Prefrontal Cortex and Action Sequences: A Review on Neural Computational Models

Ilaria Gaudiello
Department of Communication Disciplines, University of Bologna, Via Azzo Gardino 21, Bologna, 40122, Italy
ilaria.gaudiello@studio.unibo.it

Marco Tullio Liuzza
Department of Psychology, University of Bologna, Via Berti Pichat, 5, Bologna, 40127, Italy
mtliuzza@gmail.com

Daniele Caligiore
Institute of Cognitive Sciences and Technologies, National Research Council, (ISTC-CNR) Via San Martino della Battaglia, 44, 00185, Roma, Italy
daniele.caligiore@istc.cnr.it

The prefrontal cortex (PFC) can be considered the central executive of cognitive control, responsible for the flexibility of human behavior. By a switching-mechanism PFC can update rules and goals representations stored in working memory, so as to performance novel task and accomplish complex routines. PFC functional organization and relation with specific subcortical areas give an account of representations active maintenance that allows to achieve a goal through a series of sub-goals. On the basis of the most recent studies, we present a review of the theories concerning PFC role and neural computational models. The paper incudes a focus section on models developed to study the role of PFC in action-sequences learning and performing.

Keywords: Actions sequences; Prefrontal Cortex; Neural networks; Time integration.

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1. Introduction

Human behaviour is characterized by a great flexibility. Flexibility is what allows us to adapt to novel situations and environment contingencies. But this flexibility has a cost: it potentially exposes us to face interferences and confusion. A high order processing of the different stimuli is needed, as well as a temporal organization in order to coordinate huge amount of variable input and consequent beaten in time behaviour. There is a wide agreement on the important role played by PFC in cognitive control. It seems to be involved in flexibility behavioral mechanism and temporal organization,\textsuperscript{1,2} internal representations of rules and goals, representations active maintainance,\textsuperscript{1} action sequences performance,\textsuperscript{3,4} and categorization facilitating higher-order planning based on memory.\textsuperscript{5,6}

This paper aim is to review theories and models on the integrative regulation function of PFC as well as its role in temporal organization of action sequences. Hence, the first part of the inquiry consists of a brief description of PFC functional organization, whereas a further inquiry concerns PFC models and its involvement in action-sequences accomplishment. We will focus on two research direction, on the basis of a bio-inspired models\textsuperscript{3,7} and a computational framework model.\textsuperscript{4,8} A discussion is finally proposed with indication for further research towards biologically plausible models of PFC.

2. The role of PFC and its functional organization

The integrative theory of the PFC function\textsuperscript{1} provides a definition of PFC as an active memory in the service of control. In short, this means that PFC is characterized by a robust maintaining of its activity in front of incoming distractions, a multimodal and integrated representations and a high degree of plasticity. Within PFC cerebral functions reaches a high level of integration.

PFC is divided in three regions: orbital, medial an lateral. The first two regions concern the emotional behaviour, while the lateral area is involved in temporal organization of thoughts, actions, language.\textsuperscript{2} Moreover, we can give an account of the PFC structure describing it as crossed by two pathways.\textsuperscript{9} The controlled pathway includes dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC), anterior parts of the cerebellum, anterior automatic pathway includes areas like the supplementary motor area (SMA), primary motor cortex, lateral part of the cerebellum, and lateral part of the basal ganglia.\textsuperscript{2} The dorsolateral PFC (DLPFC) - lo-
cated in the upper side regions of the frontal lobe- and the ventral medial PFC (VMPFC) - located in the innermost regions extending towards the median line and the ventral surface of the frontal lobes. The location of the VMPFC implies close connections with the limbic system.\textsuperscript{10} Hence the VMPFC has been implicated both in emotional processing as well as in higher-order sensory processing, it is considered to play an important role in 'decision-making' processes.\textsuperscript{11} The location of the DLPFC implies close connections with the sensory and motor areas. Hence, the DLPFC concerns motor control, as well as performance monitoring, goal-directed behavior and executive functions, particularly in the areas of attention and working memory.\textsuperscript{12} The DLPFC is also strongly implicated in a task involving the active maintenance and continual updating of recent information. As mentioned before, PFC has a great role in the explanation of flexibility. Flexibility in human behaviour implies the ability of accomplishing habitual task according with rules and goals, and novel task by a mechanism of switching rules. PFC can store in working memory so as to switch the rules of behavior in correspondence to relevant events.

