In Search of the Brain’s Executive
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Abstract—In unpublished work over about ten years starting in 1995, John Taylor, Raju Bapi, Guido Bugmann, Neill Taylor, and I developed a network theory of the cognitive functions of the frontal lobes. We dealt with the long popular notion of the prefrontal region as executive of the brain [1]. Some cognitive neuroscientists had called for abandoning the executive idea because the functions of planning, organizing, and controlling behavior were distributed over many brain regions and not run by a single “homunculus.” Yet we believed that the executive concept was still useful if we analyzed it in system terms, including the executive functions of the prefrontal’s connections with other areas, notably basal ganglia and thalamus; parietal, premotor, and secondary sensory cortices; and amygdala.

1. ANALYZING THE EXECUTIVE

The prefrontal cortex, the association cortex of the frontal lobes, has long fascinated neuroscientists because it is the most evolutionarily advanced part of our brains. In the Nineteenth Century the famous case of Phineas Gage, whose personality changed overnight from sober to impulsive after prefrontal damage, suggested that this brain region plays a prime role in organizing and controlling behavior (see [3] for review). Yet after that time the fashion among neuroscientists shifted from theories based on localized representations to theories based on distributed representations, and the unique functions of any single brain regions were de-emphasized for much of the early to middle Twentieth century. Belief in the prefrontal lobes’ unimportance inspired the use of frontal lobotomy to control brain disorders such as epilepsy, which won a Nobel Prize (in 1941) for the neurosurgeon Egas Moniz.

Frontal lobotomy turned out to have more severe side effects than expected, notably inability to plan behavioral sequences. The work of such scientists as Pribram and Luria in the 1970s [1] again highlighted the prefrontal cortex’s executive role. Yet the brain executive concept remained controversial because of increasing evidence that no single brain region fully controls behavior.

In the mid-1990s, John Taylor embarked on a research project to revisit the notion of the brain executive as a system including interactions of prefrontal cortex with other brain regions such as basal ganglia, thalamus, amygdala, and parietal cortex. This project involved several scientists resident or visiting at King’s College London and the University of Plymouth: Raju Bapi, Guido Bugmann, Neill Taylor, and me. Our network theory was built on the notion that brain’s executive is hierarchical but distributed. We identified three overarching executive subfunctions, all of them necessary for setting goals and subgoals. These three subfunctions are (1) establishing and connecting working memory representations; (2) forming and deciding between complex behavioral schemata; (3) integrating information about affective values of stimuli and potential actions to guide responses (Fig. 1).

Perhaps because of his background in the hard physical sciences, John more than the rest of us could never quite abandon the idea that there might possibly be a single area that can in some sense qualify as “chief executive” of this distributed hierarchical system. His suggestion for the chief executive was the anterior cingulate cortex (ACC), perhaps because of its connections to emotional evaluation. Yet more recent work ([3], [4]) points to the ACC becoming activated when there is a known or potential conflict between rules of operation and then recruiting the dorsolateral prefrontal cortex (DLPFC) to search working memory for evidence that would decide between the rules. Neither of those functions seems to be more “chief” than the other.

The fundamental unit in our theory of the frontal lobes was the cortical-basal ganglia-thalamic loop (Fig. 2). Taylor and Taylor [5] showed that a multimodal network based on one of the loops could reproduce data on motor sequence storage and generation in monkeys. They proposed the corresponding network, which they called ACTION, as the basis for our three key executive functions.

We proposed that the first function, linking working memories together, could be treated by regarding each working memory as the continued activity of neurons in a recurrent loop of one of several coupled ACTION networks. Connection weights in that network can be chosen so that this activity continues circulating even when there is no input, thereby holding a memory of the initial input, now removed, which started the activity. The links between those loops are the same type required to learn motor sequences.

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Fig. 1. Schematic of three overarching subfunctions postulated for the prefrontal executive.

Fig. 2. Links between cortex, basal ganglia, and thalamus. Arrows are excitatory, circles inhibitory. STN = subthalamicus; GPe = external globus pallidus; GPi = internal globus pallidus; SNc = substantia nigra pars compacta. (Adapted from [5] with the permission of Elsevier Science.)
As for the second function, learning and deciding between schemata, the learning process has already been started in the linking of two working memory ACTION net loops together. These two loops must be coupled sequentially to produce a full schema, which itself will therefore be composed of numerous separate working memory activations. There must also be connections that turn off earlier working memory loops. This can be described as the creation of coupled attractor basins in a set of ACTION net architectures, so that activity is sequentially transferred from one to the next, the previous one being turned off.

