

Research report

Encoding behavioral context in recurrent networks of the fronto-striatal system: a simulation study

Peter F. Dominey^{a,b,*}, Driss Boussaoud^{a,b}

^a *Vision et Motricité, INSERM Unité 94, 16 Avenue du Doyen Lépine, 69500 Bron, France*

^b *Institut des Sciences Cognitives, CNRS UPR 9075, 69008 Lyon, France*

Accepted 18 March 1997

Abstract

This research addresses the hypothesis that behavioral context is encoded in recurrent networks of the fronto-striatal system. Behavioral context influences the processing of subsequent brain events, including responses to sensory inputs, thus providing a basis for context-dependent behavior. We define context-dependent behavior as the adaptive ability to produce the appropriate response to a given stimulus, dependent upon the context in which it appears. Behavioral context can change with a time-scale on the order of seconds to tens of seconds or more. This suggests a flexible mechanism that encodes context via an ensemble of neural activation that will appropriately influence the processing of subsequent sensory stimuli. We present a functional model of context encoding in recurrent connections of the fronto-striatal system with simulation results that correspond closely to empirical data. Neuronal activity in monkeys that perform a context-dependent task indicate that the prefrontal cortex and striatum participate differentially in this kind of context encoding. Likewise, simulated neurons in our model of the fronto-striatal system, which performs the context-dependent task, display task-related activity remarkably similar to that found in monkey frontal cortex and striatum, supporting our hypothesis. © 1997 Elsevier Science B.V.

Keywords: Basal ganglia; Fronto-striatal system; Neural network model; Recurrent network

1. Introduction

As behavior becomes more advanced in the hierarchy of cognitive function, the related processing becomes more abstract, less directly related to specific sensory or motor systems. From a neurophysiological perspective, the corresponding requirements for direct sensory and motor connections diminish, while those for associative connections increase, with this trend culminating in the complex planning-related functions of the prefrontal cortex (PFC) [18]. Thus, it is not surprising in this context that PFC lesions leave a number of primitive sensorimotor processes intact, while producing impairments at more abstract behavioral levels, in particular those situations in which the correct behavior is dependent on a context established by an earlier stimulus [19,31]. This suggests that indeed the capacity to generate appropriate context-dependent behavior relies on the prefrontal cortex and the neural networks

of which it is a part. Questions remain, however, about the mechanisms by which the PFC achieves this capability. In reference to such questions, the current study attempts to reconcile data from studies of primate neuroanatomy and electrophysiology with those from an anatomically structured neural network simulation of context-dependent behavior.

We define context-dependent behavior as the adaptive capacity to respond appropriately to a given stimulus in different ways, dependent upon the behavioral context in which that stimulus appears. A classic measure of this capacity is provided by the Wisconsin Card Sorting Test (WCST [29]), in which the same card must be differently sorted, either by color, number or shape, dependent on the context in which that card appears. The WCST is a classic test for detecting frontal cortical dysfunction [30], although it is not pathognomonic for frontal cortex.

The approach that we take in this study starts with a theoretical analysis of the information processing resources required to learn to perform context-dependent behavior. The neuronal mechanisms underlying these processes are then examined through the analysis of data recorded while

* Corresponding author. Fax: +33 (4) 72-91-34-01; E-mail: dominey@lyon151.inserm.fr

primates performed a complex context-dependent behavioral task [8,9,27,28]. We then attempt to understand the architectural basis of these neurophysiological mechanisms by examining the neuroanatomy of the primate frontal cortex and corticostriatal system [2,5,19,24,39,45] (see [7,20] for review). This leads to our hypothesis concerning the neurophysiological basis of context representation. In particular we advance the idea that recurrent cortical and cortico-subcortical circuits provide the basis for context encoding as suggested by Houk and Wise [23] and Dominey et al. [14].

This hypothesis is then tested on an anatomically structured neural network model of the fronto-striatal system that we have used to study context representation for sensorimotor sequence learning [14,16]. We demonstrate that this model is capable of learning a context-dependent task. Of greater interest, single units in the model's simulated frontal cortex and striatum show task-related properties that are strikingly similar to those found in monkey frontal cortex and striatum. In addition, we note that prefrontal neurons in a context-dependent task [8,9] and in a sequence learning task [6] display quite similar context-dependent coding properties, and these are both reproduced by our model. This commonality suggests a shared mechanism for both sequential and context-dependent behavior, including the possibility that each item in a sequence is selected in the context of what has preceded it. We conclude that recurrent connections in the primate fronto-striatal system participate in a generalized context encoding function that supports sequence learning and other forms of context-dependent behavior.

2. Context-dependent learning and behavior

The ability to learn an appropriate response to a given stimulus is an important aspect of adaptive behavior. This

function can be realized by an associative memory mechanism in which representations of given stimuli become associated, through learning-related internal changes, with the appropriate response. That is, a set of mappings between stimuli and responses is learned. This can be expressed as a one argument function $f()$, that takes a stimulus as input and returns a response:

$$f(s_i) = r_j, \text{ for stimulus } s_i \text{ in the set of stimulus } S,$$

$$\text{and response } r_j \text{ in set of response } R \quad (1)$$

In the current framework, context-dependent learning extends this function to take two instead of one arguments so that the mapping between stimuli and responses is determined by the context. That is, in context c_1 the stimulus s_1 may be associated with response r_1 , but in context c_2 the same stimulus s_1 is to be associated with response r_2 . Thus, it is no longer the stimulus alone that unambiguously determines the response, but the combined stimulus and context pair, as described in Eq. (2).

$$f(s_i, c_j) = r_k, \text{ for stimulus } s_i \text{ in } S, \text{ context } c_j \text{ in } C,$$

$$\text{and response } r_k \text{ in } R \quad (2)$$

Note that in this definition, behavioral context is neither necessarily fixed nor stable and can in fact change with roughly the same frequency as the stimulus. To provide a more concrete example of context-dependent behavior, we now consider a task developed by Boussaoud and Wise [8,9] to dissociate attentional and visuomotor processes. The task was performed by primates seated in front of a video display on which visual stimuli were presented (Fig. 1). A subject could generate motor responses by moving his hand from a central resting position to one of two pads located to the left and the right of the central position. At the core of the stimulus-response component of the task were two predefined rules that associated visual motor instruction cues (MICs) with left- or rightward motor

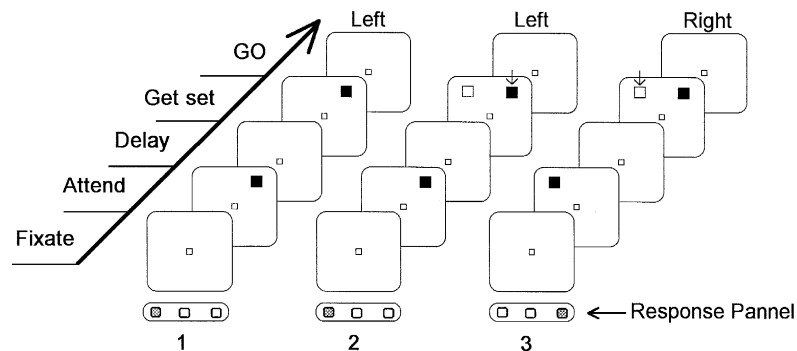


Fig. 1. Schematic representation of the task. Three types of trials are shown (1–3). Within each trial are illustrated the response panel (bottom) with three touch pads (central, left and right), and the status of the video screen at selected points in the trial. The small square at the center of each screen represents the visual fixation point, the larger squares indicate the location of the stimulus. Filled squares indicate a red stimulus, open squares indicate green stimuli. From bottom to top, the five panels show five major periods of the trials. *Fixate* – the subject visually fixates the central square. *Attend* – the spatial attentional cue (SAM) is presented. *Delay* – a delay period. *Get set* – a motor instructional cue (MIC, one or two squares) is presented. If it is ambiguous (two squares) the ambiguity can be resolved by the preceding SAM cue. *GO* – after the go signal (offset of the MIC) the subject responds to either the left or the right touch pad (hatched square on the response panel) based on the decoded value of the MIC. The vertical arrow indicates the square to attend to as identified by the SAM when there are two squares (trials 2 and 3). See text for details of the behavioral paradigm.

responses. Specifically, a red MIC cue is to be associated with a leftward response, and a green MIC with a rightward response. These two rules make up the simple associative learning aspect of the task that could be learned by the associative memory function Eq. (1) described above.

