Computational Principles Underlying the Functioning of Amygdala in the Affective Regulation of Behaviour

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Abstract. This paper presents a short review, compiled with a computational perspective, of the empirical neuroscientific evidence related to amygdala, a brain complex situated at the core of various brain systems underlying motivations and emotions. The functions of amygdala are fundamental for organisms' adaptive behaviour as they allow them to assign subjective saliency and value to experienced world states, so enhancing the adaptive power of their cognitive processes. In this respect, the major goal of the review is outlining the main computational functionalities of amygdala emerging from the neuroscientific investigations on affective processes so as to contribute to highlight the general architectural and functioning mechanisms underlying organisms' emotional processes. This effort is also expected to fertilise the design of robot controllers exhibiting a flexibility and autonomy comparable to that of real organisms.

1 Introduction: Exploiting the Synergies Between the Neuroscientific Research on Amygdala and Embodied Artificial Intelligence

In decades of research, neuroscience has produced a large amount of data and insights relative to the neural substrates underlying emotions. These are now seen as a fundamental product of evolution that allows organisms to suitably regulate and flexibly modify behaviours on the basis of their survival and reproduction needs. Emotions play a central role in the behavioural flexibility exhibited by real organisms, and for this reason their study is important not only for the advancement of their overall scientific understanding but also for

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the design of autonomous robots capable of tackling unpredictable and non-stationary environments with a versatility similar to that of organisms. These principles have been investigated in depth in some models developed within the embodied artificial-intelligence community, for example see [1–3]. These works have the merit of outlining the general principles underlying emotions and of giving a general account of them in terms of embodiment and dynamic coupling with the environment (see [4] for a review). However, they usually present models that are only weakly related to the aforementioned empirical data. This implies missing important synergies in the study of emotions that might stem from the integration of the two approaches.

This paper introduces the first results of the theoretical and reviewing efforts of a research agenda directed to contribute to build those synergies and to lead the two research threads to have a stronger integration. In particular, the paper introduces relevant empirical evidence related to *amygdala* (Amg), probably the most important brain system integrating processes involving *external stimuli*, internal *cognitive processes*, and *internal states* related to organism's needs and homeostatic regulations. In doing so, the focus will be on the neuroscientific research showing the core functionality implemented by Amg. In this respect, we anticipate that the general function of Amg is to associate "unlearned behaviours", internal body and brain states, and internal body and brain modulations, to neutral stimuli coming from the external world so that they can acquire a biological salience and play a role in the regulation of various behaviours and cognitive processes. (note that, in the following, the expression "unlearned behaviours" will be used to refer to behaviours that might be either innate or developed during the first phases of life under strong genetic pressures and general environmental constraints, cf. [5]).

As mentioned above, the review of Amg's properties will be done with a computational perspective in mind (adaptive functions, neural mechanisms, etc.) and with the aim of isolating the fundamental principles underlying the functioning of the main brain systems involved in the regulation of emotions, motivations and learning. This effort is expected to produce insights that should be useful as a general framework for designing and implementing detailed computational embodied models, as it already happened in three of our previous works [6–8].

2 The Amygdala Anatomy and Core Functions

The Amg is an almond-shaped group of nuclei located within each medial temporal lobe of the brain. Figure 1 illustrates the broad anatomical organisation of Amg. In particular the figure shows that Amg is formed by three major sets of nuclei each playing a major distinct functional role: lateral amygdala (LA), basolateral amygdala (BLA) and central nucleus of amygdala (CeA). The graph also shows the main connections of these nuclei with other brain areas with which the Amg's nuclei form various brain sub-systems implementing several functions related to affective regulation of behaviour (discussed in Section 3).