As for the third function, affective evaluation of sensory inputs and motor responses, such valuation could be stored both in the anterior cingulate and the amygdala. The amygdalar valuation in a simulation of the Wisconsin Card Sorting Task [6] arose from external penalty inputs, and was sent on from the amygdala to the ventral striatum and its associated ACTION network loop to alter any stored strategy held there. Penalty signals are assumed to inhibit ongoing strategies and allow for alternative strategies that can be attempted until there is no penalty. ACTION networks can also incorporate effects of reward, some of them involving dopamine [7].

2. PREFRONTAL SUBREGIONS

Each of the major subdivisions of the frontal lobes, both the motor parts and the prefrontal association parts of the frontal cortex, has its own loop with corresponding areas of the basal ganglia and thalamus, and there are numerous interactions between loops both at the frontal and striatal levels. More recent work clarifies specific and dissociable functions of different prefrontal regions, especially the ACC, DLPFC, and orbital and medial prefrontal cortex (OMPFC) (see [7] for a summary).

The OMPFC is the area that was damaged in the famous 19th century patient Phineas Gage, and in other patients with deficiencies in decision making and in socially appropriate behavior [2]. Based on such clinical observations and animal lesion studies, neuroscientists believe that the OMPFC forms and sustains mental linkages between specific sensory events in the environment and positive or negative affective states. The DLPFC is a working memory region, and is involved with information processing at a higher level of abstraction than the OFC. For example, in monkeys, OFC lesions impair learning of changes in reward value within a stimulus dimension, whereas DLPFC lesions impair learning of changes in which dimension is relevant [8]. Recent fMRI studies show that DLPFC is important for working memory organization and linkage [9]. The ACC is activated when a subject must select or switch among different interpretations or aspects of a stimulus. Recent theories of anterior cingulate function have emphasized its role in detection either of potential response error or of conflict between signals promoting competing responses ([2], [3]).

In [10] I suggested that the functions of these three large regions of prefrontal cortex were analogous to the three branches of the United States government: legislative, executive (in a more restricted sense), and judicial. OFC is legislative: as the integrator of social and affective information, and the judge of appropriateness of actions, it is the part of the system that has the “pulse of the people” (the “people” being the subcortical brain and its needs). DLPFC is executive in that sense: it has the level of specialized expertise that allows it to create and try out significant policies. And ACC is judicial: as an error-detector it acts as a brake of sorts on possible activities of the other two areas that stray too far from underlying principles of effective behavior.

My own recent model of emotionally influenced risky preference decision [11] combines an adaptive resonance module [12] connecting OMPFC and amygdalar layers with the frontal-basal ganglia-thalamic connections (see Fig. 3). In the adaptive resonance module the ACC plays the role of the reset node that causes a shift in categorizations at the OMPFC level if an option being considered mismatches an existing category. As in [5] the signals from amygdalar positive affect representations to the striatal direct pathway and from amygdalar negative affect representations to the striatal indirect pathway have a major role in converting affective preferences into behavioral choices. The amygdalar-mediated striatal gating mechanism was used previously in simulations of choices between decks in the Iowa Gambling Task due to Bechara and Damasio [13].
Fig. 3. Neural network for making choices between risky options, used in [11] to simulate data from [14] on gambles involving affectively rich versus poor items. A and B represent risky or sure) alternative stimuli or responses to those stimuli. An adaptive resonance module connects amygdala (affective input processing); OFC (categorization); and ACC (reset). The amygdalar dipole field allows positive or negative affective values for each attribute of each alternative to be compared with corresponding values for competing options. The OFC dipole field allows removal from consideration of categories that the inputs are found to mismatch. Positive amygdalar representations excite the striatal direct pathway, which is part of the fronto-striato-thalamic loop for approach. Negative amygdalar representations excite the striatal indirect pathway, which is part of the fronto-striato-thalamic loop for inhibiting approach. (Adapted from [15], with the permission of Springer-Verlag.)

3. CONCLUSIONS

The ACTION network framework that John Taylor developed led to a variety of interconnected models of many tasks requiring executive control (e.g., [5], [6], [16]). Among these tasks are the Wisconsin Card Sorting Task, delayed response, and motor sequence learning.

John’s contributions to high-level cognitive modeling survive in current modeling efforts by this author and many others. He was one of the pioneers in incorporating fMRI, EEG, and lesion data on specific brain regions into real-time mathematical and computational models.

REFERENCES