Now, superimposed on this task is an additional component that brings into play the need for attentional context. Imagine an ambiguous MIC that consists of two visual stimuli – a red square at one location and a green square at another. Given this ambiguous MIC, how can the subject know whether to select the green stimulus and respond left, or to select the red stimulus and respond right? In one solution, the ambiguity can be resolved by an attentional context cue that indicates one of the two locations. Specifically, prior to the dual MIC, a single spatial attention

mnemonic (SAM) cue is presented as illustrated in Fig. 1. This cue indicates the location at which the relevant element of the ambiguous MIC will appear. The subject can then select the MIC component at the cued location, discriminate its color and make a limb movement according to the core rules described above. Thus, when MIC consists of two squares at the same time, the subject must interpret the MIC dependent on the *context* established by the SAM cue.

3. Neural coding of context

The context-dependent behavior problem defined above can be reformulated more generally in terms of the opera-

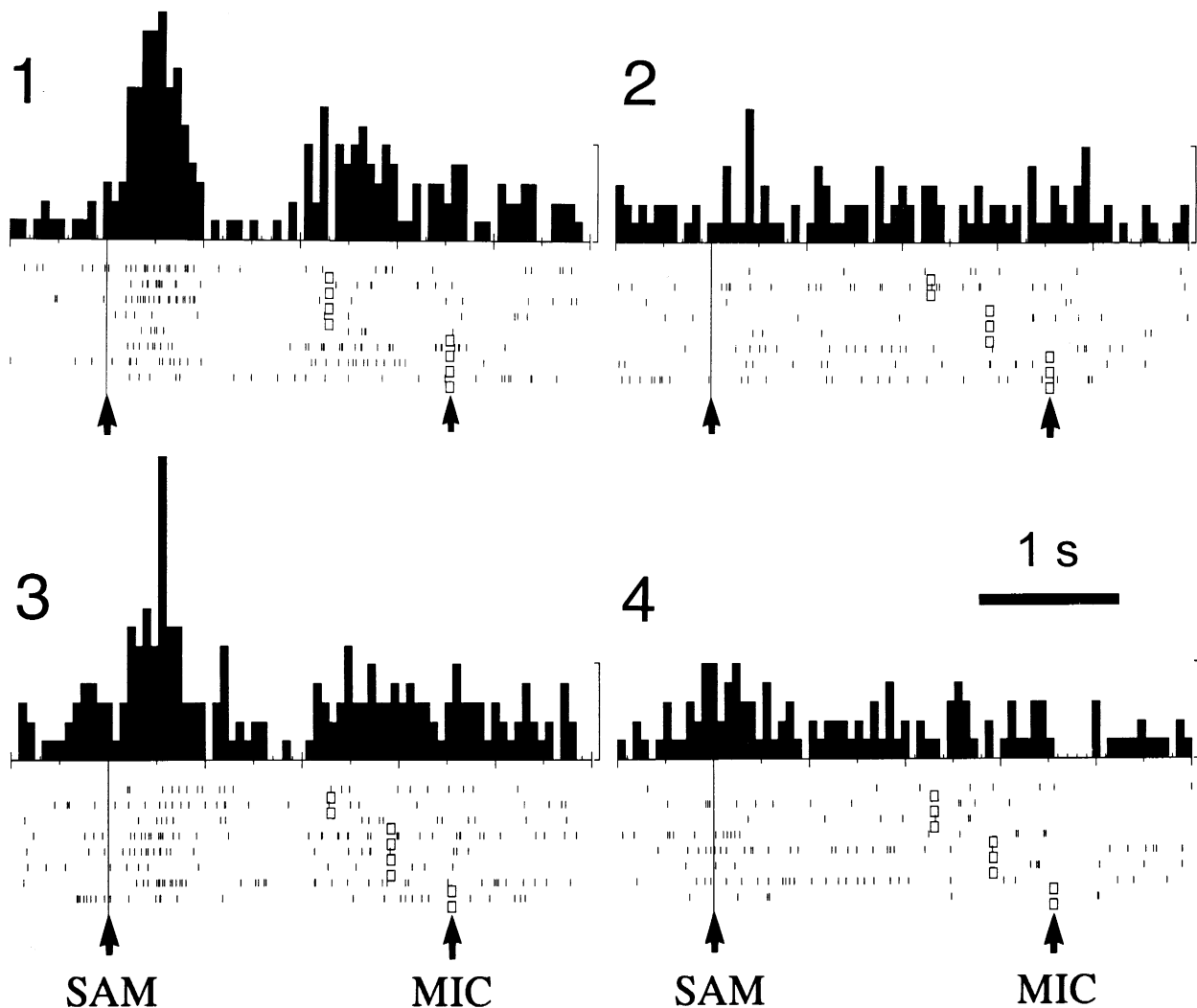


Fig. 2. An example of SAM > MIC activity of a prefrontal cortex neuron. Rasters and histograms of the neuronal activity are represented for four groups of trials (1–4), corresponding roughly to the four behavioral conditions defined in Table 1. In each group, each line of the rasters represents one trial, and each dot corresponds to the time of occurrence of an action potential. The trials are aligned on the onset of the SAM cue (vertical line); the squares indicate the onset of the MIC cue. The histogram in each group represents the discharge frequency of the neuron. 1: SAM and MIC cues were both presented within the lower visual hemifield. 2: the SAM and MIC cues were both presented within the upper hemifield. 3: the SAM cue was within the lower visual field and the MIC was in the lower and upper field. 4: SAM was in the upper field and the MIC was in the upper and lower field. Note the substantial increase in the activity following SAM presentation in the lower visual field in 1 and 3. Vertical scale: 100 imp/s.

tion of a machine that is capable of maintaining an internal state. In response to an input, the machine can make a transition to a new state and/or generate an output, depending on its current state. Thus in the example of Fig. 1, the SAM in trial 2 puts the system in state ξ_1 , while the SAM in trial 3 puts the system in state ξ_2 . The same MIC is used in trials 2 and 3 and the system must learn that in state ξ_1 , MIC1 should generate a leftward response, whereas in state ξ_2 it should generate a rightward response. In applying this formulation to neurophysiological data, we would like to know the mechanism that allows the maintenance of these internal states. In other words, how can a previously presented visual input modify the processing of a subsequent visual input in order to determine the appropriate response?

This could be realized by a structure that meets two conditions: first, it should receive sensory inputs and, second, it should receive recurrent inputs that allow previ-

ous states of activity to influence subsequent sensory processing. The prefrontal cortex is a likely candidate for this role in that it satisfies both these requirements. Fulfilling the first condition, prefrontal cortex receives visual inputs from both the dorsal and ventral visual processing systems (see [7] for review), and thus has direct access to the visual cue information that establishes the behavioral context. Fulfilling the second condition, the prefrontal cortex has two types of recurrent connection that subserve a form of working memory: (1) intrinsic connections between local cortical subdivisions [5]; and (2) extrinsic connections linking the prefrontal cortex through the basal ganglia and thalamus back to the prefrontal cortex [2,24,39,45] (see [7] for review).

In order to evaluate the proposal that prefrontal cortex encodes behavioral context, we can compare the neural activity evoked by the same stimulus when it is presented either as the context cue (SAM) or the instruction cue

