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What Affective Neuroscience Means For Science Of Consciousness

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ABSTRACT

The field of affective neuroscience has emerged from the efforts of Jaak Panksepp in the 1990s and reinforced by the work of, among others, Joseph LeDoux in the 2000s. It is based on the ideas that affective processes are supported by brain structures that appeared earlier in the phylogenetic scale (as the periaqueductal gray area), they run in parallel with cognitive processes, and can influence behaviour independently of cognitive judgements. This kind of approach contrasts with the hegemonic concept of conscious processing in cognitive neurosciences, which is based on the identification of brain circuits responsible for the processing of (cognitive) representations. Within cognitive neurosciences, the frontal lobes are assigned the role of coordinators in maintaining affective states and their emotional expressions under cognitive control. An intermediary view is the Damasio-Bechara Somatic Marker model, which puts cognition under partial somatic-affective control. We present here our efforts to make a synthesis of these views, by proposing the existence of two interacting brain circuits; the first one in charge of cognitive processes and the second mediating feelings about cognitive contents. The

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coupling of the two circuits promotes an endogenous feedback that supports conscious processes. Within this framework, we present the defence that detailed study of both affective and cognitive processes, their interactions, as well of their respective brain networks, is necessary for a science of consciousness.

Key Words: Affective neuroscience; Cognition; Consciousness; Emotions; Endogenous feedback; Feelings

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Introduction

The cognitive revolution that occurred in the last decades was an interdisciplinary movement arguing – among other ideas - that emotions are mental states that fall outside the domain of cognitive explanation. For instance, Gardner (1987^[31]) argued that one of the five main features of the cognitive revolution was the lack of emphasis on affective/emotional and nonconscious aspects of brain functions.

According to Damasio, the cognitive revolution neglected the role of emotions in human and animal behaviour, on the basis of the following assumptions: (i) emotions cannot be trusted (neither in real life, nor in the laboratory); (ii) emotions are too subjective; and (iii) emotions are elusive and vague (Damasio, 2000^[22]). Neuroscientists and cognitive scientists for some time had therefore been much more interested in cognitive aspects of the mind than in affects, emotions, and nonconscious processes.

Within the cognitivist perspective, the shaping of a conceptual framework devoted to the study of emotions and nonconscious processes would have been unnecessary or inadequate (LeDoux, 1999^[46], 2000^[47]). Researchers prioritised the analysis of mental states that could be translated in terms of computational operations, e.g., perception, learning, and memory. This keen interest in our cognitive functions partially explains why cognitive scientists did not include the study of affects and emotions among the research interests of the cognitive neurosciences (LeDoux, 1996^[44], 2000^[47]).

The cognitive revolution began to be overcome from the remarkable work of Darwin (1872/1998^[19]). The attempt to complement and overcome the limitations and misconceptions inherent in the cognitive revolution gave rise to the emergence of an "affective revolution", associated with the understanding that affects and emotions indeed play a key role in intelligent life (Panksepp, 2004^[55]; Panksepp, 2001^[53]; Davidson and Suton, 1995^[23]). The new approach to the matter of unconscious emotions highlighted the limits of the cognitivist conception (Berridge and Winkielman, 2003^[12]; Dubois, 2010^[26]). Human actions have since been

conceived as being greatly influenced by implicit processes that may not reach conscious attention (Bechara, 2004^[8]; Bechara, Damasio and Damasio, 2000^[9]; Burns and Bechara, 2007^[15]; Damasio, 1994^[20]; Dubois, 2010^[26]), but may be considered within the range of "affective consciousness" (Panksepp, 2005a^[56]).

In this paper, we analyse the work of Jaak Panksepp and Joseph LeDoux and introduce our perspective on the role of affects and emotions in a theory of consciousness. This perspective is based on the Endogenous Feedback Model, which suggests that affective/emotional and cognitive processes are mediated by distinct and interacting brain networks, and that degrees of consciousness correspond to the level of resonance of the networks (Augustenborg, 2010^[4]; Carrara-Augustenborg and Pereira Jr., 2012^[17]). After a brief historical review, we summarise central concepts present in current approaches to affects and emotions, make a brief review of their neurobiological basis, and propose a framework to define their role in a theory of consciousness.

