Learning functions in different cortical regions

In this section, we describe the properties of three neural networks made of column-like processing units, corresponding to different architectures and different columnar operations. Each network is inspired by the architecture of a known cortical network and reproduces its function.

Learning invariant recognition

Two important transformations are performed by the visual system: 1) a low level transformation resulting in the perceptual grouping of textured surfaces; and 2) a higher level transformation resulting in invariant recognition of objects. Neurobiological data give some insights in the nature of these transformations. Low-level processing is probably performed at early stages of the visual system. Visual information is then processed at least in two parallel streams (fig 3A), the dorsal stream to the parietal lobe for target location (the Where pathway) and the ventral stream to temporal lobe for target identification (the What pathway) (Ungerleider and Mishkin, 1982). The more anterior portions of the temporal lobe tend to be critical for storing prototypes of visual objects in a form that is accessible even with large variations in texture, position, orientation and size. The posterior regions are more concerned with addressing transforms of the retinal images to the stored prototypes (Weizkrantz and Saunders, 1984) and receive projections from the parietal stream which can be involved in geometrical transformations necessary to match the incoming signal with the stored prototypes. The main constraint of visual processing is to capture the diversity in the flow of visual information and to form invariant internal representations.

The network model of the visual system has a Y-like double-branched multilayered architecture (fig 3B), with one input (the retina) and two parallel outputs, which model the parietal and temporal pathways (Otto *et al,* 1992). Several steps transform the retinal information into a prototype in an object-centered reference frame in the temporal branch, and into an oculomotor command in the parietal branch: i) primary areas perform low-level processing, such as elementary feature extraction, on the retinal information; ii) secondary areas perform more elaborated processing using larger receptive fields, but still with a retinal reference frame; iii) associative intermediate

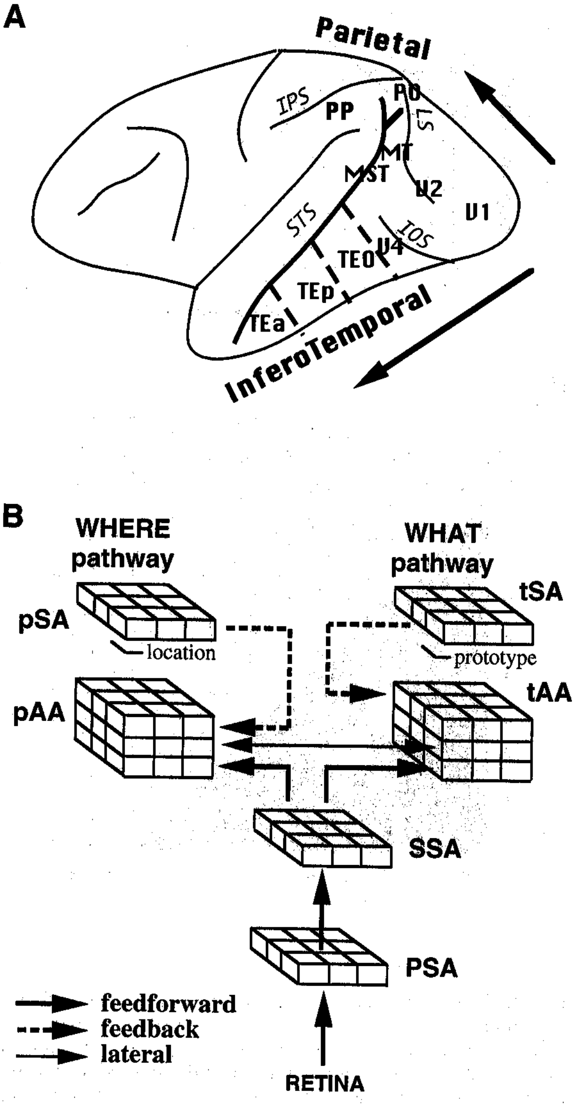

Fig 3. A. Cortical network for invariant recognition. Visual information is first processed by V1 and V2 and then by two major pathways: a ventral pathway toward the inferotemporal lobe rather involved in object recognition and the dorsal pathway toward the parietal lobe rather involved in localization and motion detection. The figure shows some important functional steps in each stream: V4 and IT subdivisions (TEO, TEp, TEa) in the ventral pathway, PO and PP (including 7a and LIP) in the dorso-medial pathway and MT and MST in the dorso-lateral pathway. **B.** Architecture for invariant pattern recognition. The global architecture of the network is Y-like shaped with a What pathway performing pattern recognition and a Where pathway encoding the location of the pattern. PSA, primary sensory area; SSA, secondary sensory; tAA, temporal associative; tSA, temporal semantic; pAA, parietal associative; pSA, parietal semantic.