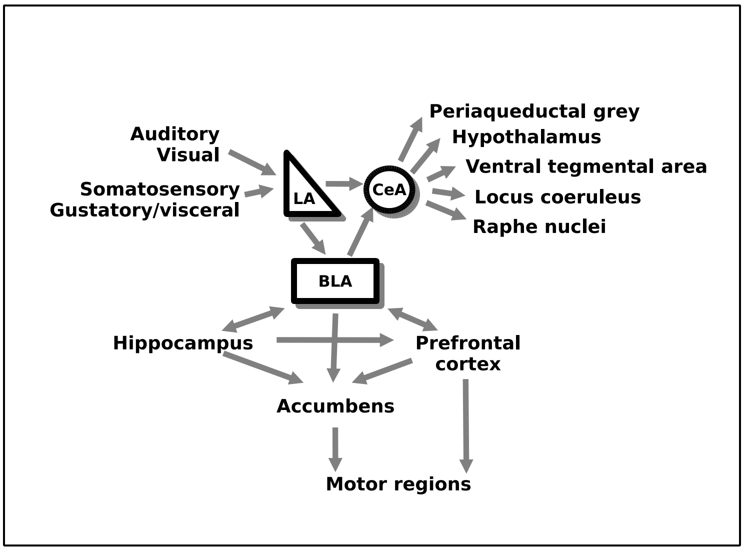

Fig. 1. Major connections between the main nuclei of Amg and between these nuclei and other brain districts with which it forms important brain sub-systems underlying various affective regulations of behaviour. LA receives afferent connections from many cortical and subcortical areas and projects mainly to other nuclei of Amg. CeA receives afferent connections from other nuclei of Amg and projects efferent connections to many subcortical systems. BLA has complex reciprocal connections with prefrontal cortex, hippocampus and nucleus accumbens.

The role that Amg plays in such affective regulations relies upon three functions (Figure 2). The first function is based on unlearned associations existing between a number of *biologically-salient stimuli* with the direct triggering of various appetitive and aversive unlearned responses directed to the environment, the body and the brain itself. In particular, some kinds of tastes and olfactory stimuli, as well as nociceptive stimuli [9], can, via unlearned Amg's pathways, *directly* contribute to trigger unlearned behaviours (e.g., salivation, freezing, startling, and approaching), to regulate emotional body states (e.g. heart rate and blood pressure), to broadly activate whole brain areas and regulate learning processes (e.g., via the neuromodulation processes performed by the nuclei of the reticular formation).

The second Amg's function is based on the strengthening of the neural pathways which allow *neutral stimuli* from the environment to trigger the aforementioned unlearned reactions. Amg can implement this process on the basis of two associative mechanisms.

The first associative mechanism is based on the creation of *direct* neural associations between the representations of *neutral* stimuli and the aforementioned unlearned reactions (these are S-R types of associations). S-R learning occurs at the level of the LA-CeA pathway, via connections that depart from LA units

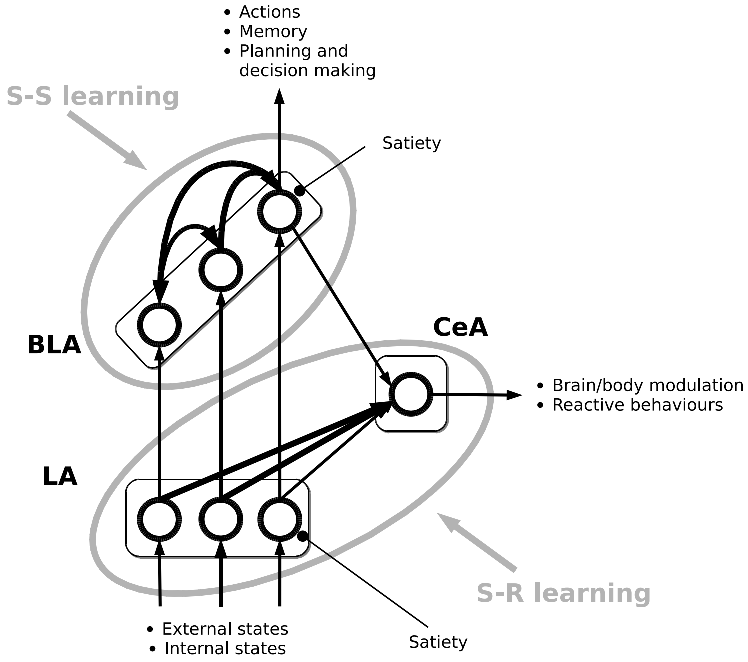

Fig. 2. Major learning processes involving the three main nuclei of Amg. Circles indicate clusters of neurons representing stimuli or reactions received from or directed to the environment, the body or the nervous system itself (for simplicity, the graph represents only few units). Bold connections represent associations formed during learning, whereas plain connections represent unlearned associations. S-R learning is implemented by the LA-CeA pathway: this allows external stimuli activating LA to directly trigger the unlearned reactions of CeA. S-S learning is implemented within BLA. Only few BLA units are associated with the CeA units: other BLA units representing external stimuli can trigger CeA reactions only by forming lateral associations with those units. Importantly, internal states, such as satiety, can modulate *on the fly* the triggering of Amg's responses by acting on the representations of the unconditioned stimuli, e.g. by inhibiting them (connections with a dot head).

representing stimuli from the world and converge to CeA which triggers the unlearned reactions. With learning, each LA unit can become directly associated with CeA reaction units.