At the onset, it is relevant to clarify our understanding of the concepts of *affect*, *feeling*, and *emotion*. These concepts are used with slightly different meanings by authors. We assume the terminology proposed by Russell (2003^[64]; 2009^[65]), by which *core affect* defines a state grossly characterised by positive or negative valence (Baars, 2008^[6]). Such state conveys the degree of agreeableness of specific stimuli and events with respect to the organism's contextual state and current intentions. Proposed as a constant flow (Barrett, 2005^[7]), core affect relate to neural changes determined by detection and processing of internal and external stimuli^a. The subjective result of these processes is the *feeling*, a category that includes sensations as pleasure and pain, affective states as being happy or sad, and also cognitive intuitions as grasping the meaning of a word or a sentence.

While the ability to produce core affect is present at birth (Barrett, 2005^[7]), automatic processes such as attention can influence the feelings that compound it. They can be modified by associative learning, and in turn they can affect our behaviour. Feelings can then be expressed into overt behaviours, in terms of *emotions* (anger, sadness, happiness, shame expressions), which William James (1884^[40]) defined as the *experience* emerging from individual's self-perception of automatic processes (see also Prinz, 2005^[62]).

We can therefore define emotions as expressed bouts of affect, which we are able to explicitly assess in terms of intensity, quality, and contextual appropriateness, and also to convey by means of symbolic language (e.g., facial mimic). Emotions, which Freud (1950^[29]) considered to be always conscious, can therefore express feelings, but they do not necessarily reflect them (i.e. someone

^aDamasio's model (1994²⁰) grants a role of primary relevance to core affect and to feelings in the generation of conscious experience. In Panksepp's terminology, "basic emotional systems" (Panksepp, 1998, p.51⁵²) would correspond to systems that generate core affects, and "core emotional feelings" (Panksepp, 2005b⁵⁷) to core affects.

can mimic sadness, without necessarily experiencing it). Therefore, there should always be a degree of consciousness related to our feelings and emotions, but such a consciousness may occur without awareness (attention to represented content). For instance, a hungry and thirsty person in a restaurant remains conscious of her hunger while choosing a drink, although her focus of attention is directed to the items of the beverage menu. Therefore, in the framework presented here we classify this sensation of hunger as an example of a peripheral, non-attended, or unaware conscious state. Affects and feelings frequently occur in our conscious life in this modality.

The major premises of Panksepp's affective neuroscience

Affective neuroscience is an area of research that focusses on the neural bases of emotions, and assumes a role of great relevance for emotions and affects in the modulation of cognition and behaviour. The approach advocated by Panksepp (1998^[52]) is an attempt to understand, among other things, (i) the genesis of affective consciousness; (ii) how basic emotions and feelings are organised in the brain; and (iii) how the basic emotional processing systems of the brain generate internally experienced feelings.

'Internally experienced affective states' is an expression used by Panksepp and others to refer to mental events that "reflect our neurobiological ability to subjectively experience certain states of the nervous system" (Panksepp, 1998, p9^[52]). Based on this conception, the approach advocated by Panksepp aims at showing how neurobiological systems mediate basic emotions (such as fear and anger). It further attempts to show how these systems elicit, "the valenced affective feeling states that provide fundamental values for the guidance of behavior" (Panksepp, 1998, p. 122^[52]).

These purposes are grounded in the idea that emotional processes are experienced feelings, which play a key role in "the causal chain of events that control the actions of both humans and animals" (Panksepp, 1998, p14^[52]). "Internal feelings" (corresponding to our concept of *core affect*) arise from neurobiological events that mediate and modulate the instinctual nature of many human action patterns, and that provide efficient ways to ensure human behavioural adaptation to environment. The causal chain of internal feelings that controls the actions of both humans and nonhuman animals is largely crafted from non-conscious processes (Panksepp, 2001^[53]). This is why one of the major premises of Panksepp's affective neuroscience is that feelings sustain some unconditioned behavioural tendencies, and play a key role in the unconscious constitution of new behaviours through providing mechanisms that allow organisms to categorise world events efficiently so as to control future behaviours (Panksepp, 1998, p14^[52]).

