

The Hierarchical Organisation of Cortical and Basal-Ganglia Systems: A Computationally-Informed Review and Integrated Hypothesis

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Abstract. To suitably adapt to the challenges posed by reproduction and survival, animals need to learn to select when to perform different behaviours, to have internal criteria for guiding these learning processes, and to perform behaviours efficiently once selected. To implement these processes, their brain must be organised in a suitable hierarchical fashion. Here we briefly review two types of neural/behavioural/computational literatures, focussed respectively on cortex and on sub-cortical areas, and highlight their important limitations. Then we review two computational modelling works of the authors that exemplify the problems, brain areas, experiments, main concepts and limitations of the two research threads. Finally we propose a theoretical integration of the two views, showing how this allows to solve most of the problems found by the two accounts if taken in isolation. The overall picture that emerges is that the cortical and the basal ganglia systems form two highly-organised hierarchical systems working in close synergy and jointly solving all the challenges of choice, selection, and implementation needed to acquire and express adaptive behaviour.

1 Introduction

A distinctive feature of animal behaviour is that it supports multiple sensorimotor activities directed to satisfy multiple survival and reproduction needs in variable conditions. The point of departure of the analysis of this paper is that hierarchical behaviour in animals can be considered as the result of three pivotal classes of processes (cf. [Alcock, 1998](#); [MacFarland, 1993](#)): (a) those leading to the acquisition and expression of specific *sensorimotor/cognitive transformations*, or *skills*; (b) those leading to the *selection* of such skills in different circumstances depending on the needs and goals pursued by the animal; (c) and those *guiding* the learning processes underlying the latter selection and the acquisition of skills based on motivations. The implementation of these processes requires a strongly structured brain architecture organised at multiple functional levels where the

top ones exert control over the lower ones but at the same time are influenced by them in their functioning (Meunier et al., 2010). This architecture is inherently *softly-modular*: on one hand, it encodes in distinct neural populations different skills, goals, and other elements that support behaviour so that they do not interfere with each other; on the other hand, if such elements are similar they are encoded in partially overlapping neural populations so to exploit generalisation. The brain architecture is also *hierarchical* to allow the implementation of sensorimotor/cognitive transformations, and selection of chunks of behaviour, at multiple levels of abstraction.

The psychological and neuroscientific literature investigating the hierarchical organisation of brain and behaviour is currently basically split in two research threads having strong characterising features in terms of topics, concepts and methods, and limited interactions. The first research thread, mainly involving the sub-fields of *cognitive neuroscience*, *primate neuro-physiology*, and *neuro-psychology*, focusses mainly on the study of cortical systems, runs behavioural/cognitive experiments with human and non-human primates, investigates the non-human primate brain with neurophysiology and the human brain on the basis of brain-imaging techniques, natural brain impairments, or transcranial magnetic stimulation (e.g., Cisek and Kalaska, 2010; Gazzaniga, 2004; Rizzolatti and Craighero, 2004; Walsh and Cowey, 2000). The second research thread, mainly involving the sub-fields of *bio-behavioural studies* and *comparative psychology*, focusses mainly on the study of sub-cortical brain structures, runs experiments with rats and sometimes non-human primates, uses behavioural experiments, investigates the brain based on brain lesions and sometimes physiological recordings (e.g., Cardinal et al., 2002; Yin and Knowlton, 2006).

The two research threads tend to focus on two critical but distinct classes of phenomena and concepts related to the hierarchical organisation of brain and behaviour. This leads the two threads to produce an incomplete account if taken in isolation. The objective of this work is to show that the integration of the knowledge coming from the two pieces of literature solves most of those problems, gives a better explanation of the system-level organisation of brain and behaviour hierarchies, and offers a view that uncovers new challenges for empirical and modelling research.

To achieve this objective we will first briefly present the view of the hierarchical organisation of brain and behaviour offered by the two research threads and then we will highlight their limitations and those of the computational models with which they are supported (Section 2). Second, we will further characterise the two views on the basis of a rather detailed review of two of our computational models, one focused on the brain hierarchy involving cortical systems (Caligiore et al., 2010; Section 3) and one focussed on the brain hierarchy involving sub-cortical systems (based on Mannella et al., 2010; Section 4). This review will allow us to specify at a computational level the typical functions and mechanisms implemented by the two cortical and sub-cortical systems in support of hierarchical behaviour. Third, based on these analyses, and on other knowledge from the neuroscientific literature, we will advance an integrated view of the

system-level organisation of brain underlying hierarchical behaviour (Section 5; some ideas and problems expanded here are introduced in Thill et al., 2013). This will allow us to overcome the explanatory limitations of the two accounts and their related models, and at the same time will furnish the basis to identify new problems that might be investigated empirically or with computational models.

2 Two research threads on hierarchical brain and behaviour: features and limitations

The cognitive neuroscience literature tends to explain the hierarchical organisation of behaviour in terms of the underlying hierarchical organisation of cortical pathways (Hamilton and Grafton, 2007; Kilner, 2011; Lestou et al., 2008; Thill et al., 2013). For example, Fuster (2001) proposes that such organisation, sketched in Figure 1, is formed by cortical pathways implementing sensorimotor mappings at increasing levels of abstraction. Within it, higher levels control lower ones by performing more integrative computations by encompassing an increasing number of information sources at an increasing level of abstraction. The literature on brain system-level organisation has further specified the components of such hierarchy. The first *sensorimotor pathway* directly maps primary sensory cortex (e.g., somatosensory cortex encoding the current state of the musculoskeletal system) to primary motor cortex (encoding motor commands to muscles) (Pavrides et al., 1993; Tokimura et al., 2000). A second *dorsal neural pathway* goes from visual cortex to associative visual/somatosensory parietal areas (encoding affordances; Evangeliou et al., 2009; Fogassi et al., 2005), and then to premotor cortex (encoding action plans; Rizzolatti and Craighero, 2004; Rizzolatti et al., 1996) that exerts control on primary motor cortex. This neural pathway is in turn formed by multiple streams (Jeannerod, 1999) controlling different actuators, in particular the arm (e.g., for reaching), the hand (e.g., for grasping), and the eye. A third *ventral neural pathway* goes from visual cortex to temporal visual areas (encoding information on relevant aspects of world, such as the identity of objects), and then to prefrontal cortex (integrating various sources of information to form the agent’s goals) and, via supplementary cortex, again to premotor/motor cortex (Fuster, 2001; Miller and Cohen, 2001; Thill et al., 2013).

With respect to behaviour, this literature mainly focuses on the expression of overt/motor behaviour (within the sensorimotor and dorsal pathways) and on the higher-level control exerted on it by the brain executive functions (ventral pathway). The specific functions implemented in each pathway can be described by referring to the research addressing the different transformations. So, the direct sensorimotor pathway supports the encoding and expression of dynamic sensorimotor transformations based on a close loop between the somatosensory and motor cortex (Graziano, 2011; Todorov and Jordan, 2002). In parallel, the dorsal pathway integrates the sensory patterns *collected from the external world* with the information on the musculoskeletal system to form affordances within

the parietal cortex (e.g., “the seen object can be grasped with a precision grip”) and then contributes to form and control motor plans at the level of premotor cortex (Cisek and Kalaska, 2010; Rizzolatti and Craighero, 2004). At the highest level, the ventral pathway processes information on the identity/nature of the objects in the environment (adaptively, these are relevant as they represent resources potentially useful for the animal) based on temporal areas. This information reaches the prefrontal cortex that suitably integrates such information with the one on the agent’s goals and on this basis contributes to the selection of the possible plans of actions prepared within the dorsal pathway (Fuster, 2001; Koehlin and Summerfield, 2007; Miller and Cohen, 2001; Wallis et al., 2001).

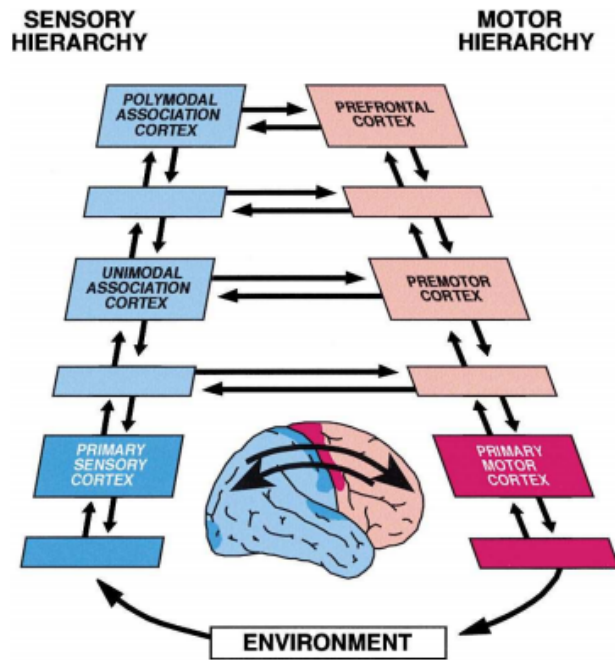


Fig. 1: Sketch of the hierarchical organisation of cortex. Reprinted from Fuster (2001) (Copyright 2001, with permission from Elsevier).

The bio-behavioural literature, instead, tends to focus on the sub-cortical hierarchy of the brain. This involves the basal-ganglia system and its rostro-caudal organisation based on multiple cortical-striatal macro-loops (Figure 2; the striatum is the input stage of basal ganglia) encompassing (Redgrave et al., 2010; Yin and Knowlton, 2006): the *limbic loop* (involving the ventral striatum, also called accumbens), the *associative loop* (involving the striatum portion called dorsomedial striatum in rats and caudatum in primates), and the *sensorimo-*

tor loop (involving the striatum portion called dorsolateral striatum in rats and putamen in primates). At the highest level, the hierarchy also involves the amygdala complex (Mirolli et al., 2010; Pitkänen et al., 1997) and the hippocampal system (Bast, 2007; Lisman and Grace, 2005; Voorn et al., 2004) as generators of motivations and as loci of associations between objects/experiences and their subjective “value” (biological relevance, novelty, etc.). Finally, they involve the dopaminergic systems (substantia nigra pars compacta and ventral tegmental area) controlling dopamine, the most important neuromodulator for the guidance of learning and for the energization of behaviour (Berridge and Robinson, 1998).

With respect to behaviour, this literature has a strong focus not only on its expression but also on the learning processes that lead to its acquisition, in particular within the context of the numerous classical and instrumental learning paradigms (Cardinal et al., 2002), and on the role that *value and motivations* play in these processes (e.g., supported by dopamine). Overall, the hierarchy contributes to generate behaviour based on the following principles. At the highest levels, some sub-cortical structures (e.g., the amygdala) interface the brain with the *body homeostatic regulations*, and on this basis allow the assignment of value to environmental stimuli and experiences. This allows the highest levels of the cortico-basal ganglia systems communicating with such structures, the limbic cortico-striatal loop, to suitably direct behaviour based on the activation of specific high-level goals (goal-directed behaviour) (Balleine and Dickinson, 1998). The limbic cortico-striatal loop is also an important regulator of dopamine (via its connections to dopaminergic areas), which in turn guides the learning processes leading to the acquisition of behaviour (Grace et al., 2007). The goals selected within the limbic loop then influence the selections involving attention, affordances and sensory processing taking place within the associative loop, on the basis of a number of “cross-loop” mechanisms (e.g., thalamo-cortical connections and “dopamine spirals”, (Haber, 2003a,a)). Based on similar mechanisms, the associative loop in turn influences the selections of the lower-level processes taking place within the sensorimotor loop.

In part forcing the distinction for the sake of clarity, it appears that the two research threads tend to study the respective brain structures and processes quite in isolation from each other. Indeed, they often present an account of the functioning of hierarchical brain almost as if the studied cortical or sub-cortical systems taken alone were not only necessary but also sufficient for the acquisition and expression of the investigated behaviour. This is problematic as the cortical and sub-cortical brain components play partially overlapping but also distinct functions. In this respect, such accounts have important limitations with respect to the three classes of processes supporting hierarchical behaviour illustrated at the beginning of the chapter, namely the implementation of sensorimotor transformations, their selection, and the guidance of the learning processes leading to the acquisition of such transformations.