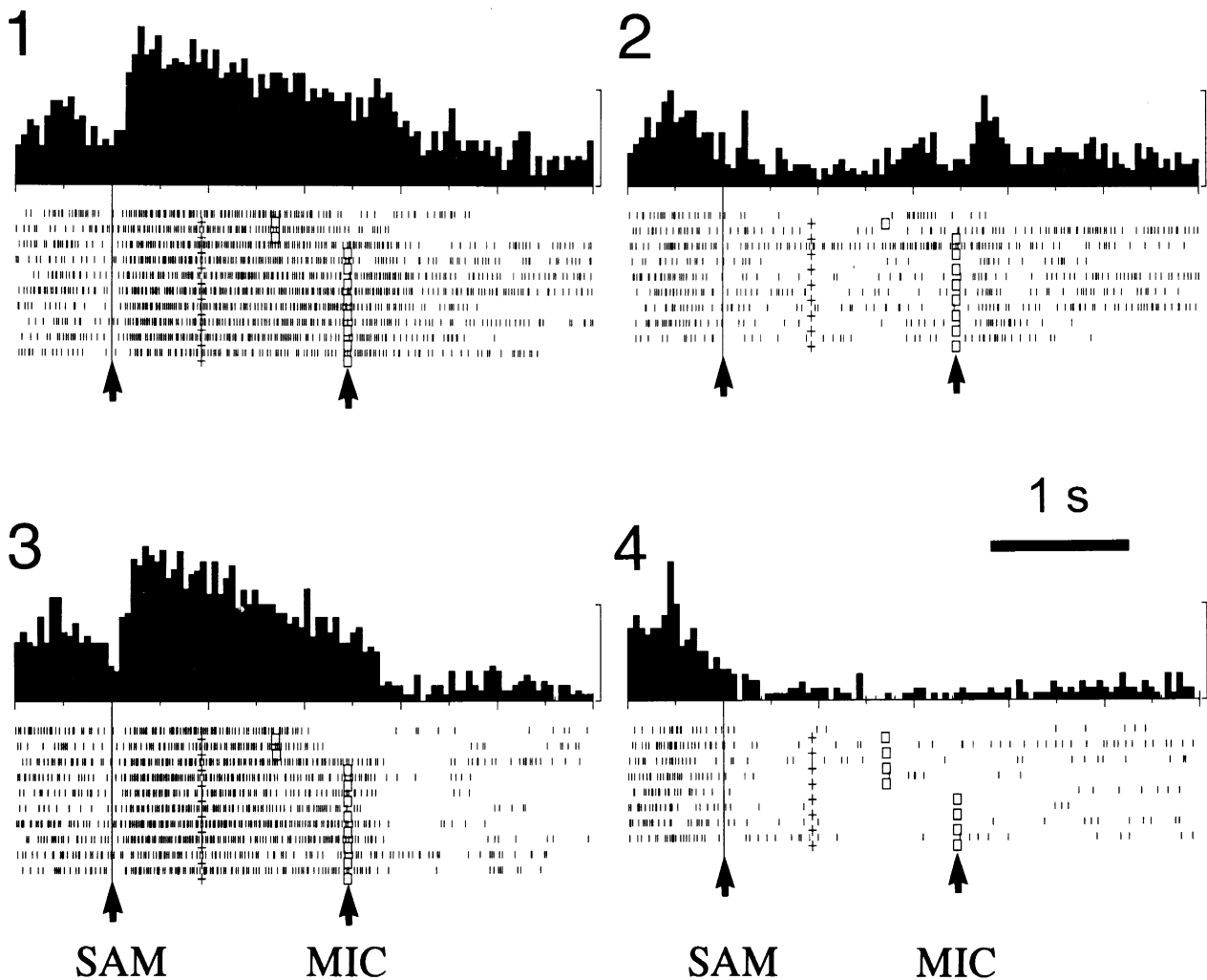


Fig. 3. An example of SAM tonic activity of a frontal cortex neuron. Notation as in Fig. 2. Panels 1–4 correspond to the neural activity of this neuron in the four behavioral conditions defined in Table 1. SAM and MIC cues were presented within the left or right visual hemifields. 1: when SAM and MIC are both presented in the left visual field, the neuron begins a tonic activation that persists until the trial's end. 2: if only MIC is presented in the left field, the neuron begins to discharge shortly after MIC onset. 3: SAM in the left field triggers a tonic discharge that is then cut off when MIC is in the opposite, right field. 4: with SAM and MIC in the right field, there is no discharge. Vertical scale: 50 imp/s.

(MIC), in prefrontal cortex and in other brain regions believed to participate in sensory and motor aspects of this context-dependent task. Thus, on some trials, MIC cues consisting of a single square were presented at the location of the SAM cue to permit observation of the neural activity related to the same physical stimulus as both a context-setting stimulus (SAM) and an instruction stimulus (MIC). A cell that responds selectively to a given stimulus when it appears as the SAM cue but not as MIC is labeled SAM-specific, or SAM > MIC. Such cells can be considered to participate in establishing the internal state or context in which the subsequent MIC is interpreted. Examples of neurons recorded in the study of Boussaoud and Wise [8,9] are displayed in Fig. 2, Fig. 3 and Fig. 4 to illustrate the most salient properties of frontal neurons in the context-dependent SAM-MIC task.

The activity of a typical SAM-specific cell is displayed in Fig. 2. This cell responds to the SAM when it appears in

the lower visual field (Fig. 2_{1,3}), but does not respond to the same stimulus when it appears as MIC (Fig. 2_{2,4}). Fig. 3 presents a related cell termed SAM tonic. This neuron displays a tonic discharge for the SAM when it appears in the left visual field (Fig. 3_{1,3}) and continues to discharge until the end of the trial if the SAM and MIC are the same (Fig. 3₁). However, if MIC is different from SAM, the tonic discharge is abruptly terminated shortly after MIC onset (Fig. 3₃).

Cells for which a phasic response is more purely stimulus driven, independent of whether the stimulus is SAM or MIC, are labeled SAM = MIC. An example of this type of response is displayed in Fig. 4. This cell responds to stimuli presented in the right visual field, independent of whether that stimulus is SAM or MIC.

In contrast to SAM-related activity, cells have also been recorded that display selective responses for a stimulus when it is MIC as opposed to when the same stimulus

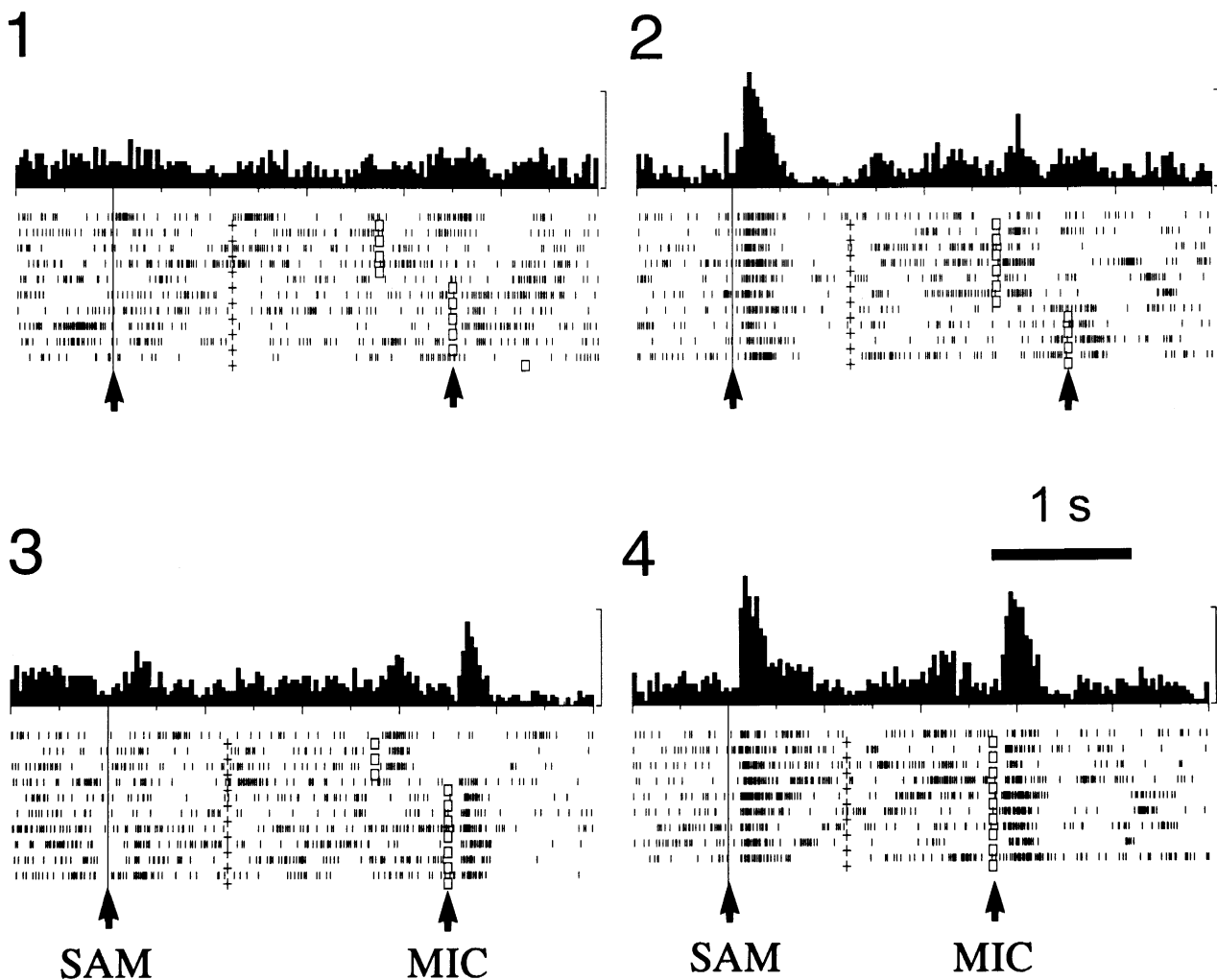


Fig. 4. An example of SAM = MIC activity of a prefrontal cortex neuron. Notation as in Fig. 2. The “+” signs represent SAM offset. Panels 1–4 correspond to the neural activity of this neuron in the four behavioral conditions defined in Table 1. 1: when both SAM and MIC are in the left field, there is no activity. 2: SAM in the right field triggers activity in the neuron, while there is no response to MIC in the left field. 3: in contrast, SAM left generates no response, while MIC right activates the neuron. 4: when both SAM and MIC are in the right field, both trigger phasic discharge from this neuron. Vertical scale: 100 imp/s.

serves as a SAM. Their response to the MIC is dependent on the SAM that precedes it, termed a movement effect [9]. That is, their activity reflects the context-dependent decoding of the meaning of the MIC.

