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NETWORKS MODELING THE INVOLVEMENT OF THE FRONTAL LOBES IN
LEARNING AND PERFORMANCE OF FLEXIBLE MOVEMENT SEQUENCES

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Abstract

Networks that model the planning and execution of goal-directed sequences of movements are described, including the involvement of both the prefrontal cortex and the corpus striatum. These networks model behavioral data indicating that frontal damage does not disrupt the learning and performance of an invariant sequence of movements. If the order of performance of the movements is allowed to vary, however, frontal damage markedly reduces ability to perform the sequence.

I: Introduction

The frontal lobes have been implicated in forming strategies for goal-directed behavior (see Nauta, 1971; Fuster, 1980; and Stuss and Benson, 1986 for summaries). This general function seems to involve co-ordination of subsystems that integrate motivational and cognitive information (e. g. Milner, 1964; Pribram, 1961) with other subsystems that link past events or actions across time (Pinto-Hamuy and Linck, 1965; Fuster, 1980, 1985) and anticipate future events or actions (Ingvar, 1985; Gevins et al, 1987).

The motivational-cognitive linkages have previously been simulated in neural networks by Leven and Levine (1987) and Levine and Prueitt (1989). The network architectures used in those simulations were based on principles such as adaptive resonance (Carpenter and Grossberg, 1987) and opponent processing (Grossberg, 1972). In this article, we look at networks that model data of Pinto-Hamuy and Linck (1965) on the performance of movement sequences by frontally damaged monkeys.

The function of learning goal-directed sequences involves classification of spatiotemporal patterns. Hence, based on an idea of Dawes (1989), we combine the adaptive resonance architecture, which classifies spatial patterns, with the avalanche architecture (Grossberg, 1978) which generates sequences. The simple spatiotemporal processing areas would seem not to be located at the prefrontal cortex, but possibly in the corpus striatum. The frontal cortex, we believe, exerts higher-order controls over the functions of this sequence-classifying region. Some of these controls enable formation of complex rules for

sequence classification (see Dehaene and Changeux, 1989, for another model of this process). Others cause biases in the competition between sequence representations, favoring longer over shorter sequences to facilitate attention to a motor plan. Possible architectures for such higher-order controls will be described in Section III.

II: Experimental Data

Some effects of frontal lesions on performance of sequential tasks were studied by Pinto-Hamuy and Linck (1965) in immature macaque monkeys. Postoperative retention was assessed in two types of test: one, in which the subjects were to respond in such a way that they had to push all of several cued panels without repetitions but in any order (internally ordered or flexible sequence test), and another, in which they had to respond in an exact order by pushing a series of panels based on given cues (externally ordered or invariant sequence test). The hypothesis was that frontally damaged subjects would have difficulty retaining or relearning flexible sequences, as it would call for interaction between an internal representation of a sequence and a flexible recall based on previous action performed so as to avoid repetitions. In the case of invariant sequences, on the other hand, the frontals would not have difficulty, as there are sensory cues (lighted panels) available for guiding motor actions).

The experimental results for one subject are illustrated in Figure 1, which shows the percentage of correct responses for one each of the externally and internally ordered sequences both pre- and post-operatively. The subjects were to respond in the internally ordered test situation, for example, if an "O" and a green circle are lighted, by pressing them in either order. In the externally ordered situation, for example, the subjects were to respond by pressing a green circle and a red circle, lighted on a panel, exactly in that order.

Another experiment, by Poppen et al (1965), explored the effects of frontal lesions on sampling and search in human patients, wherein the subjects were to modify their strategies for winning candy, working through a sequence of twenty programs. In each program, only one of the geometric figures displayed randomly on a four-by-four panel set-up is rewarding. These patients had similar difficulties to the frontally lesioned monkeys in maintaining the strategy required to complete the task to criterion. Involvement of the frontal lobes in coordination of movement sequences is also supported by single cell data on the contingent negative variation or expectancy wave (see Fuster, 1985 for discussion). Though this work does not directly suggest neural architectures modeling the capacity for spatiotemporal pattern

processing, it give some evidence of where possible timing controls lie.

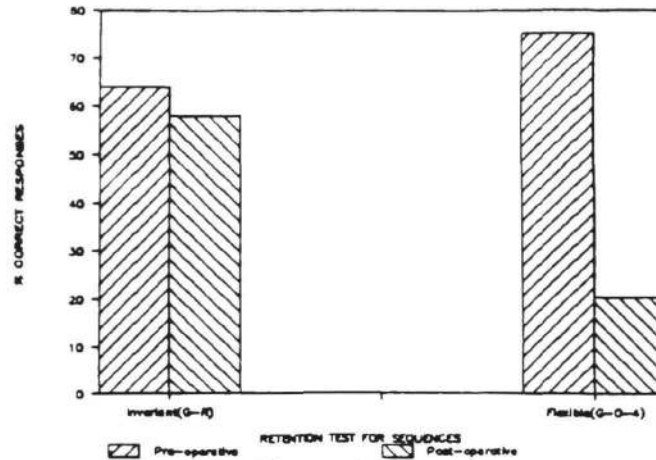


Figure 1

In the next section, we describe possible neural networks that can capture these various events and ways of integrating them. In particular, we discuss methods for qualitatively simulating the results of Pinto-Hamuy and Linck (1965).