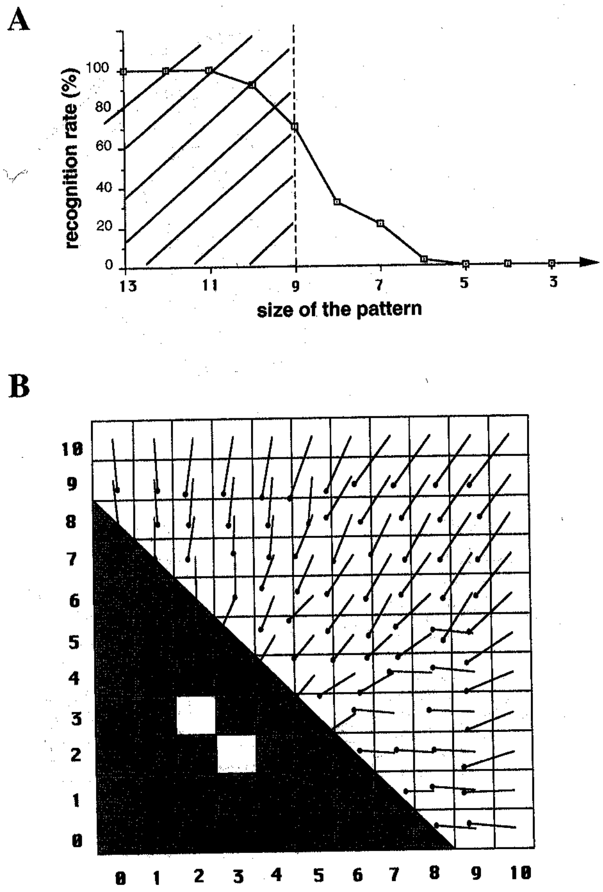

Fig 4. **A**. Performances of the temporal pathway: effect of changing size only. The network is trained to recognize 28 patterns of fixed size (size 12, 24 × 24 pixels) presented in the central position. During the recognition session, the patterns are presented, in the central position, but with varying sizes: from a size 13 (26 × 26 pixels) down to a size 3 (9 × 9 pixels). Note that the recognition rate remains above 70% despite decreases from the learned size of up to 33%. **B**. Cooperation between temporal and parietal pathways. A pattern is presented during the recognition session with varying sizes and position shifts on the retina of up to 10 ± 10 'pixels'. This figure shows the behavior of the double-branched network for a prototype (here the capital letter 'X') presented with one size (size 10, 20 × 20 pixels) in all the positions (in the upper quarter of the retina, the other quarters can be deduced by symmetry). The dark region represents the positions where the pattern is directly recognized by the What branch. Lines (black circles indicate the direction) represent the vectorial population coding of an ocular movement performed in the Where branch when the What branch fails to recognize the pattern. Notice that these vectors contain the directional information needed to reset the pattern closer to the positions where it is directly recognized (dark squares). Furthermore, the amplitude of the vector increases with the distance of the pattern from the center.

areas learn to relate the resulting pattern of activity with the iv) highest-level steps which store the learned prototypes. The temporal and parietal branches differ by the size of the receptive fields in associative and semantic maps. Receptive fields in the parietal branch become very large. Global information about the direction and the distance of the retinal stimulus from the center of the retina is extracted and helps to produce an oculomotor command. Receptive fields in the temporal branch remain smaller and precise information on the shape of the retinal stimulus is extracted) and helps for recognizing the stimulus.

Within each map, the processing units are three-layered cortical columns which combine three types of inputs: i) feedforward inputs, providing sensory information from the outside world that has already been subject to selective filtering through previous processing steps; ii) feedback inputs from higher stage units, which control the ascending flow of information; and iii) lateral inputs provided by similar units in the other flow (in the associative and semantic maps).

Cooperation of parietal and temporal pathways for recognition (external shift)

Patterns are learned in the central part of the retina. Each pattern is presented on the retina while the units corresponding to the prototype of this pattern are activated on the semantic maps. Learning occurs through *adaptive tuning if gating* when inputs from feedforward and feedback flows are in register in the associative maps. Receptive fields of associative units are 'photographies' of the pattern (after transformation in primary and secondary areas) taken when gating from prototype units occurs.

After learning, the temporal and parietal branches cooperate for recognition (Otto *et al,* 1992): 1) if the pattern is presented in the central zone of the retina, the temporal branch of the network succeeds in immediate recognition, for sizes and positions within a limited range of variation (fig 4A); 2) when variations in size and location are increased, the pattern is not directly recognized by the temporal branch, but the population activity in the parietal branch provides information on the direction and amplitude of the eye movement which can reset the pattern in the center of the visual field where it can be recognized by the temporal branch (fig 4B).