These limitations, summarised in Table 1, are now illustrated. In this description we distinguish between the empirical and the computational literatures

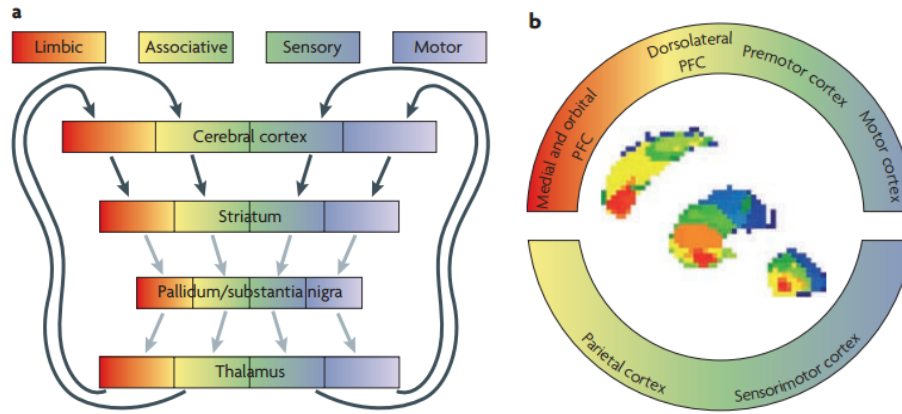


Fig. 2: The parallel basal ganglia-cortical loops forming the subcortical hierarchy. Reprinted by permission from Macmillan Publishers Ltd: *Nature Review Neuroscience*, Redgrave et al. (2010), copyright 2010.

supporting each view as the two do not always coincide. The empirical literature focussing on the cortical hierarchy (e.g., cognitive neuroscience) investigates to a large extent the sensorimotor-mappings of the dorsal pathways affording and implementing actions, and their control by the ventral-pathway/prefrontal cortex, but rarely tackles the issue of the specific mechanisms that the brain used to select alternative affordances and actions (e.g., Munakata et al., 2011). Moreover, when it investigates the phenomena related to the ventral/prefrontal control of behaviour, it faces the problem of how higher-level goals bias top-down selections (e.g., Miller and Cohen, 2001) but it usually neglects the motivational aspects leading to the ultimate formation and selection of goals, and to the guidance of the learning mechanisms leading to the acquisition of the selection capabilities at all levels (perception, action, goals, etc.).

The computational literature focussed on the cortical hierarchy develops models giving detailed accounts of the dorsal/ventral cortical pathways (e.g., Fagg and Arbib, 1998; Oztop and Arbib, 2002; see also the example in Section 3) but generally neglects the motivational processes at the origin of the overall guidance of behaviour selection and learning processes. On the other side, those same models often incorporate selection mechanisms based on lateral competition (e.g., Cisek, 2007; Erlhagen and Schoner, 2002), probably because computational implementations make evident the need of having some type of selection mechanism.

The empirical literature (e.g., bio-behavioural neuroscience) focussing on the sub-cortical hierarchy gives a prominent importance to the study of the selection mechanisms, of the learning mechanisms, and of the motivational processes driving them (Cardinal et al., 2002, for a review). However, such literature tends to give accounts of hierarchical behaviour assuming the existence of already acquired whole actions (e.g., “pressing a lever”) readily available to be selected

	Literature focussing on cortical hierarchy			Literature focussing on sub-cortical hierarchy		
	Moti- vation	Selection	Sensorimotor mapping	Moti- vation	Selection	Sensorimotor mapping
Empirical research	v	X	V	V	V	X
Computational modelling	X	v	V	v	V	X

Table 1: Summary of limitations of the different literatures studying the hierarchical organisation of brain at the cortical and sub-cortical level. “V” and “X” respectively indicate that the literature respectively accounts or not for the classes of issues indicated at the top of the column (“Motivation”, “Selection”, “Sensorimotor mapping”). “v” indicates a minor account of them.

or associated with stimuli (e.g., based on S-R associations). This is a limitation as, although several Pavlovian actions are indeed innately encoded in brain, the same is not true for most instrumental actions: in this case the sensorimotor mappings implementing the actions are acquired with progressive learning processes.

The computational literature on the sub-cortical hierarchy relies upon one of the most successful examples of synergies between empirical and computational research, namely the one based on reinforcement learning models (Barto et al., 1983; Houk et al., 1995; Joel et al., 2002; Sutton and Barto, 1998). These models are focussed on the learning processes leading to acquire the capacity to select actions by trial-and-error (Table 1), and have been also developed to capture the hierarchical organisation of the brain (Botvinick et al., 2008; Daw et al., 2005; Solway and Botvinick, 2012). The models have also been developed to some extents to capture the ultimate motivational sources of learning signals (primary rewards) and behaviour drives (e.g., Barto et al., 2004; Mirolli et al., 2013; Venditti et al., 2009). As for the related empirical literature, however, when used to account for empirical phenomena these models tend to represent “primitive actions” at a rather high level (e.g., “moving from one place to another”) that abstracts from the sensorimotor mappings needed to implement them (Table 1). Other times, when they do not assume high-level primitive actions but work on the basis of fine movements, these computational models tend to give a view of striato-cortical loops as learning by trial-and-error to implement fine sensorimotor/cognitive transformations that map sensations to actions. As we shall see in Section 5, this view is in contrast to the overall anatomical organisation of striato-cortical loops where cross-loop flows of information tend to be top-down (from goals to actions) rather than bottom-up (from sensations to actions), and to the evidence that fine sensorimotor/cognitive transformations are implemented in cortico-cortical pathways rather than in striato-cortical loops.

3 Cortical Hierarchies

This section will present a more detailed view of the organisation of the cortical hierarchy and its functioning and learning mechanisms by reviewing in depth a specific computational model by the authors (Caligiore et al., 2010, 2012). This will allow us to exemplify more in detail the nature, and also the limitations, of the accounts of the brain hierarchy given by the views focussed on cortex.

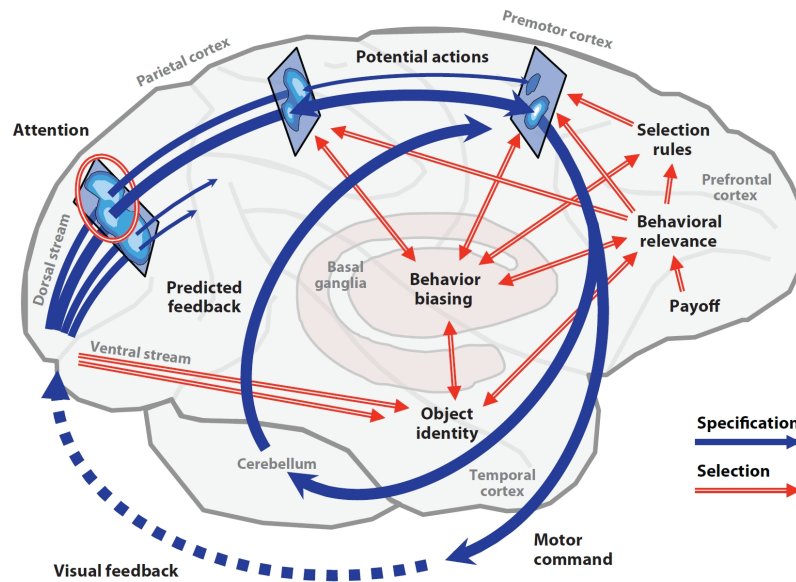


Fig. 3: Illustration of the brain cortical hierarchy addressed by the TRoPICALS model. The processes of action specification (represented by dark blue arrows) begin in the visual cortex and proceed rightward across the parietal lobe: these processes transform visual information into representations of potential actions (affordances). Along the dorsal route, sensorimotor transformations leading to produce different actions compete for further processing. This competition is biased by the input from prefrontal cortical regions that collects information for action selection (red double-line arrows). The final selected action is released into execution and causes overt feedback through the environment (dotted blue arrow). Note that TRoPICALS, as most of the literature it refers to, does not take into consideration the basal ganglia, the cerebellum, and the sources of the “payoff” illustrated in the figure. Reprinted from Cisek and Kalaska (2010) (copyright 2010, permission from Annual Reviews).

The model departs from two principles involving two cortical pathways considered in the previous section (see Figure 3): (a) the dual route hypothesis

(Milner and Goodale, 2008; Ungerleider and Mishkin, 1982), according to which the cortical brain responsible for visual processing is organized into the dorsal and ventral neural pathways; (b) the role of the prefrontal cortex as a source of top-down biasing that instructs the neural competitions between potential alternative actions at the level of the premotor cortex (Cisek, 2007; Cisek and Kalaska, 2010; Miller and Cohen, 2001). The two principles are now illustrated in detail.

In the original dual route proposal (Ungerleider and Mishkin, 1982), the ventral stream runs from early visual cortex areas to inferotemporal cortex and carries information about the identity of the objects (“what” pathway). Instead, the dorsal stream runs from visual cortex areas to the parietal cortex and processes spatial information concerning the location of objects in the visual field (“where” pathway). The scope of this theory was later extended (Milner and Goodale, 2008) by proposing that the ventral stream communicates visual information to support higher cognitive processing taking place in prefrontal cortical regions (e.g., not only object recognition but also decision making on actions to be executed and higher-level reasoning). In contrast, the dorsal stream transfers visual information to support on-line performance of actions in downstream motor cortex areas (e.g., not only location of objects, but also implementation of the sensorimotor transformations needed to detect affordances and visually guide action).

The sensory system of primates and humans provides detailed information about the external world and on this basis the motor system can perform a large repertoire of actions. This introduces a great potential for flexibility but also for interference. To effectively cope with the multitude of possible actions to perform, the brain has acquired mechanisms that coordinate low-level sensory and motor processes on the basis of goals, external context and internal motivations (Fuster, 2001). The prefrontal cortex plays a key role in these processes especially when “top-down” control based on goals (and motivations) is needed (Fuster, 2001; Miller and Cohen, 2001; Wallis et al., 2001). More in details, within the ventral pathway the prefrontal cortex can use information from the outer context and the agent’s needs to form high-level goals. Based on this information, the prefrontal cortex can act on the dorsal pathway by biasing the selection of affordances and actions. This biasing activity is based on various features of the prefrontal cortex, including its capacity to integrate multiple sources of information, to implement working memory, and to form complex behavioural “rules” (Deco and Rolls, 2003).

The computational model TRoPICALS (Figure 4, Caligiore et al. (2010, 2012)) proposed to account for compatibility effects studied in cognitive psychology (Ellis and Tucker, 2001)¹, integrates the key features of the cortical

¹ In a typical compatibility effect experiment participants are asked to produce actions which are either in agreement (compatible) with the actions typically associated with the objects (e.g., a precision grip with a small object) or in contrast (incompatible) with those actions (e.g., a precision grip with a large object) in tasks where the objects size is irrelevant. If the participants exhibit longer reaction times and higher

hierarchical organization discussed above. More in details, TRoPICALS incorporates in its architecture the *dorsal/ventral pathways organisation* of cortical areas (Milner and Goodale, 2008); the *guidance/biasing* of action selection based on prefrontal cortex “instructions” (Miller and Cohen, 2001); and the selection of actions within premotor cortex based on a *competition* between affordances and alternatives actions under a bias from the prefrontal cortex (Cisek, 2007; Cisek and Kalaska, 2010). The acronym “TRoPICALS” summarises these principles: Two Route, Prefrontal Instruction, Competition of Affordances, Language Simulation (the latter principle, less relevant here, was introduced to account for compatibility effects involving language; Barsalou, 2008).

TRoPICALS reproduces the main functions of several dorsal and ventral cortical areas (see Figure 4 for the acronyms). The model was tested within an embodied system formed by a simulated eye (camera) and a simulated robotic arm/hand (see Figure 5). The input of the model is formed by three neural maps (VC), encoding an RGB visual input, and a somatosensory map (SSC), encoding the arm angles. The output of the model is the desired posture of the hand encoding different grips (PMCl) or the desired posture of the arm encoding a reach target (PMCd). Downstream VC and SSC, the model divides into two main neural pathways: the dorsal pathway, which implements suitable sensorimotor transformations needed to perform actions on the basis of perception, and the ventral pathway, which allows flexible control of behaviour thanks to the biasing effects exerted by PFC on action selection. In turn, the dorsal pathway is formed by a stream controlling grasping and a stream controlling reaching.

With respect to function and learning, the VC performs image edge extraction based on Sobel filters (Sobel and Feldman, 1968). Based on this, within the dorsal pathway the AIP extracts the shape of objects, and within the ventral pathway the VOT categorises objects using a self-organising map (SOM; Kohonen (2003)) (see Figure 6).

Within the dorsal pathway, the AIP-PMCl and PRR-PMCd streams (i.e., the two dorsal neural streams transforming affordances into grasping and reaching actions) are trained on the basis of a Hebbian learning process (Dayan and Abbott, 2001; Hebb, 1949) that allows the system to learn to associate suitable actions (PMCl, PMCd) to available affordances (AIP, PRR). Importantly for this paper, the Hebbian process is based on a motor babbling of the hand/arm, and connections are formed only when the hand/accomplish a successful grasp/reach: this means that the *system ultimately uses a trial-and-error mechanism to learn the association that allows it to select the proper actions*.