III: Network Architectures

First consider how a specific sequence of movements might be encoded in a neural network. One possible mechanism is shown in Figure 2. This architecture was originally developed by Grossberg (1978) and was based on his own previous notion of an avalanche. The avalanche is a network for performance of a ritualistic sequence of motor acts. The network shown here extends the avalanche to include sensitivity to external feedback. The nodes $v_{i,1}$ in that figure are motor representations. The $v_{i,1}$ are active in succession, but external events can alter¹ the exact timing of their firings, or even interrupt the sequence altogether. Hence, the goal-directed actions encoded by the network can be overridden by significant changes in context. Each $v_{i,1}$ has corresponding to it a $v_{i,3}$ to keep it reverberating in short-term memory as long as needed, and a $v_{i,2}$ (influenced by an arousal source) to shut off its reverberation. Each $v_{i,2}$ also activates the next stage $v_{i+1,1}$ of the sequence.

If the sequential performance network of Figure 1 is combined with a two-layer network such as ART (Carpenter and Grossberg, 1987) for coding spatial patterns, the result can be a network for coding spatiotemporal patterns (Figure 3). In Figure 3, each of the $v_{1,i}$ from Figure 2 becomes a node at the category level $F_{2,i}$. The nodes at F_2 learn categories of activity vectors at the input level F_1 . During learning, if the input pattern at F_1 mismatches the

pattern of synaptic weights from F_2 to F_1 , node A causes short-term memory reset, leading to testing of a new category at F_2 .

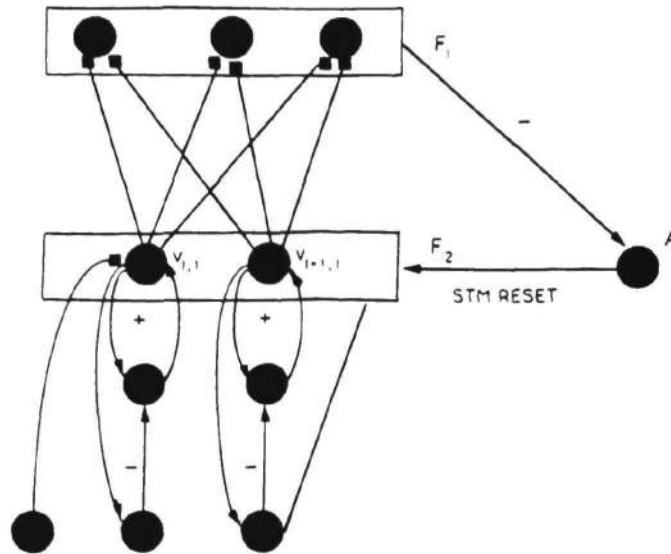


Figure 2

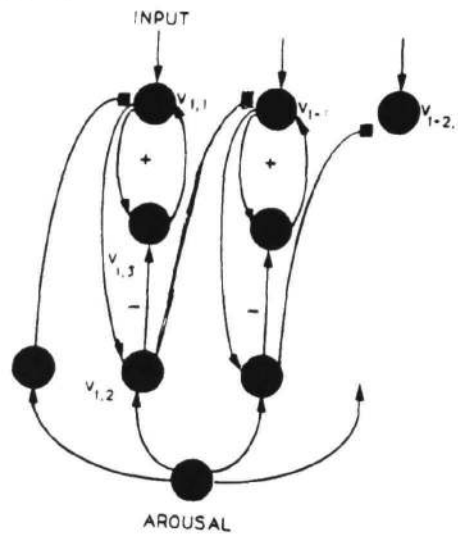


Figure 3

Nigrin (1990) developed another ART-based architecture for coding spatiotemporal patterns, with particular application to speech recognition. His network differs from ours in that it transforms spatiotemporal patterns into purely spatial patterns before encoding them, whereas our network includes the time dimension explicitly.

Recall from above the result of Pinto-Hamuy and Linck (1965) that learning and performance of externally ordered sequences is not disrupted by prefrontal lesions. Hence, if the spatiotemporal categorization network of Figure 3 is analogous to any real brain locus, it is probably elsewhere

than the prefrontal cortex. One good candidate location for such a motor control structure is the corpus striatum, a part of the basal ganglia. Extensive functional connections exist between the prefrontal cortex and corpus striatum (see, e. g., Gerfen, 1989). In the network of Figure 3, such controls could be exerted through the arousal node. This network hypothesis is in line with the general theory (Nauta, 1971; Levine and Prueitt, 1989) that the frontal lobes, through their reciprocal connections with the limbic system and hypothalamus, mediate motivational influences on cognitive and motor functions.