Studies on cerebral development show that the PFC is not completely developed in the early stages of life, and is not completely developed by late adolescence. Rather it is still developing into adulthood, and perhaps achieves maturation only in the third decade of life. A large debate is today focused on whether the DLPFC development occurs in the same amount of time as VMPFC development. Several studies support the idea that the DLPFC has evolved from the motor region and is the later brain region to mature.\textsuperscript{13,14} One point is that childhood is characterised by difficulties in performing action-sequences. It has been observed that difficulties in memory enhancement of action-sequences derive from protracted maturation of prefrontal cortex.\textsuperscript{15} It has also been shown that children observation of shorter sequences leads to better deferred imitation of single goal actions compared to action sequences.\textsuperscript{13,15} Moreover, children ability to identify the goal of an action-sequences is related to their ability to planfully solve a similar sequence. The ability to solve complex problems is close linked to the functions of the working memory, that allows to hold temporarily on-line constraints relevant to the current context. But the development of working memory too, proceeds gradually.

Hence, problems in recall, recognition, performance and encoding of temporal information concerning action-sequences can be attributed to the gradual development of PFC and to the gradual emerging of high-order processing functions, such as active maintenance and goal-directed behaviour.
Flexibility seems to depend on the ability to store abstract rule-like representations. How these representation develop? Instead of rely on representation explicitly designed for specific tasks, a model should explain the way such representations emerge by: in short, a model should try to simulate a self-organizing system. Neuroimaging evidence shows that abstract and schematic representations, such as representations of sequential actions, as well as the general rules of motor performances, remain represented in prefrontal networks. The same does not apply for the automatic aspect of motor performances, that can be relegated to lower structure. Further studies give evidence for the coexistence of two neural substrates of active representation: representations for the recent past and representations for anticipated future. The two substrates are anatomical overlapped and belong to the same cortical network of long-term memory.2

2.1. Involvement of PFC on hierarchical organization of behaviour and cross-modality integration

The high-cognitive processes, as behavioral and linguistic actions, are hierarchically organized in the prefrontal cortex, while primary motor and premotor areas constitutes the lowest levels.16 Koechlin and colleagues show that motor processing and control are processed from anterior prefrontal through caudal prefrontal, to premotor cortex: the information processed from the former level arrives to the next one, moving down in this top-down process.12 In a task performed by subjects whose were registered their brain activity by fMRI, Koechlin and colleagues showed that stimulus activated premotor area, its context was processed by the caudal prefrontal cortex and the instructional cue by the rostral PFC. These results seems confirm an ontogenetical hypothesis by which phyletic memory is innate, while higher levels are the results of further cortical associations. Executive memory is so stored in the PFC: its lowest level will be the primary motor cortex, while the highest levels should represent more complex schemas and plans of goal-oriented actions. Because the execution of these schemas or plans requires the mediation of cross-temporal contingencies, PFC is supposed to be crucial in the temporal organization of behavior.

Complex behaviors require integration of both perceptive and executive hierarchies. To do it, long corticocortical fibers connect areas involved in these hierarchies. At each stage, upper frontal areas process global aspects of the sequence, while sensory signals occur. In this process sensory inputs from posterior cortex are progressively more concrete and more dependent on immediate temporal and spatial context.16 There are some sig-
nals (episodic) that are processed in a wider temporal context that implies actions dependent from a high degree of temporal integration. In this case a simultaneous activation can be seen in the posterior cortex as in the rostral PFC. So, signals are processed at the same time in both cortices, being integrated with previous information (rules, instructional cue...) before lowering down. This integration provided by PFC is not just across the time but is also cross-modal.

A study on cross-modality in PFC have focused on the associations between visual stimuli and motor actions. This study shows the evidence of the role of PFC in integrating visual and auditory stimuli across the time. The paired association by PFC cells take place across modalities, across time and towards a goal. Thus, Dorsolateral prefrontal and premotor cortices are involved on the management of temporal behavior, as motor sequels are. This role may be crucial also for the organization of the language that can be considered as a subset of motor sequence and that depends on the temporal integration of stimuli encoded in the two sense modalities.

3. Models of PFC functioning

Several neurophysiological studies on non-human primates and neuropsychological and neuroimaging researches on the task conditions under which PFC is engaged. However it is still missing an exhaustive understanding of the mechanisms of PFC control. For this reason bio-inspired models simulating the PFC can help us to understand better how the top-down cognitive control works through it. In this section will be given an account of main computational models contributes proposed in last years, focusing on models developed in order to understand the role of PFC in action sequences learning and performing.