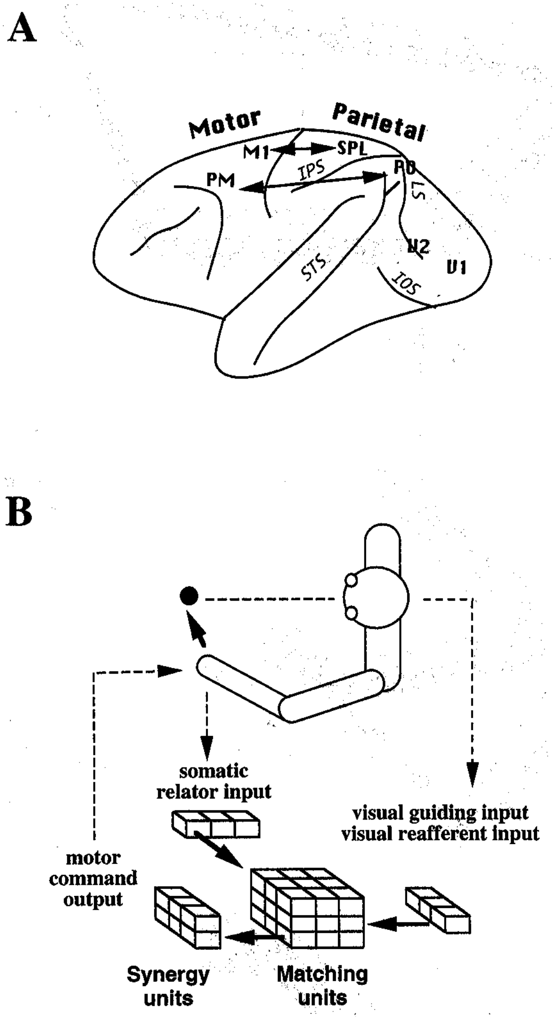

Fig 5. A. Cortical network for visually-guided arm movements. Cortical areas involved in the control of reaching behavior in the primate are the primary motor cortex (M1), the premotor cortex (PM), and the posterior parietal cortex areas (SPL, IPL, PO). **B.** Architecture of the neural network modelling the operations performed by the cerebral cortex for visuomotor transformations. The processing units model the cortical column, with inputs and outputs organized in layers. A set of synergy units and a set of matching units are reciprocally connected. Each synergy unit addresses a motor command to a subset of motor units, whose contraction produces a vectorial effect on the hand position. A matching unit receives sensory information from two sources: a somatic input (on its somatic layer-division) which encodes the initial arm position, a visual input (on the visual layer-division) which codes for the desired trajectory and feedback information (on the feedback layer-division) from active synergy units. Each matching unit projects to synergy units. Synergy units receive a feedforward input from matching units a lateral input from other synergy units. Input connections to synergy and matching units are adaptive and are tuned by the feedback loop produced by spontaneous movements.

Cooperation by direct temporo-parietal interactions (internal shift)

Direct anatomical relations have been described between the temporal and the parietal pathways (Morel and Bullier, 1990). An important contribution of the parietal lobe areas to recognition could be to provide the positional information directly to the temporal areas. This information could be used to shift the ascending input pattern, when displayed in perifoveal zone, within the temporal pathway, in order to match it with the previously stored information (Boutkhil and Burnod, 1992; Otto *et al,* 1992). This intracortical shift could be sufficient to efficiently perform the recognition process without ocular movement (Olshausen *et al,* 1993). An additional interesting property of such a process would be the possibility that such partial shifts could be used to correct local deformations.

The operation for invariant object recognition in the temporal branch which is modelled by sigma-pi networks (Glünder, 1987; Boutkhil and Burnod, 1992; Olshausen *et al,* 1993) is quite similar to the visuomotor transformation performed in the parietal branch (Burnod *et al,* 1992; see below). This operation transforms retinotopic information into an object centered reference by using positional information, exactly as the operation in the parietal branch for visually-guided reaching movement which transforms the retinal information in a motor reference frame by using a positional information on gaze and arm position. This can be modelled by the interactions between the three layers of the units in the associative map of the temporal pathway (modelling the posterior inferotemporal area): 1) the feedforward layer which gives the information content on the restricted zones extracted by lower-level maps; 2) the lateral layer which provides positional information from the parietal associative map, and and 3) the feedback layer which signals for success or failure of recognition (Boutkhil and Burnod, 1992).

Learning visual-to-motor coordinate transformation

Following integration through the visual system, visual information arising from retinal stimulation can be used to guide visual reaching movement toward targets in space. The neural network which computes visually-guided movements in the 3D space is related to the neuronal properties in premotor, motor and parietal areas (fig 5A; Bur-