The second associative mechanism is based on the formation of neural associations between internal representations of neutral stimuli and the internal representations of the aforementioned salient stimuli (these are S-S types of associations): the activation of these representations can then trigger the unlearned responses. S-S learning occurs within BLA. Only few BLA units, representing biologically salient stimuli, are associated with the CeA units. Other BLA units, representing stimuli from the environment, can have access to CeA reactions only by forming lateral associations with the BLA units representing salient stimuli.

A last important function of Amg relies on its capacity to modulate the effects of the associations that it forms in the ways just described *on the fly* (i.e., without the need of re-learning) on the basis of current homeostatic body states and overall brain states. For example the Amg is capable of avoiding to trigger approaching behaviours towards a source of food if this has been temporarily or permanently devalued through satiation or poisoning.

3 The Functions that Amygdala Plays in Different Brain Sub-Systems

Amygdala has been associated with a wide range of cognitive functions, including emotional regulation, learning, action selection, memory, attention and perception. In particular, a large amount of studies have now firmly established the involvement of Amg in aversive behaviours such as those involved in fear conditioning and taste aversion experiments [10–12]. Recently, an increasing amount of behavioral evidence has started to reveal an Amg's involvement also in appetitive behaviours [13–16]. This is also being corroborated by anatomical investigations that indicate the existence of Amg's afferent neural pathways which carry information related to both aversive and appetitive events [17, 18].

The Amg plays a function in these aversive and appetitive behaviours as it is an important component of several brain sub-systems involving the hypothalamus, insular cortex, brain stem (in particular the reticular formation), hippocampus, basal ganglia, and prefrontal cortex. In general, the role that the Amg plays in all these sub-systems relies on its capacity to use input information related to internal body states to assign positive and negative emotional valence to stimuli from the environment on the basis of the associative mechanism described in Section 2.

The Amg exploits these associative processes to play several important affective-regulation functions within various brain sub-systems (Figure 3). The detailed investigation and modeling of these functions, only broadly described here, form the main research objectives of the research agenda mentioned in Section 1.

Three of these functions involve the affective regulation of behaviours directed to the external environment:

1. *Selection and triggering of unlearned behaviours.*
   The Amg plays an important role in triggering unlearned behaviours on the basis of USs, and in implementing Pavlovian associative learning processes that transfer such triggering to CSs. In particular, studies about both appetitive and aversive Pavlovian conditioning focused on visceral [19], freezing [10, 20, 21], startle [22], and orienting [23, 24] responses. Behavioural and anatomical evidence indicates that these kinds of reactions are triggered by CeA activations [23, 24, 19].
   Also approach and avoidance behaviours, the conditioning of which depends on the BLA functioning [24, 19], can be included in the category of primary URs that animals produce in the presence of particular USs via unlearned neural connections existing between their neural representations.