The majority of task-related neurons recorded in the primate prefrontal cortex discharge in relation to SAM cues [8]. In the proposed framework, these cells encode the context – established by the SAM cue – in which the subsequent MIC is interpreted. In PFC 69% of the cells are of the SAM > MIC or SAM = MIC types. In contrast, a smaller percentage (31%) of the PFC units display the movement effect that reflects the output side, i.e., the result of the context-dependent decoding of the MIC. While the predominance of SAM-related activity in the prefrontal cortex indicates that this region participates more in the coding of behavioral context than in coding or selection of action, the opposite is the case for the striatum. The majority of striatal neurons recorded in this task (60%) display activity that is related to the MIC and that reliably predicts the upcoming movement, 39% are SAM > MIC, and 1% SAM = MIC [26]. In summary, these neuronal responses indicate that SAM-related processing in frontal cortex participates in establishing the internal state, or context, in which the subsequent MIC can be interpreted, processing that occurs more predominantly in the striatum. The mixture of SAM- and MIC-related activity in both areas indicates, however, that this functional division is graded rather than absolute.

The prefrontal cortex has also been shown to participate actively in the representation of context in sequential motor tasks. Barone and Joseph [6] studied prefrontal cortex neurons in primates that had been trained to observe and remember a sequence of lighted push buttons and then reproduce the sequence by pressing the buttons in the order they were initially presented. Individual PFC neurons encode components of the spatial locations of targets, their temporal order in the sequence, and their “touched” or “not yet touched” status. The ensemble of PFC unit activity thus encodes an ongoing representation of the internal state, or context, of the sequence input and execution that changes as each successive element of the sequence is first seen and then reproduced. These results will be examined in more detail below.

4. Materials and methods

Based on the results reviewed above we propose the hypothesis that recurrent fronto-striatal networks provide the architectural basis for encoding context, and thus for allowing context-dependent activity. According to this hypothesis, these recurrent networks can take at least two forms: the first is made up of cortico-cortical connections within the frontal cortex and the second is made up of connections from cortex to striatum and the output nuclei of the basal ganglia, to the thalamus and back to the cortex

[2,5,19,24,39,45] (see [7] for review). Our prediction is that a system based on these architectural constraints should be sufficient for learning context-dependent behavior. In order to test this prediction in a strong sense, i.e., to demonstrate that other systems are not necessary, one might work with a neurophysiological preparation that eliminates all other candidate systems that might contribute to learning and memory. Such a preparation is difficult to implement at present. An alternative is to use a model that is made up of only these fronto-striatal networks, and demonstrate that this “reduced preparation” is capable of the desired performance. We have recently developed such a model for the study of fronto-striatal function in sensorimotor se-

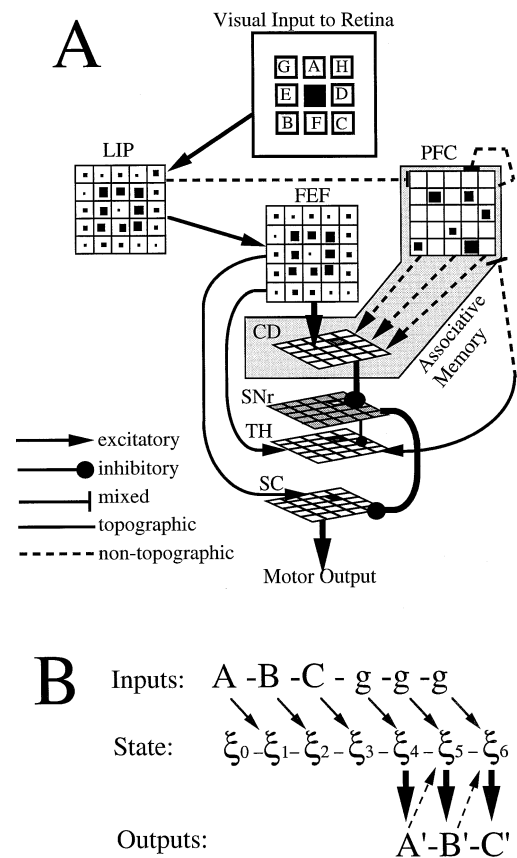


Fig. 5. Sensorimotor sequence learning model. A: model architecture. Each of the structures are 5×5 arrays. Sequences of spatial target locations (A–H) are presented in the (5×5) retina input array. During output saccade generation in the superior colliculus (SC), continuous inhibition of SC by substantia nigra (SNr) is temporarily interrupted by caudate (CD) inputs. CD saccade-related cells are influenced by topographic projections from frontal eye fields (FEF), and also by modifiable, non-topographic projections from the prefrontal cortex (PFC). PFC combines visual input from LIP (via W^{L-P} synapses), motor efferent copy from SC (via W^{S-P} synapses), and self-input (via W^{P-P} synapses) in order to generate a time varying sequence of internal states for each presaccade period in the sequence reproduction task. These states or patterns of activity become associated with caudate activity for the correct saccade by reinforcement learning mechanism that monitors responses and strengthens state-response connections for correct responses and weakens them for incorrect responses. B: schematic representation of sequence reproduction. See text (From [16]).

quence learning, and we thus proceed with a test of our hypothesis using this model.

4.1. A sequence learning model based on fronto-striatal neuro-architecture

The model [14] displayed in Fig. 5 is based on the well characterized architecture of the corticostriatal oculomotor system [15] and was developed to explain the results of prefrontal coding of sensorimotor sequences by Barone and Joseph [6]. In the model, visual input to the 2-D (5×5 element) retina produces motor output in the form of activation of the superior colliculus (SC), a 2-D map of saccadic eye movements. In the simplest case, a visual input to the retina (activation of one of the 5×5 elements) produces activation in the lateral intraparietal area (LIP) of the posterior parietal cortex [4] which then activates an oculomotor frontal eye field (FEF) [3,42]. FEF activates SC directly by an excitatory projection [41], and indirectly by disinhibition through the basal ganglia [11,21,40]. SC is under tonic inhibition from the substantia nigra pars reticulata (SNr), and this inhibition can be temporarily and selectively removed when the caudate nucleus (CD) of the striatum inhibits SNr as a consequence of activation of CD by FEF [11,22,40]. Thus, the striatum is an anatomical structure that can allow selective control of motor output choices, as suggested by Rolls and Williams [37].

In this simplest case of visually guided saccadic eye movements to a single target, the redundancy between FEF's direct and indirect (via CD and SNr) paths to the motor output in SC seems unnecessary. In the sequence reproduction task, however, at each step in the sequence, the correct one of several targets (simultaneously presented to the retina) must be chosen. In this case where a choice must be made between several targets, the brain might use PFC's selective modulation of CD to activate only the part of CD that corresponds to the correct target, ignoring the others. Indeed PFC has the required information that uniquely encodes each successive state in the sequence [6] that can be used to selectively activate CD for the correct response at each successive step.

Based on evidence of learning-related plasticity in synapses connecting cortex to caudate [10,43] we implemented an associative memory in modifiable synapses between PFC and CD [14]. The neurotransmitter dopamine (DA) is released in the striatum following reward or events that predict reward and participates in corticostriatal plasticity [10,36,38,43]. We thus use a reinforcement learning rule so that each time a correct response is made, synapses are strengthened between the state encoding elements that are active for the current state in PFC and the units in CD that participate in the generation of the correct movement.