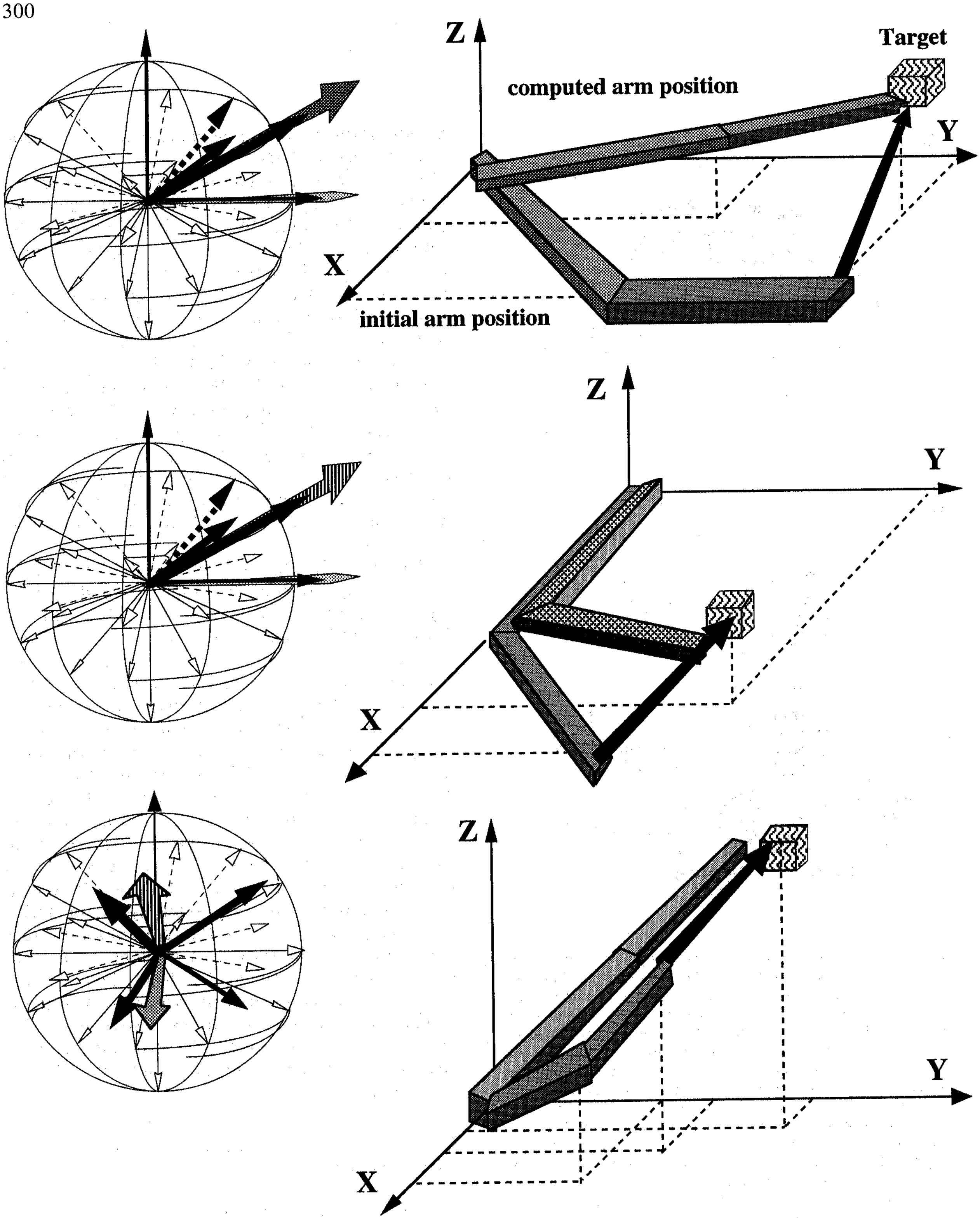

Fig 6. Invariant properties of cortical command for reaching movements. **Right.** Three different movements are shown, with the target position, the initial position and the direction of the movement. **Left.** The vectorial contributions of synergy units and the resulting population vector (*outlined hatched vector*) are shown.

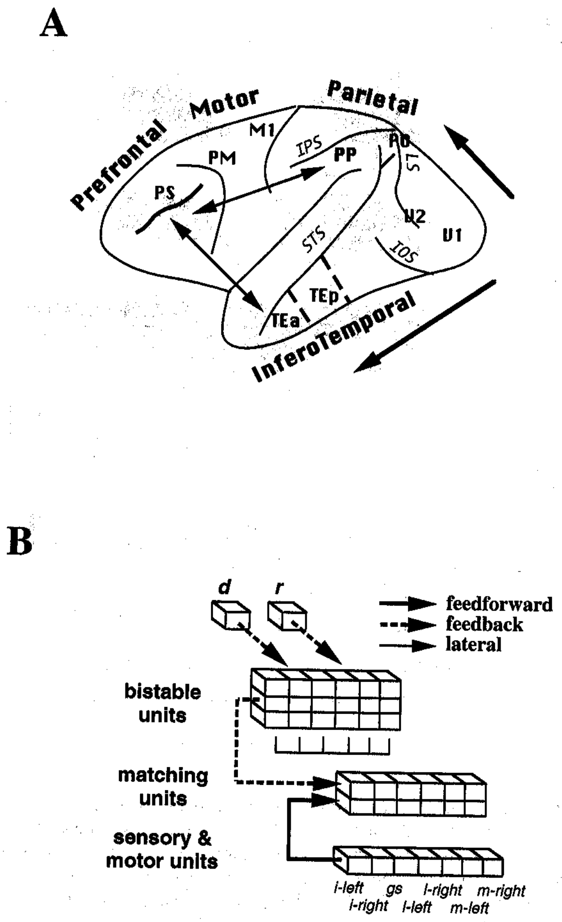

Fig 7. A. Cortical network for learning sensorimotor sequences. The prefrontal cortex (PFC) combines visual information related to discrimination and recognition provided by the higher processing steps of the temporal lobe (IT), information relative to spatial location which originates in the posterior parietal areas (PP), and interacts with structures involved in motor control (M1, PM). **B.** Architecture of the network for learning a delayed-response task. The matching layer is made of eight units. The bistable layer is made of eight groups of four units. Notations for the task events are the following: i) *l-left* and *l-right*, positions of left and right levers; ii) *m-left* and *m-right*, movements toward the levers; iii) *gs*, go signal; iv) *i-left* and *i-right*, instruction stimuli; v) *d* and *r* for drive and reinforcement, respectively. We have made the following assumptions: i) a redundant representation is used when the same event occurs in different situations (go signal); ii) all the units in a given bistable group have the same relationships with matching units; iii) there are no interfering events, except during the first training stage, where four movements (*m-left, m-right, m-up, m-down*) toward four different levers (*l-left, l-right, l-up, l-down*) are possible (but only two are correct). During this stage, the network learns to suppress the responses *m-up* and *m-down* when presented with *l-up* and *l-down*, respectively. It illustrates the ability of the network to deal with environmental interferences. Interfering events could be added at other training stages in a similar way.