Within the ventral pathway, PFC uses a second SOM to form representations that combine the seen objects (VOT) and the task to be accomplished (STC) to shape the current high-level goals used to bias action selected within PMCl or PMCd (Figure 7). The premotor regions (PMCl and PMCd) integrate affordance information from the parietal cortex (PC) (respectively from AIP and PRR

error rates in incompatible trials than in compatible ones, one can infer that seeing objects automatically elicits the representations of their affordances, independently of the performance of the experimental task.

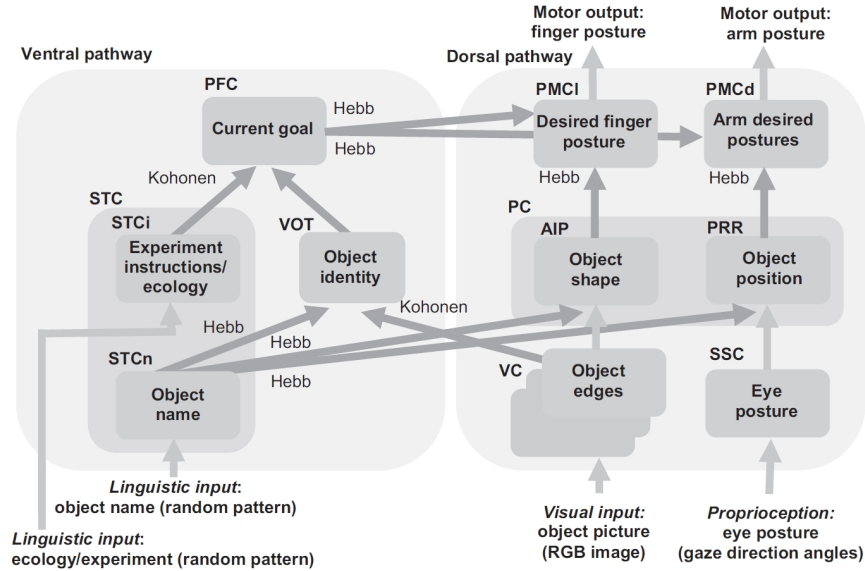


Fig. 4: Architecture of the TRoPICALS model. The boxes indicate the components of the model. The label inside each box indicates the type of information encoded by the component, whereas the acronym at its top-left corner indicates the brain anatomical area putatively corresponding to it. Light and dark grey arrows respectively indicate connections which were hardwired and connections which were updated by learning processes based on a Hebb learning rule or a Kohonen learning rule. Acronyms: AIP: the anterior intraparietal sulcus; PFC: the prefrontal cortex; PMCd: premotor cortex dorsal division PMCI: premotor cortex lateral division; PRR: parietal reach region; SSC: somatosensory cortex; STC: superior temporal cortex; VC: visual cortex; VOT: ventral occipito-temporal cortex. Reprinted with permission from Caligiore et al. (2010) (copyright 2010, APA publisher).

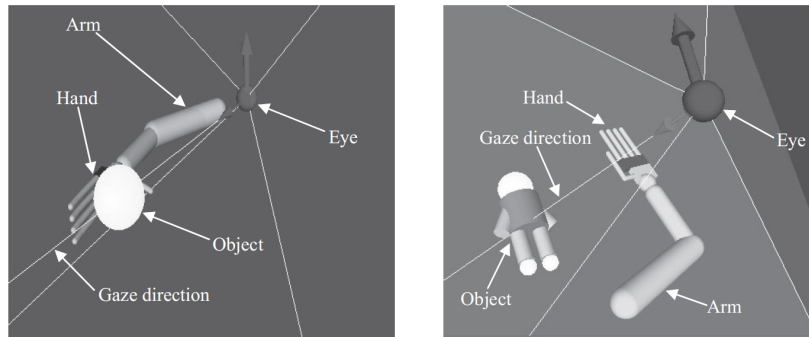


Fig. 5: The robotic set-up used to test TRoPICALS. Left: The simulated arm, hand, and eye interacting with a simulated apple. Right: The simulated arm, hand, and eye interacting with a simulated doll. In both panels, the line passing through the object indicates the gaze direction (eye control is hardwired), whereas the other four lines indicate the scope of the eye visual field. Reprinted with permission from Caligiore et al. (2010) (copyright 2010, APA publisher).

regions) and goal-based information from PFC using a dynamic neural field (Erlhagen and Schoner, 2002). The *dynamic field is then used to select actions through neural competition* taking place within premotor areas. The dynamic nature of this competition allows to account for compatibility effects: when the action suggested by affordances are congruent with the PFC command, reaction times for triggering the action are faster than when they are not congruent. Figure 8 illustrates the effect of this neural competition on the speed of the selection of actions (actions are encoded using population codes (Pouget et al., 2000) as desired postures of hand, within PMCl, and arm, within PMCd).

The presentation of the model highlighted the typical principles and topics characterising the literature focused on cortical hierarchy, and allows us to highlight the two limitations of the approach presented at a theoretical level in Section 2. TRoPICALS uses dynamic neural fields (Erlhagen and Schoner, 2002) to abstract affordances and actions selection mechanisms that in brain are mainly implemented by cortical basal ganglia loops (e.g., involving parietal and premotor areas; Alexander and Crutcher, 1990; Redgrave et al., 1999; Yin and Knowlton, 2006). In a recent extended version of TRoPICALS (Caligiore et al., 2012) developed to account for compatibility effects in the presence of a distractor (Ellis et al., 2007), the biasing effect of the PFC was augmented by adding inhibitory mechanisms which, as explicitly recognised in the paper, abstract the inhibitory effects that PFC can exert on motor cortex via the basal ganglia and the supplementary motor cortex (Nachev et al., 2008). Moreover, the Hebbian based reinforcement learning mechanism used by TRoPICALS to acquire sensorimotor mappings abstracts the role of the sub-cortical mechanisms producing the reward signals that guide the acquisition of such selection capabilities, and

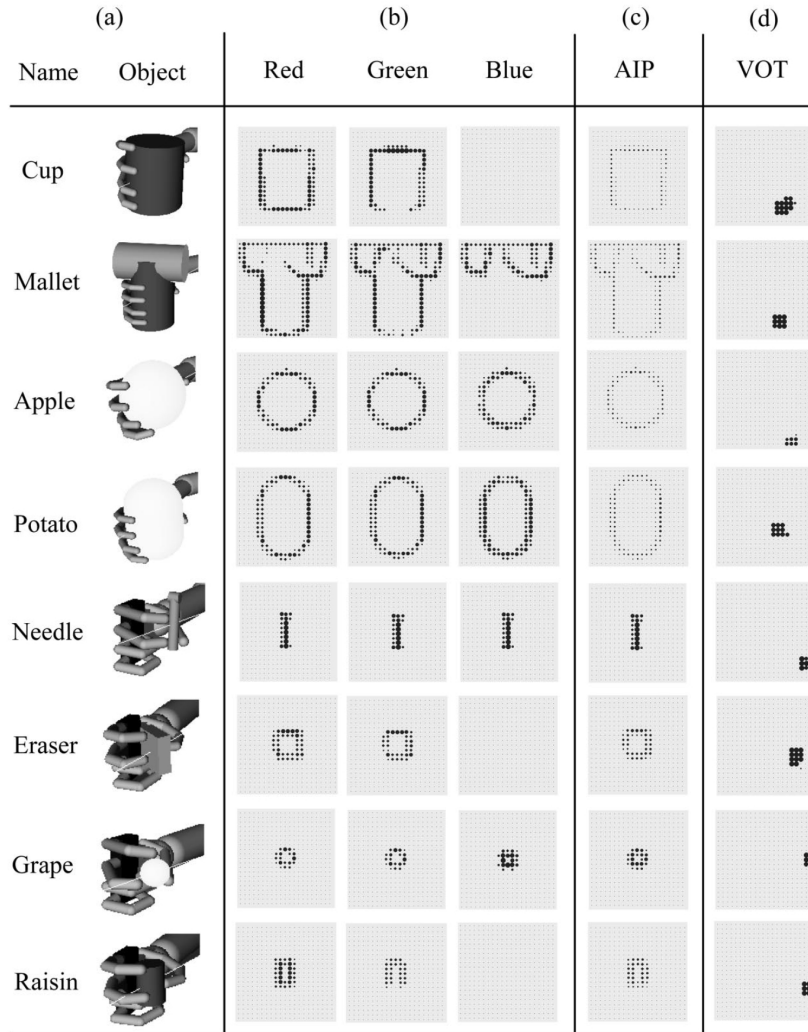


Fig. 6: Activation of the early cortical areas of TRoPICALS. The columns of the figure show: (a) the object name, appearance, and handgrip of the objects used in the compatibility effect experiment; (b) the activation of the neurons forming the visual cortex (three edge sensitive red-green-blue maps) caused by the objects; (c) dorsal pathway: the activation of AIP encoding the shape of objects; (d) ventral pathway: the activation of the VOT encoding the identity of objects. AIP: anterior intraparietal cortex; VOT: ventral occipitotemporal cortex. Reprinted with permission from [Caligiore et al. \(2010\)](#) (copyright 2010, APA publisher).

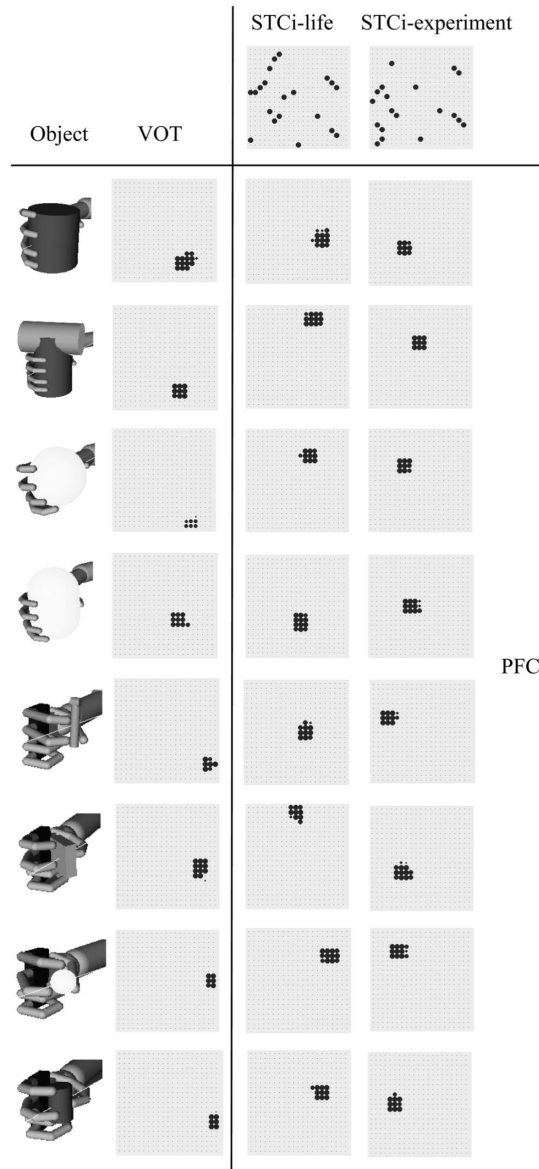


Fig. 7: The activation of the PFC caused by the different representations in VOT (objects) and the two STCi activations representing, respectively, the ecological condition experienced during life, when affordances and motor control capabilities are acquired, and the condition experienced during the psychological experiment. Notice the different representations of the various contexts and objects within the PFC: the richness of such representations is at the basis of the potential of the PFC to flexibly associate any combination of the context elements with any action. PFC: prefrontal cortex; STCi: superior temporal cortex for instructions; VOT: ventral occipitotemporal cortex. Reprinted with permission from Caligiore et al. (2010) (copyright 2010, APA publisher).

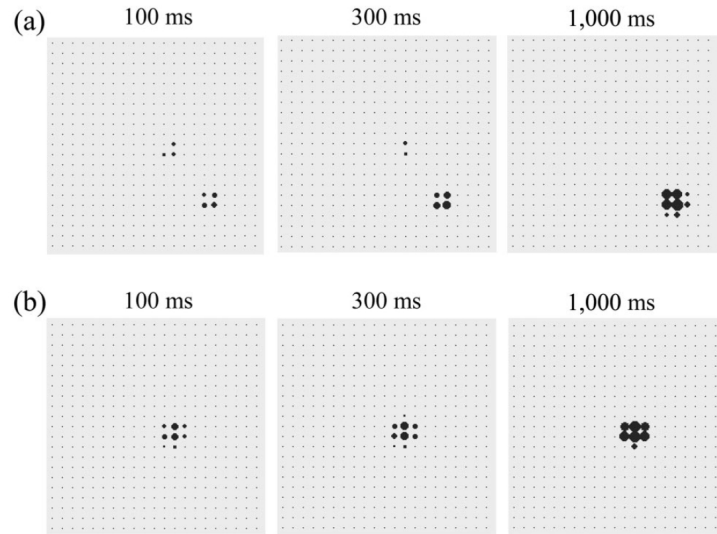


Fig. 8: The activation of the PMCl during the simulation of the compatibility effect experiments. (a) Activation of the PMCl in an incongruent trial: the biases from PFC (goals) and PC (affordances) cause two different clusters of neurons, encoding two different grasping actions, to compete until the cluster caused by the PFC suppresses the cluster caused by the PC. (b) Activation of the PMCl in a congruent trial: the biases from the PFC and the PC overlap and cause the formation of only one cluster of neurons. The panels depict the activation of the PMC after 100, 300, and 1,000 ms. Notice how in the incongruent condition the stronger top-down bias from the PFC wins. Also notice how in the congruent condition the action cluster forms more rapidly than in the incongruent one so producing faster reaction times (compatibility effect). Reprinted with permission from [Caligiore et al. \(2010\)](#) (copyright 2010, APA publisher).

the mechanisms within the basal ganglia implementing such learning processes (Joel et al., 2002; Tang et al., 2007).