In Leven and Levine (1987) and Levine and Prueitt (1989), aspects of the frontal damage syndrome, namely, perseverative behavior and excessive attraction to novelty, were replicated in neural networks by the reduction of gain from reinforcement signals. A similar decreased signal from the arousal node in Figure 3 could make a motor plan more subject to distraction by interfering events. Indeed, frontal lesions often lead to distractibility (e. g. Grueninger and Pribram, 1969; Wilkins et al, 1987).

But this simple diminution of a reinforcement parameter is far from sufficient to model all effects of the frontal lobes on behavior. We believe that the frontal lobes also exert some higher-order controls on the striatal spatiotemporal categorization field (F_2). We shall now discuss two types of controls on this field. Speculatively, we suggest that these two controls are mediated by the two major functional subdivisions of the prefrontal cortex, the dorsal and orbital regions (cf. Fuster, 1980).

One type of control is a bias in the competition between nodes at the F_2 level of Figure 3. This bias is designed to favor representations of longer sequences over representations of shorter ones, so that if a long sequence of actions is followed by reward, the entire sequence of actions, not just the set of actions close in time to the reward, is likely to be positively reinforced.

An architecture for imposing such a bias on the competition among sequence representations is the masking field, developed by Cohen and Grossberg (1987) and applied to speech recognition by Cohen et al (1987). In speech, for example, representations of an entire word (e. g. MYSELF) tend to dominate representations of parts of that word which are themselves words (e. g. MY, SELF, or ELF). An example of a masking field is shown in Figure 4. In this field, F_1 and F_2 are as in the adaptive resonance networks, but F_1 nodes are interpreted as coding items in sequences and F_2 as coding sequences. In Figure 4(a), connections from F_1 to F_2 grow randomly along positionally sensitive gradients. The nodes in the masking field F_2

grow so that larger item groupings, up to some optimal size, can activate nodes with broader and stronger inhibitory interactions. In Figure 4(b), interactions within F_2 include positive feedback from a node to itself and negative feedback from a node to its neighbors. Long term memory traces at the ends of F_1 -to- F_2 pathways adaptively tune the filter defined by these pathways to amplify the F_2 response to item groupings which have previously activated their target F_2 nodes. Tentatively, we propose that sequences represented at the corpus striatum have "copies" at the dorsal frontal cortex which are configured in a masking field.

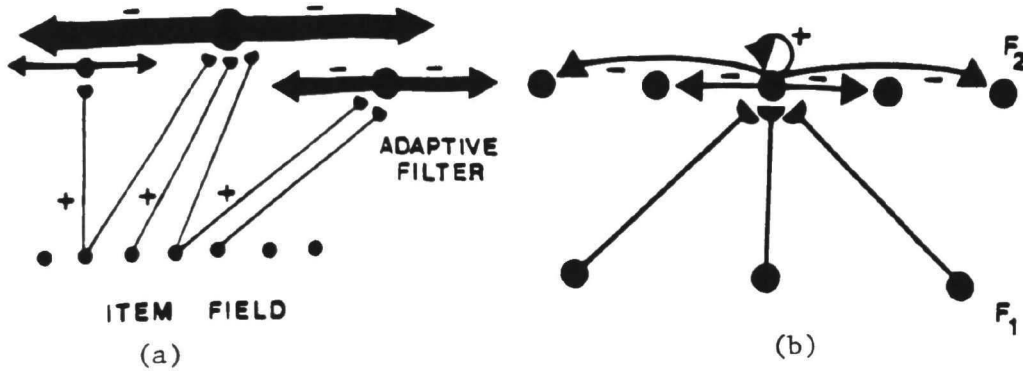


Figure 4

The other type of control that the frontal cortex is likely to exert involves categorization of possible sequences leading to reinforcement. In the case of the internally ordered sequences studied by Pinto-Hamuy and Linck (1965), a mechanism is needed for placing all possible orderings of a sequence in the same category; for example, if the panels to press are a green circle, a letter "O", and a number "4", the sequences GO4, G4O, OG4, O4G, 4GO, and 4OG should be categorized together. This classification must be mediated by the association of all these orderings with a reward. The role of the frontal lobes in such higher-order rule generation has been studied in another model by Dehaene and Changeux (1989).

We suggest that the orbital frontal cortex, through its connections with limbic reinforcement areas, may exert controls which allow many different orderings of the same sequence to be classified together if all orderings are rewarded. Such controls could be mediated by a selective-vigilance criterion for matching sequences to prototypes (see Leven and Levine, 1987, for an example of selective vigilance in an ART network). In current simulations, we are teaching the network several different orderings of the same sequence, then testing it on yet another ordering which may or may not have been presented.

IV: Discussion

The frontal lobes are widely recognized as an important part of a larger control circuit that mediates context-dependent categorizations of both sensory event sequences and motor plans. This circuit also includes parts of the limbic system, basal ganglia, and midbrain, and several monoamine transmitter systems. Foote and Morrison (1987) summarize experimental results on functions of these areas. Hestenes (1990) and several other articles in Levine and Leven (1990) relate these results to possible neural network models of mental illness. Our work herein is part of this larger body of modeling research.

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