nod *et al,* 1992; Johnson, 1992). In parietal areas, neurons can be tuned to visual, oculomotor, motor and somatosensory input, with combinatorial properties: they can be activated by retinal stimulation and eye position (Andersen *et al,* 1985), arm position and arm movement direction (Lacquaniti *et al,* in press), direction of visual and tactile stimuli (Colby *et al,* 1993). Studies of the neuronal activity in the motor and premotor cortices of behaving monkeys have shown that the activity of individual arm-related neurons is broadly tuned around a preferred direction of movement in 3D space (Georgopoulos *et al,* 1986; Caminiti *et al,* 1991). In both frontal areas these cell preferred directions rotate with the initial position of the arm (Caminiti *et al,* 1991). Furthermore, the rotation of the population of preferred directions precisely correspond to the rotation of the arm in space.

The visual-to-motor transformation is thus modelled by two maps (fig 5B): a map of matching units modelling neurons in parietal areas, and a map of synergy units, modelling neurons in premotor and motor areas. Matching units are three-layered cortical column-like units which combine three types of information: i) visually-derived inputs on target position; ii) a somatic information on the arm position; and iii) a somatomotor information on the motor command from the synergy units (efferent copy of the command). Synergy units receive two types of inputs in two layers: i) feedforward inputs from the matching units; and ii) lateral inputs from other synergy units. Synergy units project to motor output units modelling motor units in the spinal cord.

The network learns self-consistency between sensory and motor signals through spontaneous movements. Associations between synergy signal (output), kinesthetic signal (arm position), and reafferent visual signal following a spontaneous movement are stored by adjusting visual receptive fields of matching units through *adaptive tuning if gating* (equation 3 in the *Appendix*). These receptive fields can store a 'photography' of the sensory effect of the motor command (vision of the hand moving toward the fovea) in relation with both the motor command (from synergy units) and the relative positions between visual receptors and arm effectors. Any visual information that is collinear with this stored direction becomes after learning information which can guide the motor command in the appropriate direction.

The operation which is learned by the network from spontaneous movement can be approximated by a bilinear combination (equation 2 in the *Appendix*) which can be interpreted as a generalization of the classical coordinate transformation between two reference frames: the visual information is projected on a reference frame which rotates with the arm. The neural circuit converging toward a single neuron in the motor and premotor cortices can easily learn and generalize the appropriate command in a 2D subspace, but not in the whole 3D space. However, the uniform distribution of cell-preferred directions in these frontal areas can explain the computation of the correct solution by a population of cortical neurons. The model explains neuronal tuning properties which are observed in premotor and motor cortex, both at the individual cell level and at the population level (Caminiti *et al,* 1991; Burnod *et al,* 1992): 1) cells are tuned for a preferred direction which depends upon the initial position of the arm; 2) the population vector always predicts the movement direction, even if the initial position of the arm rotates; 3) the preferred direction of a single neuron rotates like the arm within a specific sub-space, but not in the whole 3D space; and 4) the whole population of preferred direction vectors rotates like the arm (fig 6).

Learning sensorimotor sequences

The next question is to understand how brain circuits integrate sequences of discrimination, recognition and reaching into a coherent behavior, defined by some internal or external goals (for example the getting of a reward). Convergent experimental evidence has demonstrated the critical role of the prefrontal cortex (PFC) and distributed neural networks linking associative, motor and prefrontal areas (fig 7A) in the acquisition and expression of complex behaviors (Goldman-Rakic, 1987; Fuster, 1988). Lesion studies have shown that monkeys with prefrontal lesions fail to execute a behavior which requires the memory of some recent events (Rosenkilde, 1979). Neuronal activities recorded in PFC during the delayed tasks in behaving monkeys appear to be a striking correlate of behavior (Fuster, 1973, 1988). For example, neurophysiological studies have demonstrated sustained neuronal activity during the delay between an instruction cue and the final permission to use the information contained therein for a spatial reaching movement (Fuster, 1973). The delay-related activity may reflect short-term mnemonic aspects related to the instruction cue, the expectation of forthcoming signals and the preparation of the behavioral reaction.

The neural network model, designed according to the principles of organization of prefrontal connections, was trained to execute a delayed response task (Guigon *et al,* in press). The task involves two lights mounted above two horizontally arranged levers and a trigger light. At each trial, one light (instruction stimulus) comes on for a short period; a few seconds later, the trigger light (go signal) comes on and the animal touches