These assumptions are viable if one studies phenomena such as compatibility effects, but we think that they give a limited/distorted image if one studies the overall hierarchical organisation of the brain, as they cannot account for a number of interesting phenomena and mechanisms whose study requires an explicit representation of selection and learning guidance processes.

4 Basal-Ganglia Hierarchies

This section reviews another model that focusses on the sub-cortical hierarchy of the brain and that will allow us to highlight the typical features of research focussed on such hierarchy. The review also highlights that this account has the opposite limitations with respect to the approach reviewed in the previous section: it fails to account for sensorimotor/cognitive transformations. The section first introduces the brain features captured by the model, and then explains and discusses the model itself.

The basal ganglia are a group of sub-cortical nuclei comprehending the striatum and the sub-thalamic nucleus (STN) as its main input gates, and the internal globus pallidus (GPi) and the substantia nigra pars reticulata (SNpr) as its main output components (Figure 9). These structures represent fundamental functional processing unit of the vertebrate brain that repeats at multiple functional levels and forms multiple re-entrant loops with various frontal and associative cortical areas. Different loops run in parallel and each loop starts from a cortical area, goes through a subregion of the basal ganglia, and goes back to the cortical area of origin via the thalamus (Alexander et al., 1986; Heimer et al., 1982; Humphries and Prescott, 2010; Middleton and Strick, 2000a; Romanelli et al., 2005). Each loop is involved in the *selection* of the content of the targeted cortical areas, such as a perceptual representation, an action, or a goal (Alexander and Crutcher, 1990; Redgrave et al., 1999). This selection takes place through a mechanisms that allows basal ganglia to dishinhibit the area of the thalamus, in turn in loop with the cortex, corresponding to the cortical content to be selected (Chevalier and Deniau, 1990; Gurney et al., 2001; Mink, 1996).

There is now a wide agreement on the fact that three distinct functional domains can be distinguished within the basal ganglia corresponding to the dorsolateral striatum (DLS), dorsomedial striatum (DMS), and ventral striatum (VS), the latter also called nucleus accumbens (Figure 10; Yin and Knowlton, 2006). Such domains are identifiable in rats and mice and are homologue to respectively the putamen, caudatum, and nucleus accumbens in primate striatum. These domains form distinct loops interacting with distinct portions of cortex. These distinct loops typically play different functional roles depending on the type of information processed within the targeted cortex, and hence are also called limbic, associative and sensorimotor loops. The functions of the loops are now explain more in detail.

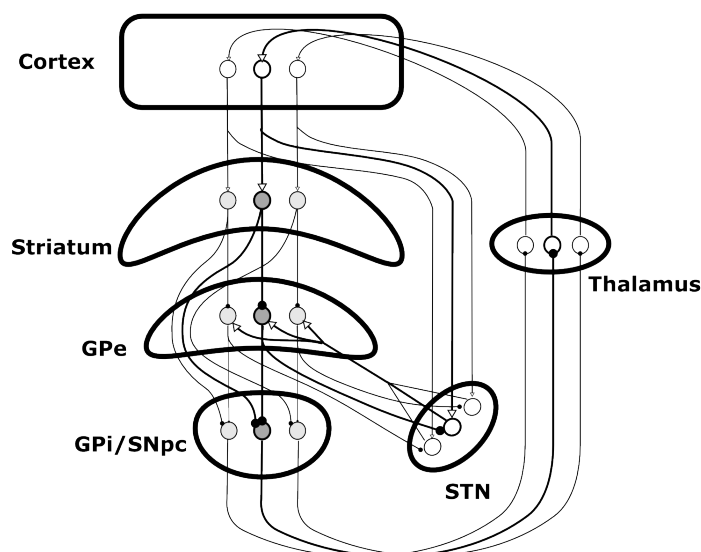


Fig. 9: A schema of the micro architecture of a single cortical basal ganglia loop. White arrowheads indicate glutamatergic projections whereas black arrowheads indicate GABAergic projections. GPe: globus pallidus, external; GPi: globus pallidus, internal; SNpc: substantia nigra, pars compacta; STN: subthalamic nucleus.

The cortical areas that reciprocate connections with the VS are various sub-regions of the prefrontal cortex (PFC), in particular the ventro-medial, orbitofrontal, and dorsolateral portions, important for the processing of biologically salient states and outcomes (Humphries and Prescott, 2010; Voorn et al., 2004; Zahm, 2000). In general, the limbic loop is involved in the selection of final goals (e.g. the achievement of a certain food), and means-to-end goals (e.g., opening a door to access a lever activating a food dispenser), based on motivations. These are important mechanisms underlying goal-directed behaviour (Cardinal et al., 2002; Corbit et al., 2001; Yin et al., 2008). The limbic loop is also important for reward and motivation based on dopamine regulation (Berridge and Robinson, 1998; Corbit and Balleine, 2011). For example, it plays an important role in the interaction between instrumental and Pavlovian processes, e.g. it allows cues previously associated with reward to energise the performance of instrumental behaviours (Corbit and Balleine, 2011; Corbit et al., 2001; Hall et al., 2001).

The cortical areas that reciprocate connections with the DMS are the temporal cortex (TE; Middleton and Strick, 1996), the parietal cortex (PC), the frontal eye-fields (FEF), and the dorsal regions of the PFC (Alexander et al., 1986; Voorn et al., 2004; Yeterian and Pandya, 1995). The associative loop is implicated in several high-level cognitive processes (Kimchi and Laubach, 2009),

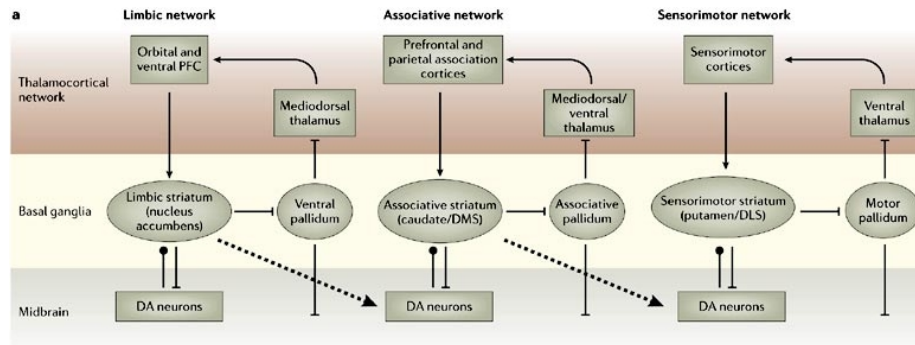


Fig. 10: A scheme of the three main cortico-striatal regions and their interconnections. Standard arrows indicate excitatory glutamate connections. Flat arrowheads indicate inhibitory GABA connections. Dot arrowheads indicate dopaminergic connections (dashed arrows indicate the cross-loop ones). Reprinted with permission from Mcmillan Publishers Ltd: *Nature Reviews Neuroscience*, Yin and Knowlton (2006), copyright 2006.

in particular it is involved in the formation of high-level visual representations (typically processed in TE; Middleton and Strick, 1996), in attention, spatial orientation, and affordance selection (involving FEF and PC, Schrimsher et al., 2002; Volkow et al., 2007), and in working memory tasks (involving various areas of PFC; Levy et al., 1997; Lewis et al., 2004).

Finally, the DLS is in loop with motor cortex (MC), premotor cortex (PMC), and supplementary motor cortex (SMC) (Romanelli et al., 2005; Tang et al., 2007). There is clear evidence that the sensorimotor loop is associated with the control of movement, in particular in the selection of final sensorimotor repertoires based on the current context (Alexander et al., 1986; Haber et al., 2000; Romanelli et al., 2005; Yin and Knowlton, 2006).

Within each of the three main loops, several discrete parallel streams run through relatively parallel pathways. For instance, the sensorimotor loop contains a somatotopic motor map that repeats at the level of striatum, globus pallidus, thalamus, and cortex, in particular in these regions separate areas can be found encoding information about arms, legs, and face (Alexander and Crutcher, 1990; Romanelli et al., 2005). Moreover, within each one of these streams there is evidence for the existence of *relatively segregated channels* capable of selecting particular cortical restricted targets, for example encoding specific actions (Chevalier and Deniau, 1990; Gurney et al., 2001; Mink, 1996). This idea is also a key assumption of most models on basal ganglia (e.g., see Joel et al., 2002 for a review). Even if no direct evidence can be given, many researchers assume that the same structure made of separate channels is present also in the associative and limbic loops given the uniformity of the striato-cortical micro-structure over the entire basal ganglia.

The three striato-cortical loops form a functional hierarchy. The decisions about motor actions, supported by the sensorimotor loop, are at a lower level with respect to the decisions about the part of the current context the animal should attend and process, which relies on the associative loop. On their turn, the latter decisions are at a lower level with respect to decisions about the motivationally salient outcomes (the high level goals of the animal) processed by the limbic loop.

Importantly, this functional hierarchy seems to be in line with neural data indicating that the cortico-striatal loops are anatomically organised in a hierarchical manner from ventral to dorsal domains. In this respect, there is evidence that cortices in different cortico-striatal loops are interconnected not only through direct projections (see previous section) but also through the thalamus so to form a cortico-thalamo-cortical pathway from higher more abstract levels to lower sensorimotor levels of the cortico-striatal hierarchy (Haber, 2003a).

Even more important for the top-down diffusion of “value” (i.e., biological relevance of stimuli) along the hierarchy, Haber (Haber, 2003b; Haber et al., 2000) discusses anatomical and functional evidence ascribing the control expressed by the ventral cortico-striatal loops to a dopaminergic modulation triggered via the so called *striato-nigro-striatal spiral pathway*. This pathway involves dopaminergic populations in the ventral tegmental area (VTA) and those in the substantia nigra pars compacta (SNpc) forming loops that reciprocate various striatal regions with a pattern *moving from the ventral to the dorsomedial and dorsolateral regions*. In particular, projections from ventral compartments of the striatum reach dopaminergic neurons (in particular within the VTA) that target ventral and medial striatal regions, and projections from medial regions contact dopaminergic neurons (in particular within the SNpc) that target medial and lateral striatal regions. Functionally, these projections diffuse the information on value of stimuli and goals from higher levels of cognition (limbic loop) to lower ones (associative and sensorimotor loops).

The model proposed by Mannella et al. (2010) (see also Mannella et al., 2011) captures the main processes illustrated above and specifies them in computational terms. In particular, the model reproduces the three cortico-striatal loops, the dopaminergic spirals, the processing of value within amygdala, and some cortico-cortical connections (which plays the role of transferring information between loops so to support learning, not of implementing sensorimotor transformations).

The model reproduces *instrumental devaluation effects* and also their absence demonstrated in multiple experiments where different areas of the sub-cortical systems reviewed above are lesioned. Figure 11 shows the simulated robotic rat used to reproduce the devaluation effects. A typical devaluation experiment is formed by three phases (Figure 12; see Balleine and Dickinson, 1998). In the first phase, a rat is first instrumentally trained to work on a manipulandum A (e.g., a lever) to obtain a reward A (e.g., food pellets), and on a manipulandum B (e.g., to pull a chain) to obtain a different reward B (e.g., a sucrose solution). In the second phase, the rat is satiated for one food (e.g., by giving free access

to the pellets). In the third phase, the rat is set in front of *both* manipulanda for the first time, and the number of actions performed on them is recorded in extinction (i.e., without reward delivery to avoid re-learning processes). The results of the experiment are that the rat acts more often on the manipulandum that corresponds to the food for which it has not been satiated. This experiment is considered a paradigmatic demonstration that the rat behaviour in the third phase is *goal-directed* as it selects the action that leads to obtain the valued outcome (goal) without the need of re-learning. Indeed, the action is selected on the basis of the value of the two goals (two foods) and not on the basis of the stimuli triggering actions (e.g., the sight of the lever and the chain) as in the case of habitual action.