The anatomical basis for this associative memory exists in the projection from prefrontal cortex to striatum [39]. Kermadi and Joseph [27] recorded single units in the striatum whose activity reflected this conditional associa-

tion between sequence state and associated motor responses, in agreement with previous findings that striatal activity often encodes associations between internal state and behavior [37].

The details of the model have been described previously [14,16]. Here we only summarize the most important features. Each of the layers displayed in Fig. 5A is modeled as a 5×5 array of leaky integrator neurons. Eq. (3) describes how the internal state of the system is updated by sensory inputs from the lateral intraparietal area (LIP), motor responses from SC (represented as routed through thalamus), and a recurrent input from PFC and thalamus (TH). The cortico-cortical connections W^{P-P} are mixed inhibitory and excitatory (corresponding to intrinsic glutamatergic and GABAergic cortico-cortical synapses), yielding the situation that a given unit's sensory response may be modulated (+ or -) by the occurrence of a previous event. These recurrent inputs thus allow the current state to influence the encoding of subsequent inputs, providing a context-dependent state transition mechanism. Eq. (4) describes how the sensorimotor input to CD from FEF is biased by PFC (via adaptive W^{P-C}) to produce the learned motor response in CD. Eq. (5) describes how connections between PFC and CD are modified during learning. When a response is evaluated, the connections between units encoding the current state in PFC, and units encoding the current response in CD, are modified as a function of their rate of activation and learning rate R . R is positive for correct responses (Learning Rate) and negative for incorrect responses (Forgetting Rate). An effective learning strategy uses Learning Rate > Forgetting Rate for initial training and then reduces values for both, with Forgetting Rate > Learning Rate for final training [16]. Note that the total projection strength or synaptic weight for each unit in PFC is conserved by normalization (not shown, see [14,16]). This avoids saturation due to continuous growth of the weights. The function $f(x)$ generates a non-linear output of its integrated inputs to x , where x is treated as a leaky integrator.

$$\begin{aligned} \text{PFC}(t + \Delta t) = & f(\text{LIP}(t) * W^{L-P} + \text{PFC}(t) * W^{P-P} \\ & + \text{SC}(t) * W^{S-P} + \text{TH}(t)) \end{aligned} \quad (3)$$

$$\text{CD}(t + \Delta t) = f(\text{FEF}(t) + \text{PFC}(t) * W^{P-C}) \quad (4)$$

$$W_{ij}^{P-C_i}(t + \Delta t) = W_{ij}^{P-C}(t) + R * \text{PFC}(t)_i * \text{CD}(t)_j \quad (5)$$

Fig. 5B shows the progression in time of the reproduction of sequence A-B-C. In all simulations, a given stimulus such as A in A-B-C is presented to the model as activation of a single element in the input array. The model PFC starts in an initial state of activity ξ_0 . Presentation of the first visual input A drives PFC to a new state, ξ_1 . Presentation of input B drives PFC from ξ_1 to ξ_2 . Then presentation of input C drives PFC from x_2 to x_3 (Eq. (3)). Presentation of the first go signal (g = illumination of A, B and C simultaneously) drives the model to state ξ_4 and

triggers the model to produce a motor output (Eq. (4)) by retrieving from the associative memory the output currently associated with state ξ_4 (dark vertical arrow). This information originates in the layer CD, corresponding to the caudate nucleus of the striatum. This activity in CD serves as a bias that influences the selection of the correct response by a winner-take-all mechanism in the layer SC, corresponding to the superior colliculus.

If the retrieved output is incorrect, the offending association between state encoding cells in PFC and motor response cells in CD is weakened (Eq. (5)), reducing the probability that the same choice will be made again. If the output is correct, A' , this association is strengthened, and the system moves on to state ξ_5 which retrieves B' from the associative memory by the same process, and so on (Eq. (5)). By this trial and error learning, this system will learn the state-output associations (indicated by the heavy arrows in Fig. 5B) and, thus, will reproduce spatiotemporal sequences as the concatenation of state-response associations. Once a trial has been successfully completed, or if an error is made, the simulator terminates that trial.

4.2. Sequence reproduction capability

Dominey et al. [14] tested the model described above in the same sequence learning task used with primates by Barone and Joseph [6]. While the model is able to learn and execute the six 3-element sequences, it also reproduces the same kind of context-dependent properties in the simulated PFC neurons as seen in the neurons of primate prefrontal cortex. Fig. 6 shows that in both the model and the primate, neurons are found that respond with a spatial preference for one of the three targets, but only when it appears at a given rank in the sequence (first, in this example).

Thus, in the analysis of Dominey et al. [14] it was demonstrated that this model not only reproduced the behavior of sequence learning and reproduction seen in primates, but also the single unit activity of PFC neurons during the sequence reproduction tasks (Fig. 6). It was later demonstrated that in addition to learning simple 3-element sequences, the model was also capable of learning and discriminating between complex sequences, such as $S: ABCDABCEABCFABCGABCH$ [16]. This sequence is complex because the repeated subsequence ABC does not have a unique successor. In order to learn a complex sequence, the system must be capable of encoding and exploiting the context established by the element four places behind. This capacity is an indication that the model developed for sequence learning displays inherent context encoding capabilities, as it can reproduce the context-dependent successors to ABC in the sequence S .

4.3. Simulation of fronto-striatal context-dependent processing

While the model thus appears to display some context-dependent capabilities, we wanted to determine if it could

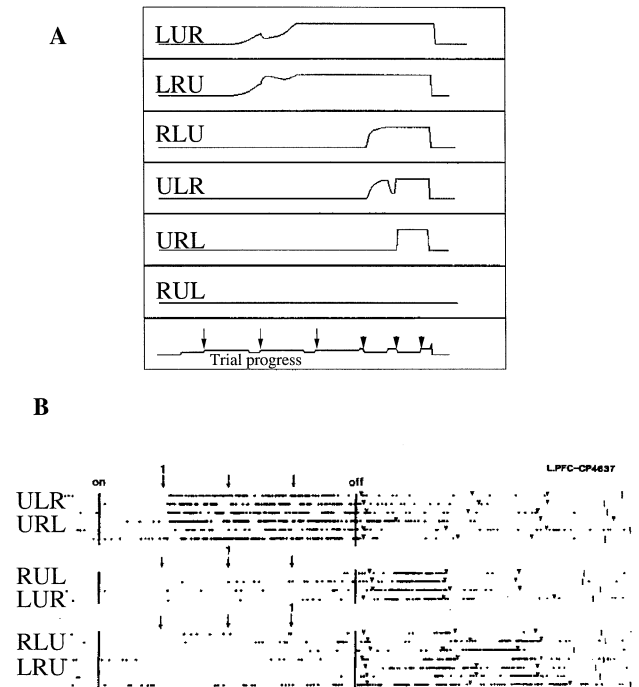


Fig. 6. Sequence context encoding in simulation and monkey. Comparison of simulated and real neural activity encoding sequence context. L, U and R stand respectively for the left, upper and right of three lighted push-button targets. Activity of the typical simulated and real neurons is displayed for each of the possible three element sequences. A: simulated neuron. Presentation of three successive targets during sequence observation phase marked with long arrows. Three successive go signals (presentation of all three targets simultaneously) and responses during reproduction phase marked with short arrows on line labeled "trial progress". Note that this unit becomes active during the presentation of the left target, but only when it appears first in the sequence, not second or third, thus encoding both the spatial location of the element and its order. B: neuron from PFC recorded by Barone and Joseph [6]. Vertical arrows indicate target presentation, and triangles following the vertical bar indicate go signal and response. This neuron responded to presentation of the upper target, but only when it appeared first in the sequence, thus encoding both location and temporal order. (From Dominey et al. [14].)

indeed learn the correct response choices for identical visual stimuli based on a context formed by a previous visual stimulus, as in the task of Boussaoud and Wise [8,9]. In order to determine if the model is sufficient for this type of context-dependent learning, we developed a reduced version of the context-dependent task in which the color dimension of the task was eliminated, as color is not represented in the model. We then attempted to train the model in this context-dependent task. In the modified version of the task, SAM and MIC can be presented in positions A or B, by activating single elements in the upper left and upper right visual fields, respectively, of the 5×5 input array. Later, responses are to be directed to either C or D, which are presented simultaneously in the lower left and lower right fields, respectively. For example, the MIC A corresponds to response C if SAM was A, and response D if SAM was B. The complete set of behavioral context-dependent contingencies is presented in

Table 1

Task contingencies for the four conditions of the simulated context-dependent task

Condition	Context cue (SAM)	Instruction cue (MIC)	Response
1	A	A	C
2	B	A	D
3	A	B	D
4	B	B	C

Table 1. In a given trial, the SAM is presented for a fixed period (corresponding to 40 network update cycles or simulation time steps (STS)). Following an equivalent delay (40 STS) after SAM offset, the MIC is then presented for the same duration. After a 40 STS delay, elements C and D are then simultaneously presented, forming the “go signal,” and the model must respond with a forced choice. While this reduced version of the task eliminates one degree of freedom from the original task, i.e., the color coding of direction choice, the essential property of interest is retained. That is, the significance of the MIC to the response of the network is completely determined by the context established by the SAM that precedes it.