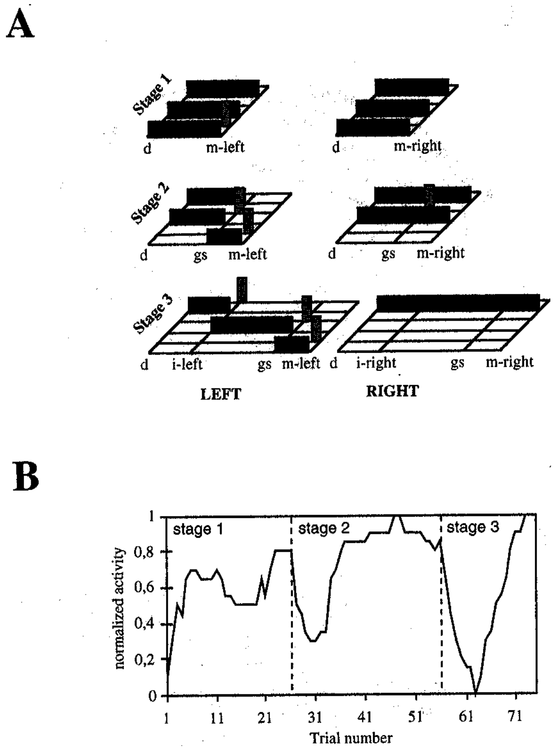

Fig 8. Computer simulations. **A**. Activities in three bistable units (dark shaded pattern) and three matching units (light shaded pattern) are qualitatively displayed for each training stage and for left and right trials. The task events are those described in figure 2. Note the gradual changes in the relationships between neuronal activity and task events and the differentiation for left *vs* right trials. **B**. Variations in the level of activity of a bistable unit during the training period. The graph is constructed from the activity during reinforced left trials. Each horizontal division corresponds to a trial. Vertical dashed lines indicate the transitions between training stages. Note the combination of increasing and decreasing activity: activity decreases at the transition between two stages and increases after the transition.

the lever indicated by the instruction: it receives a reward. The architecture of the network is shown in figure 7B. Each sensory event is coded by the all-or-none activation of a specific unit in the sensory layer, and movements towards the levers are coded in the motor layer. The network is made of two sets of units. Matching units model neurons in the associative sensory and motor areas connected to the prefrontal cortex. These units implement sensorimotor relations, such as a direct relation between the position of the lever and movement toward the lever. Bistable units model prefrontal neurons and learn to modulate these sensorimotor relations by reinforcement contingencies. Bistable units receive two types of signal in two layers: i) feedforward inputs from matching units; ii) feedback inputs which inform on motivational aspects (a drive pathway is made active at the beginning of each behavior of the network) and reinforcement (a reinforcement pathway is activated when a correct behavior is produced by the network); and iii) lateral inputs from some other bistable units. Matching units receive two types of input in two layers: 1) feedforward inputs from sensory units; 2) feedback inputs from bistable units.

The function of the network is defined by the dynamics of processing units and by the adjustable connection coefficients between processing units. Neural processing function of matching units is modelled by a non-linear interaction between inputs, which reflects the modulation of sensory inputs and motor outputs by memorized conditions (*gating* between feedforward and feedback inputs; equation 2 in the *Appendix*). Bistable units display long-lasting activities which are a selective memorization of past events (*timing* between two layers; equation 4 in the *Appendix*). They can learn to control the transition to sustained activity through *adaptive timing* (equation 5 in the *Appendix*).

Computer simulations of the neural network in figure 7B were used to train it to execute a delayed response task in three successive stages (stage 1: movement, reward; stage 2: go signal, movement, reward; stage 3: instruction stimulus, go signal, movement, reward). The rationale for this protocol is that the training protocols used with animals are progressive, stage-by-stage procedures. Furthermore, the teaching signal is an all-or-none signal indicating the correctness of the behavior. This strategy is related to reinforcement learning procedures (Sutton and Barto, 1981). At each stage, the network was presented with a number of trials, until the required behavior was obtained. The outcomes of the model reflect two aspects of short-term memory processes. First, how bistable units may contribute to the execution of the task. Second, how bistable units contribute to the acquisition of the task.

Bistable units implement short-term memory

The contribution of bistable units to the execution of the delayed response task is illustrated in figure 8A. Each graph displays qualitatively the activity of three bistable units at a given training stage. During execution of the task (stage 3), bistable units display different patterns of activity defined by the temporal relationship between task events and peaks of activity (fig 8A). Each unit is active between two successive task events. The most interesting pattern is the differential delay activity. This is a sustained activity between the onset of the instruction stimulus and the onset of the go signal specific for right *vs* left trials. All these patterns have been described in the prefrontal cortex during the delayed response task (Fuster, 1988).

At each training stage, bistable units play a complementary role in encoding the temporal structure of the task. Individual units are selective for a specific sequence of events (drive / instruction stimulus; instruction stimulus / go signal; go signal / movement), but the set of units is able to bridge all the gaps between the events of the current task. The role of matching units is also illustrated in figure 8A. These units displayed transient activity that was time-locked to sensory or motor events and that was correlated with the end of activity in bistable units. They signal the occurrence of specific sensory or motor events in the context of a specific behavior.

Long-term changes in bistable units

The experience gained at each trial in the learning period is transferred to a long-term representation of the task. This relationship changes from stage to stage, and bistable units become progressively specialized for different successions of events. At the final stage, each unit is related to a specific succession of events.

Variations in the activity of bistable units are correlated with the changes in reinforcement contingency, depending on variations in the reinforcement rate (fig 8B). Two behaviors are alternatively performed by the network when changing from stage 1 to stage 2: one is the previously correct behavior (self-initiated movements) and the other is the new correct behavior (stimulus-triggered movements). The mean activity during reinforced trials increases for leftward self-initiated movements during the first stage. During the transition from stage 1 to stage 2, activity first decreases and then increases with the increase in the performance rate. The same phenomenon occurs between stage 2 and 3 (fig 8B).