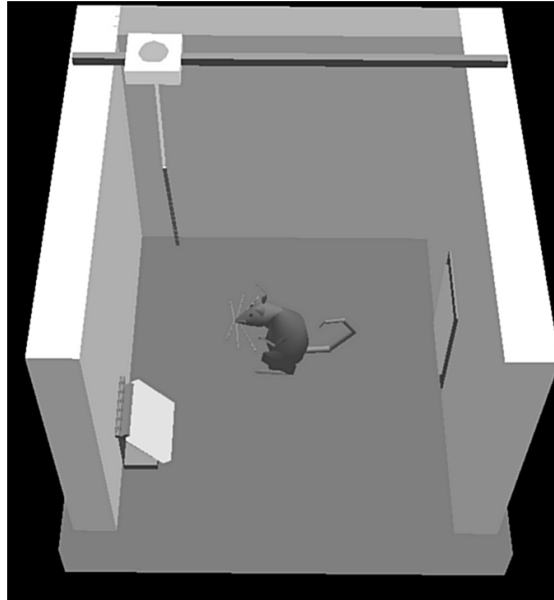


Fig. 11: A snapshot of the simulator used in the study of the devaluation experiment. The simulated rat is at the centre of the experimental chamber, the food dispenser is behind the rat, the lever is at the rat's left hand side, and the chain is at the rat's right hand side. Reprinted from (Mannella et al., 2010) (copyright 2010, with permission from Cambridge University Press).

The architecture of the model is shown in Figure 13 (Mannella et al., 2010). The model is entirely formed by leaky neurons and uses localistic representations to make its interpretation fully transparent. The model is based on two cortico-basal ganglia loops, namely the limbic and the sensorimotor loops (the associative loop was not represented for simplicity). The selection processes performed in the basal-ganglia cortical loops are represented with a neural competition tak-

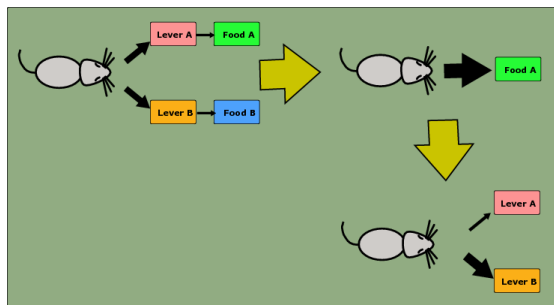


Fig. 12: A simplified schema of the instrumental devaluation paradigm. On the top-left the training phase: the animal learns to use two levers to obtain two different rewards. On the top-right the devaluation phase: the animal is satiated of one of the two rewards. On the bottom-right the test phase: the animal is presented with both manipulanda and actions toward each of them are measured in absence of any reward presentation.

ing place within premotor cortex. For simplicity, the model represents only the cortical area in loop with dorsolateral striatum (PMC in this case), whereas it abstracts away the NAcc-PFC and the PFC-PMC connections). The model also captures the reinforcement learning processes, guided by phasic dopamine (i.e., dopamine produced in strong, short-lasting bursts), that allow the two loops to acquire their selection capabilities. Finally, and importantly, the VS (nucleus accumbens) communicates with the amygdala (Amg) that informs it on the value of stimuli (e.g., the sight of a particular lever is associated with the future appearance of a valuable food). Within Amg, the value of anticipated stimuli (food A, food B) can be regulated by the internal states of the system (e.g., in the model the satiation for one food inhibits the activation of its representation).

In the simulations, during the first phase of the experiment three learning processes take place: one leading to the formation of habits, one leading to the attribution of value to previously neutral stimuli, and one assigning value to outcomes. The first process leads the sensorimotor loop to learn habits based on instrumental (i.e., trial-and-error/reinforcement learning) processes that allow the formation of associations between stimuli (the sight of the lever or of the chain) and responses (lever pressing or chain pulling) on the basis of phasic dopamine (produce by the ventral tegmental area). For example, the sight of a lever is associated to the action of pressing it as this leads to receive food A that in turn causes the production of dopamine.

The second learning process, based on differential Hebbian learning rules, leads the Amg to acquire Pavlovian associations between stimuli (the conditioned stimuli corresponding to the sight of the lever or of the chain) and outcomes (the unconditioned stimuli corresponding to the two foods). For example, within Amg the representation of the sight of a lever gets associated to the representation

of food A as these two stimuli are observed one after the other. Once formed, these associations allow the rat to “assign a value” to previously neutral stimuli, for example to recall the representation of the biologically valuable food A when the lever is seen.

The third process leads the limbic loop to associate the representations of valuable stimuli within Amg to possible outcomes (goals) encoded within VS. For example, the representation of food A in Amg gets associated with the representation of the goal get food A in VS. This association takes place within the limbic loop, and the nucleus accumbens is the nexus that links goal representations to their *current* value (i.e., their counterparts in Amg). “Current” because the Amg is capable of changing the value assigned to different stimuli on the basis of the animal current internal states, e.g. if it is hungry or satiated.

Once these associations are formed, the system can exploit them to act adaptively. In particular, the goals encoded and selected within the limbic loop are associated to the actions encoded in the sensorimotor loop. These connections rely on cortico-cortical inter-loop pathways and also on sub-cortical pathways (dopaminergic spirals). In real animals, these associations form with learning but for simplicity in the model they are hand-coded. Once these links have been learned the sole activation of goal representations in VS by the Amg (e.g., because a lever related to a valuable goal is perceived) is sufficient to bias the selection of the action that leads to accomplish the selected goal.

Figure 14 shows how the model reproduces the devaluation effect. The figure reports the number of lever presses in rats with intact Amg (intact, or “sham”, rats) and in rats where Amg has been lesioned (“BLA-lesioned” rats: the basolateral amygdala – BLA – is an important part of Amg). The figure shows that sham rats tend to press the lever more frequently when food B (previously instrumentally associated with the chain) is devalued than when food A (previously associated with the lever) is devalued. The causes of this behaviour are as follows. During the training phase, the rat acquires two habits within the sensorimotor loop, one that leads it to press the lever when it sees the lever, and one that leads it to pull the chain when it sees the chain. After the devaluation of one food, the rat is tested by setting it in front of both the lever and the chain at the same time. In this case both habits are triggered and try to recall the action related to them (pressing the lever and, at the same time, pulling the chain). If the Amg is intact, the sight of the lever and the chain recall the food A and food B representations within it. However, only one of these representations can actually manifest as the other is inhibited by the satiation internal state (say for food B). Such active representation (say for food A) can so activate the units of VS corresponding to the food A outcome and then, via the connections to cortex, to bias the selection of one action (e.g., pressing the lever). Instead, when Amg is lesioned then VS cannot preferentially select one outcome and so unbalance the selection for one or the other available actions. As a result the rat will select the two actions with a similar frequency.

This model highlights the typical features, and the limitations, of the research that focusses on the sub-cortical hierarchy of brain. First, the model emphasises

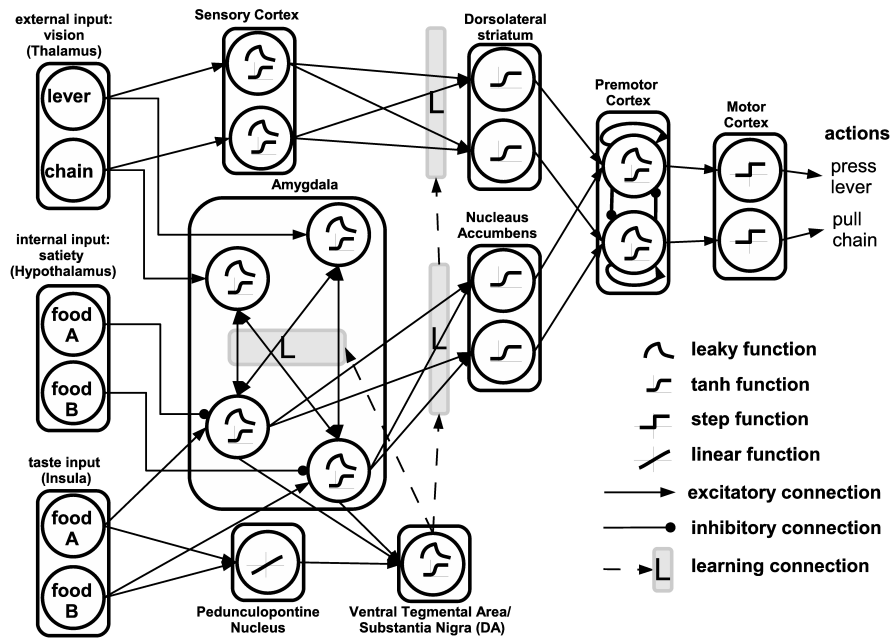


Fig. 13: The architecture of the model used to investigate the devaluation effect. Reprinted from (Mannella et al., 2010) (copyright 2010, with permission from Cambridge University Press).

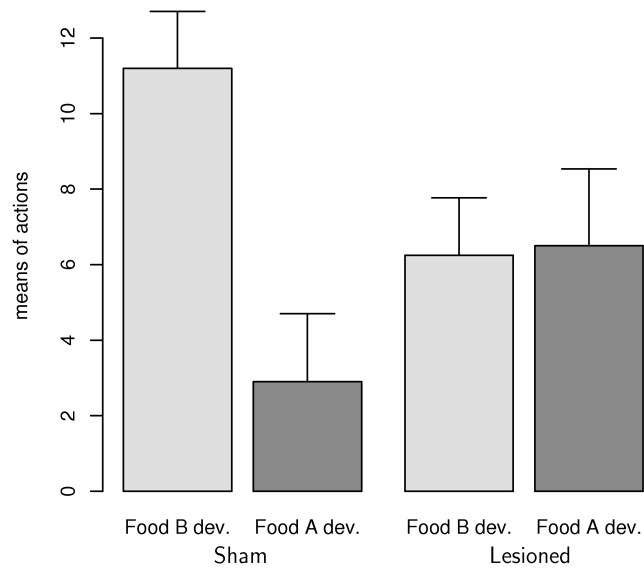


Fig. 14: Behaviour of the simulated rats in the devaluation experiment. The histogram bars show the average and standard deviation of actions performed by Sham and BLA-lesioned rats on the lever (previously instrumentally associated with food A) when either food A or food B have been devalued. Reprinted from (Mannella et al., 2010) (copyright 2010, with permission from Cambridge University Press).

the trial-and-error learning processes taking place within each cortico-striatal loop, and its fundamental role for the acquisition of their capacity to select the cortical contents. Second, such learning processes are guided by the value systems, such as the amygdala and the dopaminergic system, that lead the animal to learn to select actions and goals that are valuable for survival and reproduction (e.g., to acquire food). Third, the model captures the hierarchy existing between the different cortico-striatal loops: importantly for this review, the hierarchy captures in particular the flow of control from the higher “limbic” levels, informed on the actual needs of the animal, to the lower sensorimotor levels (notice how this contrasts with reinforcement learning models that use trial-and-error processes to mainly implement sensorimotor transformations linking the sensations from the outer world to the actions to perform).

Aside these strengths, the model has also some important limitations with respect to the explanation of brain hierarchy. The most important ones are that actions (e.g. “pressing a lever” or “pulling a chain”) are considered as ready-available wholes that the sensorimotor loop can select in correspondence to stimuli, affordances are abstracted away, and goals are assumed to be already formed and ready to be selected by the limbic loop. This means that the model does not account for the processes involving the sensorimotor/cognitive transformations happening at different levels of abstraction and accounted for by the literature focussing on the cortical hierarchy of brain, e.g. considered in the model reviewed in the previous section.

5 Integrating the cortical and sub-cortical hierarchies

Based on the reviews and the models presented in the previous sections, we can now propose an integrated view of the cortical and sub-cortical hierarchies of brain. This is summarised in Figure 15. We first present this view by focussing on the role of cortex and basal ganglia in the hierarchy, then we illustrate some detailed aspects of the different functioning mechanisms of the two, and finally we highlight important system-level open problems highlighted by the view.

The general idea is that cortex implements sensorimotor/cognitive transformations needed to perform and control action at different levels of abstraction. The sensorimotor neural pathway (SSC-MC) implements the dynamic mapping closely linking the proprioception to the control of muscles. The dorsal neural pathway (PPC-PMC-MC) encodes affordances (PPC) and possible motor plans (PMC) to be executed downstream (MC). The ventral neural pathway (ITC-dlPFC) detects the resources available in the environment (ITC) and, based on this information and higher level information from areas encoding value (OFC, vmPFC), biases the selection of motor plans (SMC-PMC; note that there are also important connections from PFC to PC, not reported here for simplicity, that allow PFC to contribute to select affordances within PC). Overall, the various pathways perform different mappings from sensation to action taking place at increasing levels of abstraction: from proprioception to muscles (SSC-MC); from visual information needed to interact with objects to motor plans (VC-

PPC–PMC–MC); from visual information on the nature of objects to high level goals (VC–ITC–dlPFC–SMC–PMC); from visceral states to biologically charged goals (Amg/Hip/Hyp–OFC/vmPFC–dlPFC).