Training proceeds based on the reinforcement learning rule described in Eq. (5). That is, for correct responses, connections (W^{P-C}) between active elements in PFC and CD are strengthened. This increases the probability that the next time the same context-dependent activity pattern is present in PFC the same (correct) choice will be made via the PFC influence on CD. Likewise, on error trials, the involved connections (W^{P-C}) are weakened, reducing the probability of a subsequent error in the same context.

5. Simulation results

The results will be presented in three parts. First, we will consider the behavioral aspect, that is, can the model learn to correctly interpret ambiguous instruction cues based on the context cues that precede them? Next, we will compare the distribution of neurons coding context vs. behavior in the model and primate cortex and striatum. The point of this comparison is to determine if the two systems (model and primate) resolve this context-dependent problem based on similar functional organization of the frontostriatal system. Finally, we will make some detailed comparisons between individual units in the primate and model prefrontal cortex, in order to illustrate how context appears to be similarly coded over time in these systems.

5.1. Behavior

Eleven instances of the model were created by using different starting values for the connections specified in

Eq. (3), Eq. (4) and Eq. (5) (W^{P-C} , W^{P-P} , W^{S-P} , W^{L-P}). The 11 models were trained to 100% correct performance by the procedure described above. In all cases, error-free performance was attained within 500 mixed trials of the four conditions or approximately 125 trials per condition. By this observation, the first requirement of our hypothesis is met. That is, from a purely behavioral point of view, a model that encodes behavioral context in recurrent networks is capable of learning the context-dependent task. It learns the behavioral significance of instruction cues as a function of the preceding context cues. In order to satisfy the second requirement we must now consider the manner in which this response was achieved.

5.2. Quantitative comparison of context and behavior coding in model and primate

If the model resolves context dependencies in a manner similar to that of the primate brain, we should see similar coding of context and behavior in model and primate neurons. In particular, as in the primate, we would expect to see a greater percentage of context coding neurons in the simulated frontal cortex, with a greater percentage of behavior coding neurons in the simulated striatum. For the model, this is because in the recurrent PFC network, context information has not yet become associated with behavioral motor responses, which takes place in the striatum via modifiable corticostriatal synapses.

The 25 PFC cells from each of the 11 models were pooled together to form a group of 275 units. Of these, 119 were task-related, while the remaining units were either never activated, or non-specifically activated. Among the 119 units, 65% responded preferentially to SAM, 23% with equal SAM and MIC response, and 12% with a preference for MIC. This distribution of response types is in good correspondence with that found in the primate, and the comparison between physiological and simulated activity revealed some rather striking similarities. Likewise, of the 275 striatal cells pooled from the 11 models, 36 were task-related. Of these 28% responded preferentially to SAM, 11% with equal SAM and MIC response, and 61% with a preference for MIC. As in the case of the prefrontal cortex, this distribution of response types is in good correspondence with that found in the primate.

These results are summarized in Fig. 7, where they are also compared with the same data from primates. We see that for both the model and the primates, in the frontal cortex there is a dominant neural coding of the behavioral context as opposed to the specific behavior to be produced. Again, in both the model and primates, this trend is reversed in the striatum.

5.3. Qualitative comparison of context and behavior coding in model and primate

Fig. 8 illustrates a neuron with phasic activity specifically related to the occurrence of the SAM cue at a

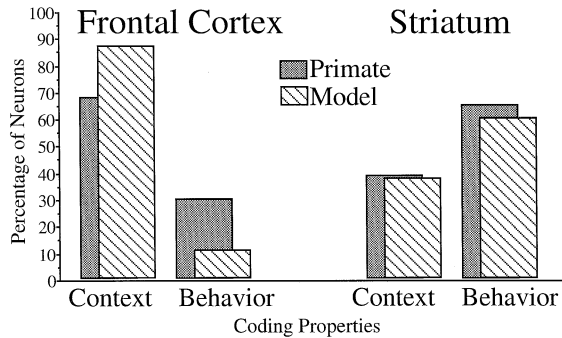


Fig. 7. Comparison of task-related neuronal responses in the model and primate frontal cortex and striatum. Primate cortex data from Boussaoud and Wise [8] and striatal data from Kermadi and Boussaoud [26]. Responses that were classified (in [8] and [26]) as SAM > MIC or SAM = MIC are considered to encode context, as their response is correlated with the context cue (SAM) independent of the behavioral response. Those neurons classified MIC > SAM are considered to encode behavior as their activity directly predicts the upcoming behavioral response. We observe that in both the model and the primate, frontal cortical neurons participate more predominantly in the coding of context than in the behavioral outcome, with the reverse holding in the striatum.

specific location. No such activity followed the presentation of the same stimulus as an instructional cue (MIC), nor with a SAM cue at another location in space. This type of neuronal activity strikingly resembles that recorded from the prefrontal cortex of primate, as displayed in Fig. 2. A similar example of SAM-specific activity found in a simulated PFC neuron is shown in Fig. 9. As in the previous case, this neuron is active following a SAM cue that appeared at a given location, but the activity is tonic in that it remains at a high level of activation until the MIC cue is presented. Also note that this neuron displays activity following the MIC cue that appears at the location for which the neuron responds to the SAM cue. Thus, the

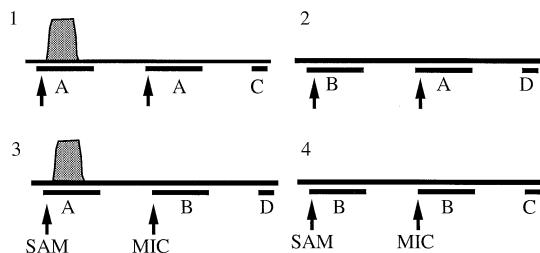


Fig. 8. Representative examples of neural responses displaying SAM > MIC activity in the simulated PFC. Same presentation format as in Fig. 2, Fig. 3 and Fig. 4. Duration of SAM and MIC presentation (corresponding to 40 simulation time steps) indicated by labeled horizontal bars. The activity of this simulated neuron is displayed in the four conditions defined in Table 1. Recall that A and B are stimuli in the upper left and right fields, respectively, and that C and D are responses to the lower left and right fields, respectively (corresponding to the primates' responses to the left and right touch-pads). In each condition, the neural activity is displayed above, and the time course of the SAM, MIC and response displayed below. The neuron discharged shortly following SAM that appeared in the left hemifield but not to the identical MIC presented within that hemifield, nor to the SAM or MIC presented in the right hemifield. Compare with Fig. 2.

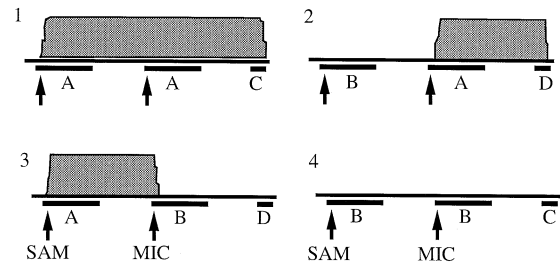


Fig. 9. SAM tonic response in a simulated PFC neuron. Same format as Fig. 8. The neuron discharged shortly following SAM in the left hemifield, remained active if MIC was in the same hemifield and stopped if not. The neuron also became active for MIC in the left hemifield independent of SAM's location. Compare with Fig. 3.

neuron is activated by the presence of a stimulus within a given part of space, independent of whether the stimulus appeared first, as the context cue, or second, as the instruction cue. Again, a parallel can be drawn between the coding properties of our simulated neurons and those in the primate frontal cortex, by comparing these simulated task-related responses with those of the real prefrontal neuron in Fig. 3.