3.1. Main Characteristics of PFC Models

Many computational studies had confirmed some hypotheses done about the identification of neural correlates of plasticity in PFC, suggesting that these may operate as mechanisms for self-organization. Some models of PFC functioning reproduce tasks of experiments in which subjects have to use game-rules, internal representations of goals, and means to achieve them. Here, PFC is simulated as a hidden layer providing a bias getting stronger when there’s a competition between automatic, strong stimulus-response mappings and controlled, weak one and favouring the seconds (e.g. model simulating the Stroop Task in). This model even shows how
an uninterrupted activity is necessary to improve a control mechanism. It still remains to show what happens in presence of a new task that requires a rapid updating of our PFC representations (e.g.\textsuperscript{20}). The updating has to be, at the same time, adaptive and robust. In\textsuperscript{18} has been proposed that Dopamine neurons (DA) may play a rule in this process gating the access to PFC by modulating the influence of its afferent connections. This process seems to be formally equivalent to what happens in many models that simulate the PFC updating mechanisms. Computational studies as the one of\textsuperscript{18} confirm the plausibility of this self-organizing bootstrapping mechanism.

3.2. PFC models and action sequences

Within PFC studies inquiries on human motor learning behavior and action sequences have a particular relevance. Here we consider four computational model of particular interest, implemented to understand the role of PFC in controlling action sequences.

The first model reviewed is that by Gupta and Noelle.\textsuperscript{7} The authors move from the hypothesis that there are two largely distinct neural pathways that control respectively the controlled and the automatic processes. The neural network is a model of the dual pathway hypothesis that uses the Leabra modeling framework\textsuperscript{21} which incorporates two ways to modify the strength of connections: a) an error correction learning algorithm b) a Hebbian correlational learning rule. For the authors, the use of Leabra is strongly compatible with modeling a dual pathway model. The task reproduces some human experiments in which the subject had to learn sequences of key pressing on a keyboard of 9 keys. The network manages a two joint planar arm that has to press keys in sequence. The model includes a cognitive control modulation mechanism. This mechanism modulates the strength of the controlled pathways contribution to the final motor output as well as the strength of the input going from the controlled pathway to the automatic one. It is interesting to note that controlled pathway learns more rapidly (in terms of trials) than the automatic one. Automatic pathway in isolation cannot produce correct motor sequences. Beside, the controlled pathway is able to compensate the automatic pathway errors. At the last stage of learning, the model suffers when excessive control is employed during the execution of an automatized motor skill. The main limit of this model, as admitted by the authors themselves, is that it does not yet capture execution-time differences between controlled processing and automatic processing. It is well established that controlled execution of a skill is slower than automatic execution.
With the aim of understanding the top-down control exerted by internally generated sub-goal and by externally provided goal, Polk and colleagues have developed a model to simulate the Tower of London TOL task. The simulation leads to a specific hypothesis about the role of the dorsolateral prefrontal cortex (DLPFC) in TOL: the DLPFC represent internally-generated subgoals that bias competition among choices toward the solution of the task. The TOL task involves moving three colored balls until they match a given goal configuration. An externally provided goal leads the system to prefer the goal-achieving move over the other legal moves. The model itself highlights the result of the combination of bottom up mechanism (or purely data driven production system) and a top down mechanism (a goal modulated system) in modern production systems. Though we still need a deeper comprehension of temporal organization mechanism and of PFC cooperation with other cortical areas.

The recent model by Botvinick and colleagues is based on a computational framework, namely the actor-critic framework. Such framework includes a hierarchical reinforcement learning (HRL) to aggregate actions in subroutines that can be used as building block to solve incoming problems. Moreover the framework is endowed with temporally abstract actions, representations that cluster a set of interrelated actions as a single higher level action or skills. These temporally abstract actions rather than specifying a single primitive action specify a whole policy to be accomplished, that is a mapping from states to actions. It is important to highlight that prefrontal representations do not implement policies directly but instead select among stimulus-response pathways implemented outside the PFC: in short, PFC working concerns the hidden layer. As the model shows a twofold relevance, neural and behavioural, an attempt has been made to map HRL on to functional neuroanatomy: a correspondence can be found between the actor and the dorsolateral striatum (DS) and between the critic with the ventral striatum (VS) and the mesolimbic dopaminergic system. Hence, representations within PFC correspond to option identifiers in HRL (an option being a sort of supergoal, e.g. prepare coffee, that calls lower-level options, e.g. adding sugar or cream), while stimulus response pathway selected correspond to option-specific policies. This mechanism can give an account of the role of the PFC to represent action as multiple, nested levels of temporal structure. Moreover it may find evidence in recent observation of primate behaviour: when cognitive planning involves a complex number of action sequences, cells in lateral PFC selectively exhibit an for a specific category of behavioral sequences. Categories of behaviors are embodied as
sequences of movements and, during the planning, their representations are present in prefrontal cells. Authors identified not only cells dedicated to plan sequences, but also cells selective for the category of the sequences themselves. This implies the existence of a unit of knowledge that specifies the macrostructure of an event series at an advanced level of unification. It seems to be confirmed the theory of hierarchical structures of behavioral plan. This research confirm other evidences of the PFC role of categorization in monkeys.  