Each loop of the basal ganglia collects a rich set of information from various areas of cortex and on this basis selects the contents processed in specific target cortical areas. These selection processes involve the whole cortex with the exception of primary cortical areas, and have an increasing importance (e.g., in terms of neural resources involved) going towards the higher levels of the hierarchy. So, at the highest level of the hierarchy the VS, supplied with rich information on value of stimuli by various sub-cortical areas (e.g., Amg, Hip, Hyp), contributes to select biologically relevant goals encoded in OFC/vmPFC (e.g., in relation to the achievement of a particular food). At a lower level, the DMS contributes to selects more abstract goals (e.g., pressing a lever) encoded in dlPFC, affordances encoded in PPC, and object identity encoded in ITC. At the lowest level, the DLS selects motor plans, encoded in PMC, and action implementation processes, encoded in MC. The hierarchy formed by basal ganglia also involve “inter-loop” mechanisms, such as the dopaminergic spirals (VTA, SNpc), that carry information on value, and cortico-thalamo-cortical connections, not represented in the figure.

The integrated view we just proposed, that assigns to cortex a special role in performing sensorimotor/cognitive transformations and to basal ganglia a special role in performing selection, in particular on the basis of value, is supported by four general system-level features of the two systems. Some aspects of these features are represented in Figure 16. The first feature involves the input/output ratio of each element of the two systems (e.g., PMC or DLS). This ratio is very high in basal ganglia with respect to cortex. Striatal neurons have a very large input from various cortical areas, whereas their output is focussed and concentrated on one specific cortical area with which it forms a loop (Redgrave et al., 1999; Wilson, 1995). This makes this funnel-like architecture of basal ganglia ideally suited to perform the selection of whole neural assemblies at the level of the targeted cortex. Instead, cortical areas usually reciprocate a similar amount of connections to the areas from which they receive an input (Felleman and Van Essen, 1991). This architecture is ideal to perform complex mappings through which detailed information (e.g. on perception) is transformed into other detailed information (e.g., on motor commands).

A second important feature is the realm of activity of the two systems. Cortex covers all aspect of cognition, from primary sensory processing to primary motor processing, from associative processing to the processing needed to implement executive functions. Instead, basal ganglia play an increasingly important role, measurable in terms of neural resources involved, going from sensory input to motor output, and from lower to higher levels of “cognition” (Alexander and Crutcher, 1990). Thus, basal ganglia do not project to primary sensory cortical areas, involved with sensory low-level cognition processes (Romanelli et al., 2005); the basal ganglia regions involving DMS have some projections to sensory associative areas (PC, IT); those involving DLS have important projections to

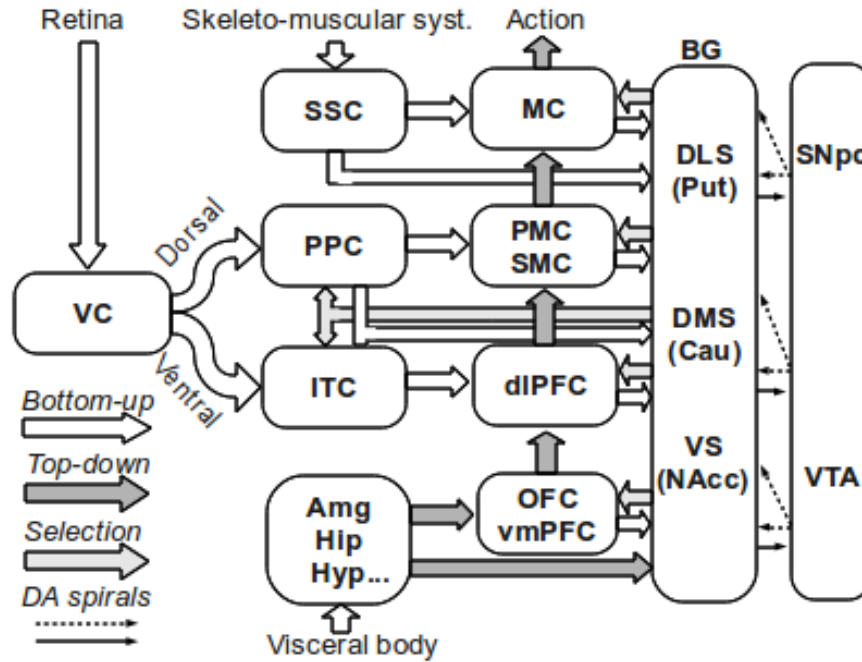


Fig. 15: An integrated view of the cortical and basal ganglia systems. Acronyms: Amg: amygdala; BG: basal ganglia; DA: dopamine; DLS: dorsolateral striatum; DMS: dorsomedial striatum; Hip: hippocampus; Hyp: hypothalamus; dlPFC: dorsolateral prefrontal cortex; ITC: inferotemporal cortex; MC: motor cortex; OFC: orbitofrontal cortex; PMC: premotor cortex; PPC: posterior parietal cortex; SMC: somatosensory cortex; SNpc: substantia nigra, pars compacta; SSC: somatosensory cortex; VC: visual cortex; vmPFC: ventromedial prefrontal cortex; VTA: ventral tegmental area.

the frontal cortex area where the brain processes action preparation and execution (PMC, MC); finally those involving DMS and VS have a major target in cortical areas implementing processes related to high-level executive functions (respectively dlPFC and OFC/vmPFC). These patterns allow cortex to perform detailed computations at all levels of cognition, while assign to basal ganglia a special role in selecting information at high levels of cognition and close to action preparation and performance.

A third feature is that the highest levels of the basal ganglia hierarchy (involving VS) are also more strongly linked to the sub-cortical areas processing value (e.g., Amg and Hip) with respect to the highest levels of the cortical hierarchy (PFC) (Graybiel and Kimura, 1995). The ventral basal ganglia are also more strongly involved in the regulation, and as targets, of dopamine than the

related cortical areas (Abercrombie et al., 1989; Berridge and Robinson, 1998). These features pose basal ganglia in an ideal position to be informed about the subjective relevance of stimuli, i.e. value, so to perform at best the selection processes.

The last feature involves the learning processes usually ascribed to the two systems. Cortex is usually seen as the locus of unsupervised or associative learning (Doya, 2000), as also indicated by the long term potentiation (LTP) processes happening in it (Iriki et al., 1989; Kirkwood et al., 1996). Basal ganglia, instead, have a micro-architecture that makes it ideal for selection (Redgrave et al., 1999) and for trial-and-error learning guided by dopamine learning signals (Joel et al., 2002).

We close this section by showing a last aspect of the integrated system-level framework, in particular how it might aid the identification of the local micro interactions of the cortical and basal-ganglia systems where they physically contact. This is illustrated on the basis of Figure 16. The cortical pathways implement detailed and focussed sensorimotor/cognitive transformations that progressively transform signals from sensory to motor areas (Cisek and Kalaska, 2010; Miller and Cohen, 2001). Instead, basal ganglia collect a wide range of information, including important information on value (Graybiel and Kimura, 1995), and then perform a targeted selection of spatially limited, cortical contents based on focussed output channels involving the striatum-pallidal disinhibition mechanism (Chevalier and Deniau, 1990). This *disinhibition* mechanism acts on the cortico-thalamic loops by freeing it from the tonic inhibition of GPi/SNpr so as to *let the information flow of the sensorimotor/cognitive transformations passing through the targeted cortical pathway stage to pass without interruption* (Mink, 1996). In particular, information that travels through the various stages of cortex is amplified/refined/preserved by the close loops of such stages with thalamus. These cortico-thalamic loops are by default interrupted (at the level of thalamus) by tonic inhibitory inputs from basal-ganglia outputs. When basal-ganglia release from such inhibition specific cortico-thalamic loops, information is free to be elaborated and flow through the corresponding cortical area. The overall idea is thus that information travels from cortical sensory areas to motor cortical areas via different sensorimotor/cognitive transformation pathways: each of these is formed by various cortical stages within which the various specific contents, part of the information flow, can be either stopped or allowed to be elaborated and pass by the specific channels of the basal-ganglia loops targeting them.

6 Conclusions

The hierarchical organisation of behaviour requires the implementation of three key functions by the underlying brain hierarchy, namely the implementation of sensorimotor/cognitive transformations at multiple levels of abstraction, the selection of various elements of such transformations, and the guidance of the learning processes. Based on this conceptual grid, the article showed how current

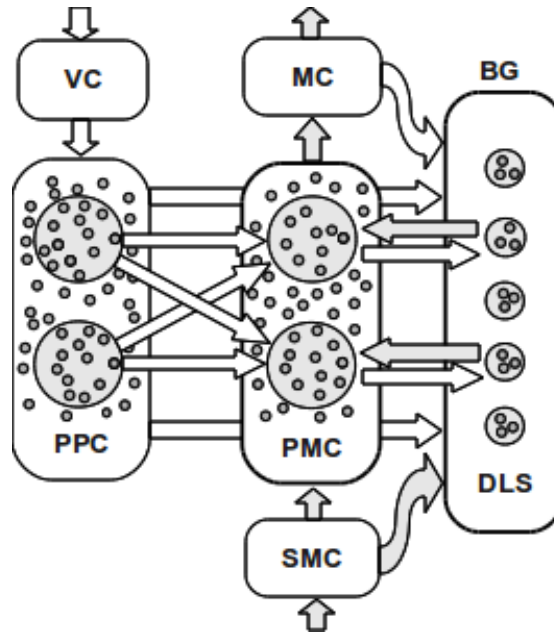


Fig. 16: Mechanisms of interaction involving cortex and basal ganglia (BG). The interactions are explained in the graph with a focus on the BG-cortical loop involving DLS and PMC. With respect to cortex, notice how: (a) PMC is part of a bottom-up information flow involving the VC-PPC-PMC cortical pathway; (b) PMC activity is modulated by a top-down information flow involving the SMC-PMC cortical pathway; (c) the VC-PPC-PMC-MC input-output pathway is “intercepted”, at the level of PMC, by a cortico-basal ganglia loop involving DLS and supporting the selections happening within the PMC itself. With respect to basal ganglia: (a) DLS forms a loop with the target PMC cortical region; (b) DLS also receives information from all cortical areas that are linked to PMC (and from other cortical areas not reported here): the ample information gathered through these connections allows DLS to perform a well-informed selection of PMC contents. The graph also schematically illustrate the neural processes happening within and between DLS and PMC: (a) the cortical cell assemblies have comparable size (e.g., those of PPC and PMC in the graph) and exchange all-to-all connections (e.g., the PPC-PMC ones): this allows cortical pathways to perform fine mappings at all levels of cognition; (b) BG receive all-to-all afferent connections from cortex, but exchange connections organised in separate channels with the target cortex (DLS-PMC connections); (c) the BG cell assemblies are much smaller than those of cortex, so implementing a notable funnelling of cortical-to-BG information, and an “abstract control” of BG over the targeted cortex. See Figure 15 for the acronyms.

research on the hierarchical organisation of brain is either focussed on the study of *cortical hierarchies*, or on the study of *sub-cortical hierarchies* formed by basal ganglia and other sub-cortical components processing value and motivations. When taken in isolation, these two approaches have important limitations in accounting for brain hierarchy. In particular, they either tend to ascribe to the systems they study all the three processes needed by the hierarchical organisation of behaviour, or they overlook some of those processes altogether. Thus, the cortical account often fails to specify the selection mechanisms needed to direct the course of action, and in large part the motivational mechanisms guiding learning processes. On the other side, in most cases the sub-cortical account fails to explain how the detailed sensorimotor and cognitive input-output mappings are learned and expressed.

The type of accounts of the hierarchical organisation of brain given by the two literature threads have been exemplified here through the presentation of two models, focussed respectively on the hierarchical processes implemented by the cortex and on the processes implemented by basal ganglia and amygdala. The two models made apparent how the two approaches mainly focus on, respectively, the explanation of sensorimotor/cognitive transformations happening at different levels of abstraction and on the explanation of selection based on value. The two models also highlighted that the computational approaches that back up the cortical and sub-cortical empirical study of brain hierarchy are affected by the same limitations and biases of the related empirical literatures.