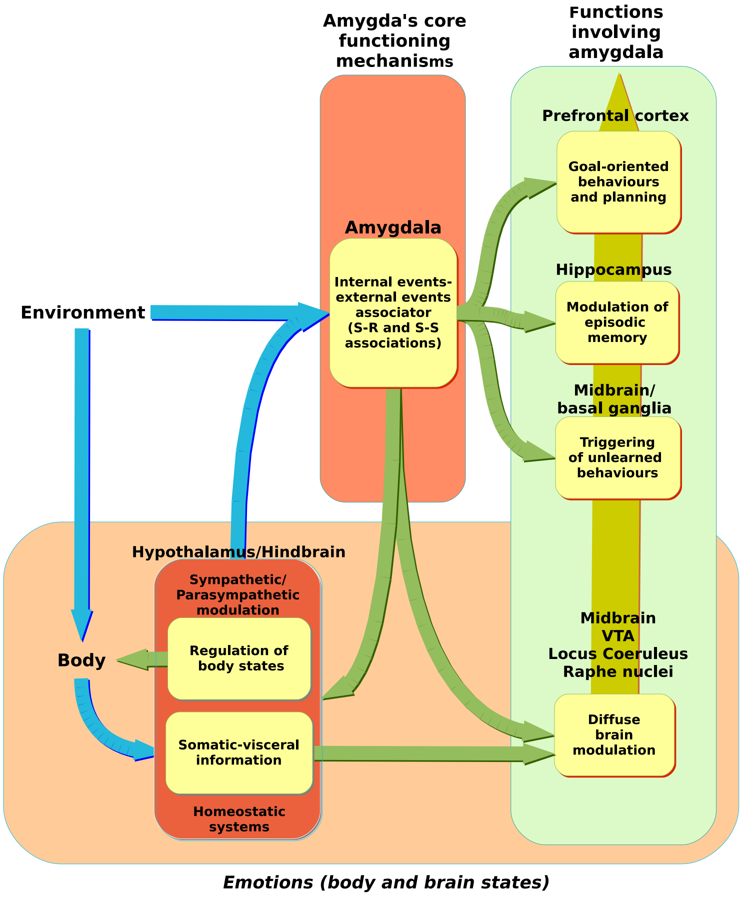

Fig. 3. A scheme indicating the main functions played by the Amg within some of the main affective regulatory systems of brain. Notice the core associative mechanisms implemented by the Amg, which subserve all such functions, and the role that Amg plays in the modulation of emotions in terms of the regulation of diffused brain states and body homeostatic states.

2. *Furnishing emotional states for the generation of fast-forming episodic memories.*

   The BLA's massive reciprocal connections with hippocampus might allow Amg to influence multi-modal fast-associative episodic memory processes taking places in it on the basis of current emotional states. In particular, as Amg is one of the main brain loci where the information on internal states and on the value of external stimuli is integrated, its input to the hippocampus might furnish the emotional context to memory formation and consolidation processes [25, 26].
3. *Emotional evaluation of stimuli for goal-oriented behaviour.*

The BLA-prefrontal cortex reciprocal connections play an important role in modulating the cognitive processes behind goal-oriented behaviours and planning, as shown by the seminal works of Balleine and Dickinson on rats [27] (see also [28]).

Within the neuropsychology literature, [29, 30] has proposed that the essential contribution of the Amg to decision making processes consists in evoking the emotions (in their terminology, the "somatic states") that are appropriate to rewards and punishments. The idea is that orbitofrontal cortex, part of prefrontal cortex, elaborates the emotional value of action outcomes on the basis of Amg's activation. Decision making processes, having prefrontal cortex as a principal actor, can then use this information for selecting actions with uncertain payoffs.

The last two functions of Amg involve the regulation of body states, diffused brain states and learning:

1. *Diffused modulation of brain functioning and regulation of learning processes.*
   Efferent connections from CeA project to ventral tegmental area, locus coeruleus and Raphe nuclei, the three main systems of departure of respectively dopaminergic, noradrenergic and serotoninergic innervations directed to virtually all districts of brain.

   Phasic dopaminergic responses at the timescale of milliseconds might underly synaptic reward-based modifications, whereas tonic dopaminergic activation at the timescale of minutes or hours might regulate the intensity of production of neural responses of the target areas [31–33].

   Also norepinephrine operates at different timescales. However, differently from dopamine, its phasic activation does not depend on the rewarding or aversive value of the stimuli, but only on its properties as a signal of novelty [34].
2. *Regulation of body homoeostatic states.*
   Animals reactions to events include unlearned patterns of modulation of homoeostatic body parameters such as blood pressure, heart rate, gastric and intestinal motility, and others. Efferent connections from Amg can control these regulatory processes (URs) depending on particular biologically-salient stimuli (USs) or neutral stimuli associated with them (CSs).

   This kind of modulation passes through the activation of the CeA and its connections to the hypothalamus and autonomic centers of brainstem, including the vagal nuclei and the sympathetic system [18, 19, 21].

4 Conclusions

This paper reviewed empirical neuroscientific evidence with the goal of showing that amygdala, at the core of various brain systems underlying emotions and motivations in organisms, can be viewed as an interface between organisms' cognitive processes and body homeostatic regulations. In particular, the review showed how amygdala implements some important mechanisms that allow the association of various environmental stimuli and context with the triggering of "behaviours" directed to regulate organisms' body states, their interactions with the outer environment and the general functioning of brain itself. These associative functions are fundamental for adaptive behaviour as they allows organisms to assign subjective saliency and value to experienced world states, so enhancing the adaptive value of their cognitive processes.

We believe that the encountering of empirical knowledge and data on emotions, re-organised within a computational perspective as done here, will help both to highlight the general principles underlying emotional regulation of behaviour in organisms and to design controllers with which endowing robots with a flexibility and autonomy comparable to that of organisms.

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