These results are consistent with experimental data. During reversal learning in a go/no-go discrimination task, Niki *et al* (1990) found some neurons that reversed their activity with the change in the reward contingency (type 2), and some that retained the same activity (type 1). The matching units of this model resemble the type 1 units since both were related to the impending behavioral response and did not change their activity with change in the reward contingency. Type 2 units (Niki *et al,* 1990) reversed their activity with the change in the reward contingency as do bistable units in the network. Although few units were studied, type 2 units were rarely found in the premotor cortex, while the prefrontal cortex contained both types of units in similar proportions (Niki *et al,* 1990). Changes in the activity of bistable units can also be compared with those found by Thorpe *et al* (1983). Neurons in the orbitofrontal cortex decrease or increase their activity depending on learning of the associative significance of a visual stimulus. The results are also consistent with the observations of Watanabe (1990) who found decreasing activity when changing the significance of a stimulus without changing the required behavioral response. Modulations of activity in bistable units may thus be related to the change in the associative significance of the current behavior (will it lead to a reward?) (Thorpe *et al,* 1983; Watanabe, 1990).

Discussion

Most neural models of brain functions are constructed using some principles of cortical organization. However, in many cases, biological principles are mixed with engineering principles (for example optimization procedures), and models become complex hybrid systems. This approach may be defined as 'top-down', since a restricted number of hypotheses are made on biological features, and outcomes are mainly derived from algorithmic constraints. Strong criticism has been formulated against this approach (see Crick, 1989).

A complementary approach is to ask how the cerebral cortex is likely to solve problems (Ballard, 1986; Burnod, 1988). This 'bottom-up' approach focuses on the structural and functional characteristics of cortical circuits and their involvement in the implementation of problem-solving algorithms. The goal is not to take into account the greatest number of biological properties, but to point to the critical aspects, which contribute to appropriate computation.

The appeal of the neocortex relies on the following facts: i) great regularity is observed in its organization; ii) cortical circuits process any set of data with a single format, whatever the modality; and iii) the phylogenetic development of the cortex is correlated with the acquisition of higher level behavior structures. However, to focus on the cerebral cortex does not deny the contribution of subcortical systems, such as basal ganglia, cerebellum, or medial temporal lobe structures. It is a means to describe the computational principles underlying various brain functions within one and the same framework.

A cortical column-like processing unit

The modelling principles encompass several levels of brain organization, including synapses, neurons, and maps. It allows multiple constraints in the construction of models of cortical functions to be taken into account. A central, original component of the framework is a multicellular processing unit (cortical column), reflecting the layered organization of the cortex and the differential laminar distribution of cell types. The architecture of the unit allows various processing and learning modes to be used as a basis for regional variations. Furthermore, the layered structure of the unit facilitates the construction of neuronal networks with various patterns of connectivity.

The unit implements two levels of processing (feature extraction and vertical integration). In this way, there is a dissociation between the specific operation performed by cortical circuits and the nature of data on which they act. It means that processing is independent of particular input codes since feature extraction provides an unique format, whatever the modalities.

Higher-order processing units have already been proposed as an alternative to the simple linear or thresholded summator, such as the sigma-pi unit (Williams, 1986) and the synaptic triad (Dehaene *et al,* 1987). A sigma-pi unit computes a sum of contributions from multiplicative clusters of inputs and thus implements a *gating* mechanism as an intrinsic property of single operating elements. Many models have stressed the computational interest of sigma-pi units to represent multidimensional receptive fields or higher-order feature detectors (Mel, 1993), to implement invariant pattern recognition (Glünder, 1987; Fukushima, 1988), to perform coordinate transformations (Kuperstein, 1988; Groh and Spark, 1992). However, there is no easy way to set the synaptic weights in a network of sigma-pi units, although Durbin and Rumelhart (1989) proposed a method based on the back-propagation algorithm.

The synaptic triad is an elementary device made up of three neurons, in which the synaptic transmission between two neurons in the triad is modulated by the third one (Dehaene *et al,* 1987). The postsynaptic neuron in the triad acts as a sequence detector on the presynaptic and the modulator neurons. A local Hebbian rule can be used within a network of synaptic triads to learn temporal sequences (Dehaene *et al,* 1987; Dehaene and Changeux, 1991).

Training neural networks: developmental stage or conditioning

Generally, neural networks are trained following the logic of classical conditioning. Learning occurs even when the output of the network is incorrect, the output being unconditionally given by the teacher. However, for the development or the adaptation of most neural systems, a teacher either does not exist or gives only raw information concerning the behavior (such as failure or success). In the first case, the system learns in an unsupervised fashion, by experiencing the environment, as it may be the case for the development of the selectivity to orientation in the visual cortex (self-organization). In the second case, the system learns by trial and error to meet at each time the requirements of the teacher.

The model of invariant recognition is trained by associations between raw retinotopic inputs and inputs corresponding to a semantic representation (Miyashita, 1993). The model of visual-to-motor transformation learns, through spontaneous movements under visual control, the consistency between visual, proprioceptive and motor signals. A similar learning seems to happen during critical periods of development in the child (Hay, 1984). A progressive, stage-by-stage procedure is used, in the third model, to encode a sensorimotor sequence in a neural network. Such a procedure is encountered when laboratory animals are operantly trained to perform a sequence of actions in order to get a reward (Delacour, 1981).