Fig. 10 shows a neuron that displays a SAM = MIC response type. Here, when a cue appears at location B, the neuron responds independent of whether that cue is a SAM or a MIC. This neuron is similar to the previous example in that it does have a visual receptive field, though the responses in this case are more phasic, whereas those in the previous case are more tonic. This neuron's activity resembles that of the real frontal neuron in Fig. 4.

As mentioned above, neuronal activity preferentially related to MIC cues is rarely found in PFC. Fig. 11 illustrates one example of such a case where the activity was specifically related to the onset of the MIC cue at a given location. In addition, this MIC-related activity is observed only if that MIC cue was preceded by a SAM cue at a different location. Thus, MIC-related activity is dependent upon the location of a previously presented SAM cue, and thus on the context-dependent behavioral significance. Interestingly, this type of neuron was just as infrequent in the primate prefrontal cortex as in the model PFC.

This set of example simulated neuronal responses and their correspondence with neuronal activity recorded in the

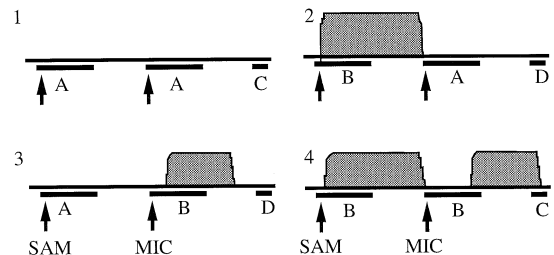


Fig. 10. SAM = MIC activity in a simulated PFC neuron. Same format as Fig. 8. This neuron discharged for MIC and SAM equally when they appeared in the right hemifield. Compare with Fig. 4.

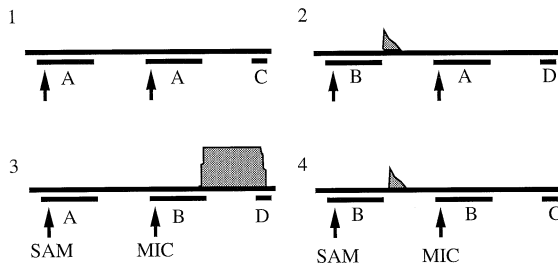


Fig. 11. MIC activity in a simulated PFC neuron. Same format as Fig. 8. The cell discharged only to the MIC in the right hemifield and only when it was preceded by SAM in the left hemifield. This shows both a stimulus effect and movement effect.

primate brain suggest at least some degree of similarity in the way that these two systems code context and its behavioral significance.

6. Discussion

In human and non-human primates, the prefrontal cortex participates less in the direct processing of sensory and motor parameters of behavior than in the more abstract manipulation of these parameters based on previously established plans or contexts [18,19,34]. This suggests that the prefrontal cortex might play a special role in the representation of behavioral context in order to correctly guide subsequent context-dependent behavior. Adopting such a position, we are then obliged to specify a hypothesis for the neural mechanisms by which the prefrontal cortex might realize this function.

The simulation results reported in this study and their correspondence with neural activity in the primate prefrontal cortex are in agreement with our hypothesis: behavioral context is encoded in recurrent connections of the fronto-striatal system in order to influence the processing of subsequent brain events, including responses to sensory inputs, in a context-dependent manner. In this sense, the prefrontal cortex appears to participate in the more general function of maintaining internal state in the classic sense of finite state machines. We propose that recurrent networks, such as the frontal cortex, encode context in that stimulus-driven responses are influenced by previous context-setting stimuli. These networks are thus sufficient for learning the context-dependent task described above. In the present simulation, the initial attentional cue established a context (i.e., a state of activity in PFC) in which the second instructional cue is “interpreted” and the resulting state of activity becomes associated, by learning, with the correct response. The finding of neurons in the model’s PFC that generate context-dependent responses similar to those recorded in primate PFC suggests that the capacity for context-dependent behavior is based in part on the organization of recurrent networks in the fronto-striatal system.

Likewise, the shift from prefrontal cortex to striatum in their respective biases for coding context vs. response selection in the primate and model suggests a dual role for striatum. While this structure participates in the recurrent, context coding loop to prefrontal cortex via the thalamus, it also participates in motor response generation via motor circuits that project to the supplementary motor area and primary motor cortex, and to the superior colliculus [2].

6.1. Functional relation between sequence- and context-related processes

A related point in the general domain of context-dependent behavior is that there is a certain degree of functional equivalence between the neural activity encoding context for sequence learning [6] and for the context-dependent task [8,9]. Comparing real vs. simulated neural activity in Fig. 2 vs. Fig. 8, and Fig. 6B vs. Fig. 6A, respectively, we see two distinct examples of simulated and real neurons that display selectivity for a given stimulus, but only when that stimulus appears in a particular temporal position in the task sequence. Though the physiological data from Fig. 2 and Fig. 6B come from different experiments, they share the similarity that the representation of external events is dependent on their serial order, and that this dependence is reflected in the neural activity. The fact that the same model can reproduce these two physiological results argues for a shared mechanism. While we do not attempt to state that context-dependent behavior and sequence learning are functionally equivalent, it is nevertheless clear that they share certain features, especially when the context is defined by a stimulus that precedes the instruction stimulus in a temporal sequence.

The model used in the present simulation was designed to test the capacity to generate a sequence of saccadic eye movements. However, the basal ganglia output signals are not directed only to the oculomotor areas of the brain (e.g. [1,2]). Striatal output signals have been suggested to be organized into multiple, partially segregated parallel pathways including the “cognitive” pathway terminating in prefrontal cortex, the “motor” pathway terminating in premotor areas, and the “oculomotor” pathway in the FEF (and SEF). Houk and Wise [23] have suggested that the principal neuron mediating the selectivity of these recurrent loops is the striatal medium spiny neuron, which is thought to act as a bistable pattern recognizer. Through the motor pathway, basal ganglia-thalamocortical signals can influence the skeletomotor system, especially the supplementary motor area (SMA) and the dorsal premotor cortex (PMd). Interestingly, in comparison to the PFC, PMd contains the opposite distribution of neuronal properties under the same task [8,9]. The majority of PMd cells are active following MIC cues, whereas in the PFC, the cells are preferentially active with SAM. It can be postulated, thus, that PMd is a further stage in sensorimotor processing where context-dependent action is selected. Context

information can get to the PMd either directly from the PFC ([7] – review) or via the fronto-striatal loop [1,2,18,31].

6.2. Related models

The use of recurrent connections has been explored as a fruitful method to encode sequential context as demonstrated in a number of recurrent sequence learning models ([17,25,32,35], see [33] for a review). It is of interest to note that our current model differs from these others in at least one fundamental fashion in that it learns by a simple reinforcement mechanism, rather than by error gradient calculation mechanisms such as backpropagation.

Independent of the specific architecture, context-dependent behavior implies the need to rely on, and thus somehow to encode, the history of previous events in order to respond correctly or predict future events. Indeed, in the domain of complex sequence learning, where the necessary context is not just from the previous element, but possibly elements several places behind, both recurrent networks [12] and alternative architectures [13,28,44] have been shown to accommodate, up to certain limits, these contextual constraints. These studies support the idea that sequence learning is a specific example of the more general class of context-dependent learning problems.

6.3. Limitations

We note that there are clearly certain limitations to the simulation of fronto-striatal function as presented here. The model does not address a number of brain functions that are likely to be involved in context-dependent behavior. However, this study demonstrates that an adaptive recurrent system is sufficient for allowing context-dependent behavior, and that this recurrent system provides a working model of the fronto-striatal system and its role in context-dependent behavior.

Acknowledgements

P.F.D. is supported by the Fyssen Foundation (Paris). We gratefully acknowledge the insightful comments of Steve Wise on a previous version of this manuscript.