Finally the model described by Hazy and colleagues adopts a radically different approach to understand how the PFC is involved in action sequences. The authors explicitly moves from the existing mechanistic models of the basal ganglia (BG) and frontal system. BG, in fact, provides a modulation of frontal action selection in terms of Go vs Not Go and this makes them play crucial role in motor control and action selection. Basal ganglia are responsible for learning by trial-and-error to automatically compose various sensorimotor primitives of the direct pathways, on the basis of a double inhibition mechanism in order to produce sophisticated behaviours. They are supposed to learn to select and compose sensorimotor skills on the basis of trial-and-error mechanisms, that can be mimicked by reinforcement learning algorithms. However, once trained basal ganglia produce quite inflexible and stereotyped behaviour, elicited by just the right stimuli. Moreover, they do not generalize well to novel situations. However the two brain districts strongly interplay to produce voluntary behaviours. In this model the BG modulates working memory representations in prefrontal area. This allows to build on more abstract executive functions, as plans, goals, task-relevant stimuli, etc. The same mechanisms that allows the BG-PFC system to learn when to update or maintain its working memory informations can be extended to the output-gating mechanism. For these reasons authors implemented a PBWM (PFC, BG, Working Memory) model that is strongly bio-inspired and has the aim to give an account the strict relationship between the BG and PFC. The hypothesis of the authors is that PFC is an evolution of the BG and the frontal cortical system mechanisms. BG modulates PFC representations in terms of Go vs Not Go and this allows PFC to develop more abstract representations that are the ones stably maintained. The task of PBWM is to resolve the 1-2-AX task, an evolution of the simple AX task, that needs the model to answer to six key functional demands for working memory: rapid updating, robust maintenance, multiple separate working memory representations, selective updating, independent output-gating for top-down biasing.
of processing: Learning what and when to gate. The PVLV (Primary Value and Learned Value) moves away from the classical time differences (TD) learning mechanisms based on the predictive nature of dopamine activity (DA) and involves two learning mechanisms, separated but interdependent, based essentially on delta-rule. Another important aim of is to elaborate a Multi-Task (MT) model, able to resolve several task and not just one as most of models early implemented. This means to reproduce our attitude to be flexible thanks of our ability in generalize, namely to abstract from specific situations. This model is just an extension of the PBWM. PFC an BG are implemented as layers of the same area interacting with the layers deputes to learn (Primary Value and Learned Value) through a reinforce ment learning mechanism that simulates the midbrain dopaminergic system and its activation via the BG and the amygdala. The algorithms used in the model are Leabra and kWTA (k-winners-take-all).

4. Discussion

PFC can be considered the central executive of our controlled behavior. We reviewed some of the most important theories that show how PFC is responsible for the flexibility of human behavior. If early theories and models helped us to understand which were the general functions of PFC, some specific aspects were still to be cleared up. It remains to understand how to capture execution-time differences between controlled processing and automatic processing, because it is clear that controlled execution of a skill is slower than an automatic one. We compared bio-inspired model with models starting from the computational-framework model as the one proposed by. We also noticed how the computational-framework model may reproduce evidence in recent observation of primate behaviour: when cognitive planning involves a complex number of action sequences, cells in lateral PFC selectively exhibit an for a specific category of behavioral sequences. There are still many opened problems as: how these models can quickly be updated when their encounter new cognitive tasks; how PFC is functionally organized; how does it work human capacity for generativity; which is the role of dopamine effects in PFC; how to give an account of PFC interaction with specific subcortical areas. We suggest to draw a biologically plausible model of PFC in order to implement the development of PFC in humans from childhood to adulthood. How does the shift work from the automatic to the controlled pathway in children that haven’t still developed PFC? We are going to keep on searching about that.
References

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