Towards an integrated model of a 'reference' task

To perform a task such as a delayed pointing toward a visual target ('reference' task), a number of fundamental processes must be carried out by the cerebral cortex: i) discrimination and recognition of the target: this step involves first the orientation toward the target and then the processing of the visual image of the target, which includes feature extraction, perceptual grouping of textured surfaces, classification, etc; ii) construction of a body-centered representation of the target: this step involves the evaluation of the distance from the body, the integration of eye, head and body position signals; iii) visual-to-motor transformation and computation of the motor command: this step involves solving the inverse kinematics and the inverse dynamics for the arm; and iv) planification of the sequence of events: this step involves the short-term memorization of the target and the preparation for response.

The neural substrate of these operations can be addressed experimentally both at the cellular level in behaving monkeys, using single unit recordings, and at the system level in monkeys and humans, using brain imaging techniques (deoxyglucose labeling, position emission tomography, functional magnetic resonance imaging). The model helps to relate these two different levels of analysis and provides a guide to a systematic experimental study of the 'reference' task using different techniques (Burnod, 1994).

Appendix

Processing unit

Each layer i ($1 \leq i \leq N$) has n_i weighted input pathways $\left\{ x_j^i (w_j^i) \right\}$, corresponding to afferences from other columns. It provides first a 'global layer input' u^i, which is internal to the column, and then an output y^i which is sent to other columns.

The global layer input u^i of layer i is calculated according to:

$$u^i(t) = f\left(\sum_{j=1}^{n_i} w^i_j(t)\, x^i_j(t)\right) \qquad (1)$$

where t is a quantized time, which describes the course of processing, and f a non-linear non-decreasing function in [0,1].

The output activity of layer i depends upon the combination of two terms: the first term expresses the influence of each layer k independently, with a *layer* coefficient (L^i_k), and the second one expresses the non-linear interaction between pairs of layers, with an *inter-layer* coefficient (Q^i_{ik}). The general form of the output y^i of each layer i is a function of the global layer inputs, and the *layer* and *inter-layer* coefficients.

Gating and adaptive tuning if gating

In this case, each layer i provides an output activity y^i according to:

$$y^i(t) = f\Big[\sum_{k=1, k\neq 1}^{N} Q^i_{ik}(t)\, u^i(t)\, u^k(t)\Big] \qquad (2)$$

where the *inter-layer* coefficients Q^i_{ik} are equal to 1. The *intra-layer* coefficients are modified according to:

$$\Delta w^i_j(t, t{+}1) = \lambda[\sigma x^i_j(t) - w^i_j(t)]\, y^i(t-1)\, u^i(t) \quad (3)$$

where λ is a positive constant determining the rate of learning and σ a positive constant. This rule expresses that the coefficient w^i_j increases toward σ with the coincidence of pre- and post-synaptic activity when the column has been previously active, and decreases toward 0 with post-synaptic activity alone in the same condition. In this way, coefficients can be tuned around values that correspond to the most probable input within layer i when this layer has been active.

Timing and adaptive timing

In this case, each layer i provides an output activity y^i according to:

$$y^i(t) = [1 - \lambda\, y^i(t-1)]\, F\left[\sum_{k=1}^{N} L^i_k u^k(t)\right] + F[\eta\, y^i(t-1)]\Big\{1 - F\Big[\Big[\sum_{k=1}^{N} u^k(t)\Big]\Big\} \qquad (4)$$

where λ and η are parameters, F is the stochastic function defined by:

$$F(u) = \begin{cases} 1 \text{ with} & \text{prob}\, f(u) \\ 0 \text{ with} & \text{prob}\, 1 - f(u) \end{cases}$$

Equation 4 implies that the output layer i has two states of activity (0 and 1) and switches between these states with a probability defined by the global layer inputs. The first term of the equation indicates that the output layer becomes active when it was previously inactive and when the global layer inputs are sufficient. The second term indicates that the output layer can stay active for a while and returns to rest following subsequent inputs.

The *layer* coefficients are modified according to:

$$\Delta L^i_k(t, t{+}1) = e^i_k(t)\Big\{\sum_{j=1, j\neq k}^{N}[-\alpha\, u^i(t)\, y^i(t-1) + \beta u^{-j}(t) y^{-i}(t) r(t)]\Big\} \qquad (5)$$

where r is a reinforcement signal, α and β are positive parameters. Using the notations of Sutton and Barto (1981), we define:

$$\begin{cases} u^{-j}(t+1) = \kappa u^{-j}(t) + u^j(t) \\ e^i_k(t+1) = \omega e^i_k(t) + u^k(t) y^i(t) \\ y^{-1}(t+1) = \chi_1 y^{-1}(t) + \chi_2 y^i[y^i(t) - y^i(t+1)] \end{cases}$$

where κ, ω, χ_1 and χ_2 are parameters in [0,1]. Equation 5 indicates that the layer coefficient L^i_k decreases when the sustained activity of the unit triggered by the layer $\underline{k}$ is stopped by some other pathways (term with -α) and increases when a reinforcement signal occurs after the sustained activity (term with +β).

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