Given these limitations, this paper has proposed a system-level framework on hierarchical brain within which the cortical and sub-cortical systems form a *whole integrated hierarchical system* and play complementary distinct roles. The principle of this integrated view can be summarised as follows:

- Cortex is formed by multiple sensorimotor and cognitive pathways that perform fine and detailed information elaborations and transformations from sensations to actions. The capability to perform the elaborations and transformations is acquired mainly through unsupervised and associative learning mechanisms. The major pathways are: (a) a somatosensory-motor pathway to implement learning and performance of motor skills (this mainly involves somatosensory and motor cortex); (b) a dorsal pathway to build affordances and to prepare actions (this mainly involves parietal and premotor cortex). (c) a ventral pathway to identify the resources in the environment and to implement the highest level cognitive processes such as the executive control of goals encoded at multiple levels of abstraction (this mainly involves temporal and prefrontal cortex).
- Basal-ganglia form multiple loops with cortex and select information at multiple levels of abstraction. The ability to perform such selections is acquired on the basis of trial-and-error learning processes. The major basal-ganglia cortical loops are: (a) a sensorimotor loop, important for selecting motor acts (this involves dorsolateral portions of the basal ganglia, and motor cortex); (b) an associative loop, important to select perceptual and high-level cognition contents (this involves medial portions of basal ganglia, and tem-

- poral, parietal, and prefrontal cortex); (c) a limbic loop, important for selecting goals and contents with high biological valence, and to regulate the dopamine system (this involves ventral portions of basal ganglia, and orbital and medial prefrontal portions of cortex).
- The highest cortical levels and the ventral basal-ganglia levels have a strong interaction with limbic sub-systems of brain, and so are informed on the motivational and biological value of stimuli, events, and experiences (this involves sub-systems such as amygdala, hippocampus, hypothalamus, and the dopaminergic centres). This information drives and guides the learning processes happening in cortical and basal ganglia systems.
 - Information flows and is finely elaborated within the cortical pathways, and within the various stages of such pathways, especially close to the output and at high-levels of cognition, basal ganglia select them by inhibiting or letting them pass through.

The integrated framework proposed here leads to overcome the limitations of the cortical and sub-cortical accounts of hierarchical brain when taken in isolation. Indeed, within the framework the limitations of the cortical theories related to the selection and learning guidance functions are overcome by the fact that such functions are mainly implemented by the sub-cortical systems. On the other side, the limitation of the sub-cortical theories related to the lack of explanation of the fine sensorimotor and cognitive transformations are overcome by the implementation of such function by cortical pathways.

Aside these strengths, the hypothesis has still some open problems. We mention few of these. As explained in Section 2, cortical systems are usually assumed to implement two forms of learning, namely unsupervised learning (especially within the perceptual areas) and associative learning (especially within the frontal areas). This raises a problem for the view proposed here when actions or other chunks of knowledge have to be acquired by the cortex on the basis of trial-and-error processes. The framework proposed here offers a solution to this problem. The solution is based on the intriguing idea that, at least when learning happens above a certain level of abstraction, basal-ganglia can acquire the mappings by trial-and-error, and then the information so acquired is progressively transferred to the cortex, which learns on the basis of associative processes under the “instruction” (supervision) by basal ganglia. There is indeed empirical evidence (Carelli et al., 1997; Tang et al., 2007) that when behaviour is first acquired and then automatized (i.e., it becomes “habitual”) the basal ganglia show a high initial activation that then decreases with the progress of learning (see also Ashby et al., 2010, for a review and Ashby et al., 2007, for a model). This hypothesis, however, needs to be further investigated in future work.

The second problem is a specification of the previous one when it is applied to the cortical acquisition of fine and detailed somatosensory-motor cortical transformations (e.g., the mapping implementing a skill). In this case, the mechanism proposed above cannot be exploited because, as shown in Figure 16, basal ganglia can select cortical neural assemblies only at a gross level given their reduced number of neurons with respect those of the targeted cortical areas. So, how

can such mappings be acquired? This is a problem left open by the framework presented here, and leading us to touch an issue that can be only introduced here and that should be tackled in future work. A possible solution to the problem might rely upon the *cerebellum*. Cerebellum, hosting more than half of the neurons of brain, plays a critical role in the acquisition and expression of motor behaviour (Houk and Wise, 1995; Kawato, 1999). The problem mentioned above could be solved by a close interplay between the cortical somatosensory loop and cerebellum. A possible idea to explore would be that cerebellum aids the cortex to acquire fine sensorimotor mappings based on the *supervised learning processes* that it implements (Doya, 2000; Rolls and Treves, 1998). In line with this, some authors propose that the cerebellum plays a key role during learning but then progressively passes the acquired information to cortex (see Hua and Houk, 1997, for a review and a model). We think that the overall motor hierarchy involving the cerebellum would see the basal ganglia, cortex, and cerebellum playing their major roles respectively at the top, middle, and lower levels of the hierarchy, so we partially disagree with this view. However, we recognise that it represents a solution to the problem we are considering. This issues need further considerations in the future and to be reconciled within the framework proposed here.

The latter observation leads naturally to highlight a further limitation of the framework proposed here, namely the need to integrate cerebellum within it. Indeed, aside the sheer computational importance that cerebellum has within the nervous systems, there are strong indications that it forms important loops with cortex similarly to basal ganglia (Middleton and Strick, 2000b). Moreover, cerebellum plays important functions not only for motor behaviour but also for cognitive processes (Ito, 2008). These aspects should be accounted for by a system-level framework of brain hierarchy like the one presented here, a further issue to be investigated in future work.

Although we recognise the existence of these and other open issues, we think that the system-level framework presented here offers a better understanding of how the brain actually implements the three key functions critical for the hierarchical organisation of behaviour – sensorimotor/cognitive transformations, selection, and learning guidance – than the cortical and sub-cortical theories of it. In this respect, the framework is an important theoretical tool usable to formulate new specific theories, to make new predictions and to design new experiments to test them, and to design new computational models on brain hierarchy.

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Bibliography

- Abercrombie, E. D., Keefe, K. A., DiFrischia, D. S., and Zigmond, M. J. (1989). Differential effect of stress on in vivo dopamine release in striatum, nucleus accumbens, and medial frontal cortex. *J Neurochem*, 52(5):1655–1658.
- Alcock, J. (1998). *Animal behavior: an evolutionary approach*. Sinauer Associated, Sunderland, MA, sixth edition.
- Alexander, G. E. and Crutcher, M. D. (1990). Functional architecture of basal ganglia circuits: neural substrates of parallel processing. *Trends Neurosci*, 13(7):266–271.
- Alexander, G. E., DeLong, M. R., and Strick, P. L. (1986). Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annu Rev Neurosci*, 9:357–381.
- Ashby, F. G., Ennis, J. M., and Spiering, B. J. (2007). A neurobiological theory of automaticity in perceptual categorization. *Psychol Rev*, 114(3):632–656.
- Ashby, F. G., Turner, B. O., and Horvitz, J. C. (2010). Cortical and basal ganglia contributions to habit learning and automaticity. *Trends Cogn Sci*, 14(5):208–215.
- Balleine, B. W. and Dickinson, A. (1998). Goal-directed instrumental action: contingency and incentive learning and their cortical substrates. *Neuropharmacology*, 37(4-5):407–419.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, 59:617–645.
- Barto, A. G., Singh, S., and Chentanez, N. (2004). Intrinsically motivated learning of hierarchical collections of skills. In Triesch, J. and Jebara, T., editors, *International Conference on Developmental Learning (ICDL2004)*, pages 112–119, Piscataway, NJ. IEEE. UCSD Institute for Neural Computation, LaJolla, CA.
- Barto, A. G., Sutton, R. S., and Anderson, C. W. (1983). Neuronlike adaptive elements that that can learn difficult control problems. *IEEE Transactions on Systems Man and Cybernetics*, 13:835–846.
- Bast, T. (2007). Toward an integrative perspective on hippocampal function: from the rapid encoding of experience to adaptive behavior. *Rev Neurosci*, 18(3-4):253–281.
- Berridge, K. C. and Robinson, T. E. (1998). What is the role of dopamine in reward: hedonic impact, reward learning, or incentive salience? *Brain Res Rev*, 28(3):309–369.

- Botvinick, M. M., Niv, Y., and Barto, A. (2008). Hierarchically organized behavior and its neural foundations: A reinforcement-learning perspective. *Cognition*, 113(3):262–280.
- Caligiore, D., Borghi, A. M., Parisi, D., and Baldassarre, G. (2010). TRoPI-CALS: A computational embodied neuroscience model of compatibility effects. *Psychological Review*, 117:1188–1228.
- Caligiore, D., Borghi, A. M., Parisi, D., Ellis, R., Cangelosi, A., and Baldassarre, G. (2012). How affordances associated with a distractor object affect compatibility effects: A study with the computational model *tropicals*. *Psychological Research*, 77:7–19.
- Cardinal, R. N., Parkinson, J. A., Hall, J., and Everitt, B. J. (2002). Emotion and motivation: the role of the amygdala, ventral striatum, and prefrontal cortex. *Neurosci Biobehav Rev*, 26(3):321–352.
- Carelli, R. M., Wolske, M., and West, M. O. (1997). Loss of lever press-related firing of rat striatal forelimb neurons after repeated sessions in a lever pressing task. *J Neurosci*, 17(5):1804–1814.
- Chevalier, G. and Deniau, J. M. (1990). Disinhibition as a basic process in the expression of striatal functions. *Trends Neurosci*, 13(7):277–280.
- Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362:1585–1599.
- Cisek, P. and Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*, 33:269–298.
- Corbit, L. H. and Balleine, B. W. (2011). The general and outcome-specific forms of pavlovian-instrumental transfer are differentially mediated by the nucleus accumbens core and shell. *J Neurosci*, 31(33):11786–11794.
- Corbit, L. H., Muir, J. L., and Balleine, B. W. (2001). The role of the nucleus accumbens in instrumental conditioning: Evidence of a functional dissociation between accumbens core and shell. *J Neurosci*, 21(9):3251–3260.
- Daw, N. D., Niv, Y., and Dayan, P. (2005). Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control. *Nat Neurosci*, 8(12):1704–1711.
- Dayan, P. and Abbott, L. F. (2001). *Theoretical Neuroscience: computational and mathematical modeling of neural systems*. The MIT Press, Cambridge, MA.
- Deco, G. and Rolls, E. T. (2003). Attention and working memory: a dynamical model of neuronal activity in the prefrontal cortex. *European Journal of Neuroscience*, 18:2374–2390.

- Doya, K. (2000). Complementary roles of basal ganglia and cerebellum in learning and motor control. *Curr Opin Neurobiol*, 10(6):732–739.
- Ellis, R. and Tucker, M. (2001). The potentiation of grasp types during visual object categorization. *Visual Cognition*, 8:769–800.
- Ellis, R., Tucker, M., Symes, E., and Vainio, L. (2007). Does selecting one visual object from several require inhibition of the actions associated with nonselected objects? *Journal of Experimental Psychology Human Perception and Performance*, 33:670–691.
- Erlhagen, W. and Schoner, G. (2002). Dynamic field theory of movement preparation. *Psychological Review*, 109:545–571.
- Evangelidou, M. N., Raos, V., Galletti, C., and Savaki, H. E. (2009). Functional imaging of the parietal cortex during action execution and observation. *Cerebral Cortex*, 19:624–639.
- Fagg, A. H. and Arbib, M. A. (1998). Modeling parietal-premotor interactions in primate control of grasping. *Neural Netw*, 11(7-8):1277–1303.
- Felleman, D. J. and Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cereb Cortex*, 1(1):1–47.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., and Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Science*, 308:662–667.
- Fuster, J. M. (2001). The prefrontal cortex—an update: time is of the essence. *Neuron*, 30:319–333.
- Gazzaniga, M. (2004). *The cognitive neurosciences III*. MIT press, Cambridge, MA.
- Grace, A. A., Floresco, S. B., Goto, Y., and Lodge, D. J. (2007). Regulation of firing of dopaminergic neurons and control of goal-directed behaviors. *Trends Neurosci*, 30(5):220–227.
- Graybiel, A. and Kimura, M. (1995). Adaptive neural networks in the basal ganglia. In Houk, J. C., Davis, J., and Beiser, D., editors, *Models of Information Processing in the Basal Ganglia*, pages 103–116. The MITT Press, Cambridge, MA.
- Graziano, M. S. A. (2011). New insights into motor cortex. *Neuron*, 71(3):387–388.
- Gurney, K., Prescott, T., and Redgrave, P. (2001). A computational model of action selection in the basal ganglia. i. a new functional anatomy. *Biological Cybernetics*, 84:401–410.
- Haber, S. N. (2003a). The primate basal ganglia: parallel and integrative networks. *J Chem Neuroanat*, 26(4):317–330.