References

- [1] G.E. Alexander, M.D. Crutcher, Functional architecture of basal ganglia circuits: neural substrates of parallel processing, *Trends Neurosci.* 13 (1990) 266–271.
- [2] G.E. Alexander, M.R. DeLong, P.L. Strick, Parallel organization of functionally segregated circuits linking basal ganglia and cortex, *Annu. Rev. Neurosci.* 9 (1986) 357–381.
- [3] R.A. Andersen, C. Asanuma, M.W. Cowan, Callosal and prefrontal associational projecting cell populations in area 7a of the macaque monkey: a study using retrogradely transported fluorescent dyes, *J. Comp. Neurol.* 232 (1985) 443–455.
- [4] S. Barash, R.M. Bracewell, L. Fogassi, J.W. Gnadt, R.A. Andersen, Saccade-related activity in the lateral intraparietal area. II. Spatial properties, *J. Neurophysiol.* 66 (1991) 1109–1124.
- [5] H. Barbas, D.N. Pandya, Architecture and frontal cortical connections of the premotor cortex (area 6) in the rhesus monkey, *J. Comp. Neurol.* 286 (1989) 353–375.
- [6] P. Barone, J.-P. Joseph, Prefrontal cortex and spatial sequencing in macaque monkey, *Exp. Brain Res.* 78 (1989) 447–464.
- [7] D. Boussaoud, G. Di Pellegrino, S.P. Wise, Frontal lobe mechanisms subserving vision-for-action versus vision-for-perception, *Behav. Brain Res.* 72 (1996) 1–15.
- [8] D. Boussaoud, S.P. Wise, Primate frontal cortex: neuronal activity following attentional vs. intentional cues, *Exp. Brain Res.* 95 (1993) 15–27.
- [9] D. Boussaoud, S.P. Wise, Primate premotor cortex: effect of stimulus and movement, *Exp. Brain Res.* 95 (1993) 28–40.
- [10] P. Calabresi, R. Maj, A. Pisani, N.B. Mercuri, G. Bernardi, Long-term synaptic depression in the striatum: physiological and pharmacological characterization, *J. Neurosci.* 12 (1992) 4224–4233.
- [11] G. Chevalier, S. Vacher, J.M. Deniau, M. Desban, Disinhibition as a basic process in the expression of striatal functions. I. The striato-nigral influence on the tecto-spinal/tecto-diencephalic neurons, *Brain Res.* 334 (1985) 215–226.
- [12] A. Cleeremans, *Mechanisms of Implicit Learning*, MIT Press, Cambridge, MA, 1993.
- [13] S. Dehaene, J.-P. Changeaux, J.P. Nadal, Neural networks that learn temporal sequences by selection, *Proc. Natl. Acad. Sci. (USA)* 84 (1987) 2727–2731.
- [14] P.F. Dominey, M.A. Arbib, J.P. Joseph, A model of cortico-striatal plasticity for learning associations and sequences, *J. Cogn. Neurosci.* 7 (1995) 311–336.
- [15] P.F. Dominey, M.A. Arbib, A cortico-subcortical model for generation of spatially accurate sequential saccades, *Cereb. Cortex* 2 (1992) 153–175.
- [16] P.F. Dominey, Complex sensory-motor sequence learning based on recurrent state-representation and reinforcement learning, *Biol. Cybern.* 73 (1995) 265–274.
- [17] J.L. Elman, Finding structure in time, *Cogn. Sci.* 14 (1990) 179–211.
- [18] J.M. Fuster, *The Prefrontal Cortex*, 2nd ed., Raven Press, New York, 1989.
- [19] P.S. Goldman-Rakic, Circuitry of primate prefrontal cortex and regulation of behavior by representational memory, in: *Handbook of Physiology*, vol. 9, The Nervous System, American Physiological Society, Bethesda, MD, 1987, pp. 373–417.
- [20] A.M. Graybiel, Building action repertoire: memory and learning functions of the basal ganglia, *Curr. Opin. Neurobiol.* 5 (1995) 733–741.
- [21] O. Hikosaka, M. Sakamoto, S. Usui, Functional properties of monkey caudate neurons. I. Activities related to saccadic eye movements, *J. Neurophysiol.* 61 (1989) 780–798.
- [22] O. Hikosaka, R.H. Wurtz, Modification of saccadic eye movements by GABA-related substances. II. Effects of muscimol in monkey substantia nigra pars reticulata, *J. Neurophysiol.* 53 (1985) 292–308.
- [23] J.C. Houk, S.P. Wise, Distributed modular architectures linking basal ganglia, cerebellum, and cerebral cortex: their role in planning and controlling action, *Cereb. Cortex* 2 (1995) 95–110.
- [24] I.A. Ilinsky, M.L. Louandet, P.S. Goldman-Rakic, Organization of the nigrothalamocortical system in the rhesus monkey, *J. Comp. Neurol.* 236 (1985) 315–330.
- [25] M.I. Jordan, Learning to articulate: sequential networks and distal constraints, in: M. Jeannerod (Ed.), *Attention and Performance XIII*, Erlbaum, Hillsdale, NJ, 1990.
- [26] I. Kermadi, D. Boussaoud, Role of the primate striatum in attention

- and sensorimotor processes: comparison with premotor cortex, *NeuroReport* 6 (1995) 1177–1181.
- [27] I. Kermadi, J.P. Joseph, Activity in the caudate nucleus of monkey during spatial sequencing, *J. Neurophysiol.* 74 (1995) 911–933.
- [28] R. Kuhn, J.L. Van Hemmen, Temporal association, in: E. Domanay, J.L. Van Hemmen, K. Schulten (Eds.), *Physics of Neural Networks*, Springer-Verlag, Berlin, 1992, pp. 213–280.
- [29] B. Milner, Effects of brain lesions on card sorting, *Arch. Neurol.* 9 (1963) 90–100.
- [30] H.E. Nelson, A modified card sorting test sensitive to frontal lobe defects, *Cortex* 12 (1976) 313–324.
- [31] R.E. Passingham, *The Frontal Lobes and Voluntary Action*, Oxford University Press, Oxford, 1993.
- [32] B.A. Pearlmutter, Learning state space trajectories in recurrent neural networks, *Neural Comput.* 1 (1989) 263–269.
- [33] B.A. Pearlmutter, Gradient calculation for dynamic recurrent neural networks: a survey, *IEEE Trans. Neural Netw.* 6 (1995) 1212–1228.
- [34] M. Petrides, Functional organization of the human frontal cortex for mnemonic processing: evidence from neuroimaging studies, in: J. Grafman, K.J. Holyoak, F. Boller (Eds.), *Structure and Functions of the Human Prefrontal Cortex*, *Ann. NY Acad. Sci.* 769 (1995) 85–96.
- [35] F.J. Pineda, Recurrent backpropagation and the dynamical approach to adaptive neural computation, *Neural Comput.* 1 (1989) 161–172.
- [36] T.W. Robbins, V. Giardini, G.H. Jones, P.J. Reading, B.J. Sahakian, Effects of dopamine depletion from the caudate-putamen and nucleus accumbens septi on the acquisition and performance of a conditional discrimination task, *Behav. Brain Res.* 38 (1990) 243–261.
- [37] E.T. Rolls, G.V. Williams, Sensory and movement-related neuronal activity in different regions of the primate striatum, In: Schneider and Lidsky (Eds.), *Basal Ganglia and Motor Behavior*, 1987, pp. 37–59.
- [38] W. Schultz, P. Apicella, T. Ljungberg, Responses of monkey dopamine neurons to reward and conditioned stimuli during successive steps of learning a delayed response task, *J. Neurosci.* 13 (1993) 900–913.
- [39] L.D. Selemon, P.S. Goldman-Rakic, Longitudinal topography and interdigitation of corticostriatal projections in the rhesus monkey, *J. Neurosci.* 5 (1985) 776–794.
- [40] G.B. Stanton, M.E. Goldberg, C.J. Bruce, Frontal eye field efferents in the macaque monkey. I. Subcortical pathways and topography of striatal and thalamic terminal fields, *J. Comp. Neurol.* 271 (1988) 473–492.
- [41] G.B. Stanton, M.E. Goldberg, C.J. Bruce, Frontal eye field efferents in the macaque monkey. II. Topography of terminal fields in mid-brain and pons, *J. Comp. Neurol.* 271 (1988) 493–506.
- [42] D.C. Van Essen, Visual areas of the mammalian cerebral cortex, *Annu. Rev. Neurosci.* 2 (1979) 227–263.
- [43] J.P. Walsh, R. Dunia, Synaptic activation of NMDA receptors induces short-term potentiation at the corticostriatal synapse of the rat, *Neuroscience* 57 (1993) 241–248.
- [44] D. Wang, M.A. Arbib, Complex temporal sequence learning based on short-term memory, *Proc. IEEE* 78 (1991) 1536–1543.
- [45] E.H. Yeterian, D. Pandya, Prefronto-striatal connections in relation to cortical architectonic organization in rhesus monkeys, *J. Comp. Neurol.* 312 (1991) 43–67.