- Haber, S. N. (2003b). The primate basal ganglia: parallel and integrative networks. *J Chem Neuroanat*, 26(4):317–330.
- Haber, S. N., Fudge, J. L., and McFarland, N. R. (2000). Striatonigrostriatal pathways in primates form an ascending spiral from the shell to the dorsolateral striatum. *Journal of Neuroscience*, 20:2369–82.
- Hall, J., Parkinson, J. A., Connor, T. M., Dickinson, A., and Everitt, B. J. (2001). Involvement of the central nucleus of the amygdala and nucleus accumbens core in mediating pavlovian influences on instrumental behaviour. *Eur J Neurosci*, 13(10):1984–1992.
- Hamilton, A. F. and Grafton, S. (2007). *The motor hierarchy: from kinematics to goals and intentions*, volume 22, pages 381–408. Oxford University Press, Oxford.
- Hebb, D. O. (1949). *The Organization of Behaviour*. Wiley, John and Sons, New York, NY.
- Heimer, L., Switzer, R. D., and Hoesen, V. G. W. (1982). Ventral striatum and ventral pallidum: Components of the motor system? *Trends in Neurosciences*, 5(0):83 – 87.
- Houk, J. C., Davis, J., and Beiser, D., editors (1995). *Models of Information Processing in the Basal Ganglia*. The MITT Press, Cambridge, MA.
- Houk, J. C. and Wise, S. P. (1995). Distributed modular architectures linking basal ganglia, cerebellum, and cerebral cortex: their role in planning and controlling action. *Cereb Cortex*, 5(2):95–110.
- Hua, S. E. and Houk, J. C. (1997). Cerebellar guidance of premotor network development and sensorimotor learning. *Learn Mem*, 4(1):63–76.
- Humphries, M. D. and Prescott, T. J. (2010). The ventral basal ganglia, a selection mechanism at the crossroads of space, strategy, and reward. *Prog Neurobiol*, 90(4):385–417.
- Iriki, A., Pavlides, C., Keller, A., and Asanuma, H. (1989). Long-term potentiation in the motor cortex. *Science*, 245(4924):1385–1387.
- Ito, M. (2008). Control of mental activities by internal models in the cerebellum. *Nat Rev Neurosci*, 9(4):304–313.
- Jeannerod, M. (1999). Visuomotor channels: Their integration in goal-directed prehension. *Human Movement Science*, 18(2-3):201–218.
- Joel, D., Niv, Y., and Ruppin, E. (2002). Actor-critic models of the basal ganglia: new anatomical and computational perspectives. *Neural Netw*, 15(4-6):535–547.
- Kawato, M. (1999). Internal models for motor control and trajectory planning. *Curr Opin Neurobiol*, 9(6):718–727.

- Kilner, J. M. (2011). More than one pathway to action understanding. *Trends in Cognitive Sciences*, 15:352–357.
- Kimchi, E. Y. and Laubach, M. (2009). Dynamic encoding of action selection by the medial striatum. *J Neurosci*, 29(10):3148–3159.
- Kirkwood, A., Rioult, M. C., and Bear, M. F. (1996). Experience-dependent modification of synaptic plasticity in visual cortex. *Nature*, 381(6582):526–528.
- Koechlin, E. and Summerfield, C. (2007). An information theoretical approach to prefrontal executive function. *Trends Cogn Sci*, 11(6):229–235.
- Kohonen, T. (2003). Self-organized maps of sensory events. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 361:1177–1186.
- Lestou, V., Pollick, F. E., and Kourtzi, Z. (2008). Neural substrates for action understanding at different description levels in the human brain. *Journal of Cognitive Neuroscience*, 20:324–341.
- Levy, R., Friedman, H. R., Davachi, L., and Goldman-Rakic, P. S. (1997). Differential activation of the caudate nucleus in primates performing spatial and nonspatial working memory tasks. *Journal of Neuroscience*, 17(10):3870–3882.
- Lewis, S. J. G., Dove, A., Robbins, T. W., Barker, R. A., and Owen, A. M. (2004). Striatal contributions to working memory: a functional magnetic resonance imaging study in humans. *Eur J Neurosci*, 19(3):755–760.
- Lisman, J. E. and Grace, A. A. (2005). The hippocampal-vta loop: controlling the entry of information into long-term memory. *Neuron*, 46(5):703–713.
- MacFarland, D. (1993). *Animal behavior*. Longman Group, Harlow, UK, second edition.
- Mannella, F., Mirolli, M., and Baldassarre, G. (2010). The interplay of pavlovian and instrumental processes in devaluation experiments: a computational embodied neuroscience model tested with a simulated rat. In Tosh, C. and Ruxton, G., editors, *Modelling Perception With Artificial Neural Networks*, pages 93–113. Cambridge University Press, Cambridge.
- Mannella, F., Mirolli, M., and Baldassarre, G. (2011). A system-level neural model of the brain mechanisms underlying instrumental devaluation in rats. In *COSYNE - Computational and Systems Neuroscience (2011), Salt Lake City, 24 February 2011*. Available from Nature Precedings: <http://precedings.nature.com/documents/5849/version/1>.
- Meunier, D., Lambiotte, R., and Bullmore, E. T. (2010). Modular and hierarchically modular organization of brain networks. *Front Neurosci*, 4:200.
- Middleton, F. A. and Strick, P. L. (1996). The temporal lobe is a target of output from the basal ganglia. *Proc Natl Acad Sci U S A*, 93(16):8683–8687.

- Middleton, F. A. and Strick, P. L. (2000a). Basal ganglia and cerebellar loops: motor and cognitive circuits. *Brain Res Rev*, 31(2-3):236–250.
- Middleton, F. A. and Strick, P. L. (2000b). Basal ganglia and cerebellar loops: motor and cognitive circuits. *Brain Res Rev*, 31(2-3):236–250.
- Miller, E. K. and Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annu Rev Neurosci*, 24:167–202.
- Milner, A. D. and Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, 46:774–785.
- Mink, J. W. (1996). The basal ganglia: focused selection and inhibition of competing motor programs. *Prog Neurobiol*, 50(4):381–425.
- Mirolli, M., Mannella, F., and Baldassarre, G. (2010). The roles of the amygdala in the affective regulation of body, brain, and behaviour. *Connection Science*, 22(3):215–245.
- Mirolli, M., Santucci, V. G., and Baldassarre, G. (2013). Phasic dopamine as a prediction error of intrinsic and extrinsic reinforcements driving both action acquisition and reward maximization: A simulated robotic study. *Neural Networks*, 39:40–51.
- Munakata, Y., Herd, S. A., Chatham, C. H., Depue, B. E., Banich, M. T., and O’Reilly, R. C. (2011). A unified framework for inhibitory control. *Trends Cogn Sci*, 15(10):453–459.
- Nachev, P., Kennard, C., and Husain, M. (2008). Functional role of the supplementary and pre-supplementary motor areas. *Nature Reviews Neuroscience*, 9:856–869.
- Oztop, E. and Arbib, M. A. (2002). Schema design and implementation of the grasp-related mirror neuron system. *Biol Cybern*, 87(2):116–40.
- Pavrides, C., Miyashita, E., and Asanuma, H. (1993). Projection from the sensory to the motor cortex is important in learning motor skills in the monkey. *J Neurophysiol*, 70(2):733–741.
- Pitkänen, A., Savander, V., and LeDoux, J. E. (1997). Organization of intra-amygdaloid circuitries in the rat: an emerging framework for understanding functions of the amygdala. *Trends Neurosci*, 20(11):517–523.
- Pouget, A., Dayan, P., and Zemel, R. (2000). Information processing with population codes. *Nature Reviews Neuroscience*, 1:125–132.
- Redgrave, P., Prescott, T. J., and Gurney, K. (1999). The basal ganglia: a vertebrate solution to the selection problem? *Neuroscience*, 89:10091024.
- Redgrave, P., Rodriguez, M., Smith, Y., Rodriguez-Oroz, M. C., Lehericy, S., Bergman, H., Agid, Y., DeLong, M. R., and Obeso, J. A. (2010). Goal-directed and habitual control in the basal ganglia: implications for parkinson’s disease. *Nat Rev Neurosci*, 11(11):760–772.

- Rizzolatti, G. and Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27:169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V., and Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research*, 3:131–141.
- Rolls, E. T. and Treves, A. (1998). *Neural networks and brain function*. Oxford University Press, Oxford.
- Romanelli, P., Esposito, V., Schaal, D. W., and Heit, G. (2005). Somatotopy in the basal ganglia: experimental and clinical evidence for segregated sensorimotor channels. *Brain Res Rev*, 48(1):112–128.
- Schrimsher, G. W., Billingsley, R. L., Jackson, E. F., and Moore, B. D. (2002). Caudate nucleus volume asymmetry predicts attention-deficit hyperactivity disorder (adhd) symptomatology in children. *J Child Neurol*, 17(12):877–884.
- Sobel, I. and Feldman, G. (1968). A 3x3 isotropic gradient operator for image processing. Presentation for Stanford Artificial Project.
- Solway, A. and Botvinick, M. M. (2012). Goal-directed decision making as probabilistic inference: a computational framework and potential neural correlates. *Psychol Rev*, 119(1):120–154.
- Sutton, R. S. and Barto, A. G. (1998). *Reinforcement Learning: An Introduction*. MIT Press, Cambridge, MA.
- Tang, C., Pawlak, A. P., Prokopenko, V., and West, M. O. (2007). Changes in activity of the striatum during formation of a motor habit. *Eur J Neurosci*, 25(4):1212–1227.
- Thill, S., Caligiore, D., Borghi, A. M., Ziemke, T., and Baldassarre, G. (2013). Theories and computational models of affordance and mirror systems: An integrative review. *Neuroscience and Biobehavioral Reviews*.
- Todorov, E. and Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination. *Nat Neurosci*, 5(11):1226–1235.
- Tokimura, H., Di Lazzaro, V., Tokimura, Y., Oliviero, A., Profice, P., Insola, A., Mazzone, P., Tonali, P., and Rothwell, J. C. (2000). Short latency inhibition of human hand motor cortex by somatosensory input from the hand. *J Physiol*, 523 Pt 2:503–513.
- Ungerleider, L. G. and Mishkin, M. (1982). Two cortical visual systems. In Ingle, D. J., Goodale, M. A., and Mansfield, W. R. J., editors, *Analysis of Visual Behavior*, volume 549, pages 549–586. The MIT Press, Cambridge, MA.
- Venditti, A., Mirolli, M., Parisi, D., and Baldassarre, G. (2009). A neural-network model of the dynamics of hunger, learning and action vigor in mice. In Serra, R., Villani, M., and Poli, I., editors, *Artificial life and evolutionary computation - Proceedings of Wivace 2008*, pages 131–142. World Scientific, Singapore. Venice, Italy, 8-10 September 2008.

- Volkow, N. D., Wang, G.-J., Newcorn, J., Telang, F., Solanto, M. V., Fowler, J. S., Logan, J., Ma, Y., Schulz, K., Pradhan, K., Wong, C., and Swanson, J. M. (2007). Depressed dopamine activity in caudate and preliminary evidence of limbic involvement in adults with attention-deficit/hyperactivity disorder. *Arch Gen Psychiatry*, 64(8):932–940.
- Voorn, P., Vanderschuren, L. J. M. J., Groenewegen, H. J., Robbins, T. W., and Pennartz, C. M. A. (2004). Putting a spin on the dorsal-ventral divide of the striatum. *Trends Neurosci*, 27(8):468–474.
- Wallis, J. D., Anderson, K. C., and Miller, E. K. (2001). Single neurons in prefrontal cortex encode abstract rules. *Nature*, 411:953–956.
- Walsh, V. and Cowey, A. (2000). Transcranial magnetic stimulation and cognitive neuroscience. *Nat Rev Neurosci*, 1(1):73–79.
- Wilson, C. J. (1995). The contribution of cortical neurons to the firing pattern of striatal spiny neurons. In Houk, J. C., Davids, J. L., and Beiser, D. G., editors, *Models of Information Processing in the Basal Ganglia*, pages 29–50. The MIT Press, Cambridge, MA.
- Yeterian, E. H. and Pandya, D. N. (1995). Corticostriatal connections of extrastriate visual areas in rhesus monkeys. *J Comp Neurol*, 352(3):436–457.
- Yin, H. H. and Knowlton, B. J. (2006). The role of the basal ganglia in habit formation. *Nature Reviews Neuroscience*, 7:464–476.
- Yin, H. H., Ostlund, S. B., and Balleine, B. W. (2008). Reward-guided learning beyond dopamine in the nucleus accumbens: the integrative functions of cortico-basal ganglia networks. *Eur J Neurosci*, 28(8):1437–1448.
- Zahm, D. S. (2000). An integrative neuroanatomical perspective on some subcortical substrates of adaptive responding with emphasis on the nucleus accumbens. *Neurosci Biobehav Rev*, 24(1):85–105.