'Natural internal values' is an expression used by Panksepp (1998, p14^[52]) to refer to the set of types of values upon which we carry out complex behaviours,

efficiently categorise events and control future behaviours. These values are triggered by the arousal of various subcortical circuits, located in evolutionarily ancient areas of the mammalian brain. One of the best ways to understand how the values are composed is to delineate a 'natural taxonomy' of these systems through an analysis of the brain circuits from which such tendencies arise. Based on these assumptions, Panksepp intends to demonstrate that the function of emotional systems is to integrate many types of behavioural responses and physiological processes in the brain and rest of the body. More so, Panksepp defends the view that emotional systems trigger subjectively experienced feeling states that provide efficient ways to guide and sustain behaviour patterns and certain types of learning (Panksepp, 1998, p15^[52]). He believes that such a psychoneurological analysis of human and animal emotions makes possible an understanding of the basic underlying nature of the human mind. All mammals "come into the world with a variety of abilities that do not require previous learning, but which provide immediate opportunities for learning to occur" (Panksepp, 1998, p25^[52]). These emotional abilities emerge from basic systems in the brain, and their development depends on the interactions with higher brain areas that allow the organisms to make effective behavioural choices.

The human brain contains seven "basic emotional systems" (Panksepp, 1998, $P 51^{[52]}$), among them four primal circuits. These circuits - i.e. seeking, rage, fear and separation distress panic -- mature early in life to ensure the survival of individuals.

The seeking-system is the neural network that provides us efficient ways to elaborate "energetic search and goal-directed behaviours in behalf of any of a variety of distinct goals objects" (Panksepp, 1998, p52^[52]). The rage-system is easily aroused by thwarting and frustrations, helping us to defend ourselves and prompting behaviour when we are irritated or restrained (Panksepp, 1998^[52]). The fear-system tries to minimise the probability of bodily destruction. This specific circuit arose during animal evolution and it serves to reduce pain (Panksepp, 1998^[52]). Finally, separation distress panic is a neural system that is very important in the constitution and elaboration of social emotional processes related to attachment: "to be a mammal is to be born socially dependent" (Panksepp, 1998, p54^[52]). This system provides both safeguards to assure that parents (usually the mother) "take care of the offspring and that offspring have powerful emotional systems to indicate that they are in need of care" (Panksepp, 1998, p54^[52]).

Panksepp (1998, p54^[52]) adds to the above primal circuits, three socio-emotional systems, which are engaged at appropriate times in the lives of all mammals, namely: (i) lust, (ii) maternal care, and (iii) play. These systems depend on abilities acquired during mammalian evolution, being developed in the individual by the action of specific hormones and social interaction. In addressing *lust*, Panksepp (1998, p225^[52]) says that there are specific brain circuits that promote both sexual instinct and maternal motivation (Panksepp, 1998, p54^[52]).

Regarding *care*, Panksepp (1998, p246^[52]), illustrates the existence of intrinsic brain systems that promote nurturing behaviours of mothers and fathers. Finally, when Panksepp designates the rough-and-tumble *play* as an emotional system (Panksepp, 1998, p280^[52]), he understands that playing may reveal some major secrets of the brain and yield important insights into certain childhood psychiatric problems, among them autism and attention deficit disorders. Panksepp (1998, p297^[52]) postulates that many children diagnosed with ADHD may, in fact, be exhibiting heightened play tendencies. He writes:

Their hyperactivity, impulsiveness, and rapid shifting from one activity to another may be partly due to their unconstrained and unfocused playful tendencies. Indeed, the medications that are used to treat the disorder – psycho-stimulants such as methylphenidate (i.e. Ritalin) and amphetamines – are all very effective in reducing playfulness in animals. (Panksepp, 1998, p297^[52]).

From the standpoint of clinical neuroscience and clinical psychiatry, Panksepp's affective neurosciences aims at showing that it is possible that many cognitive deficits could be ameliorated by tackling the underlying emotional feelings (Panksepp, 2001^[53]).

This objective cannot be reached by using a single disciplinary approach. Indeed, neuro-scientific terminology is not sufficient by itself to embrace the full nature of brain processes related to both emergence and constitution of internal emotional states (Panksepp, 2001^[53]). Behavioural and psychological perspectives are not sufficient either. The demarcation of the neurobiological nature of human and non-human animal feelings requires the synthesis and further integration of behavioural, psychological, and neurobiological perspectives. Many disciplines have contributed to the improvement of our knowledge of how emotions arise from ancient brain circuits, but Panksepp (1998^[52]) remarks that there is a missing piece that can bring all these disciplines together. In his words, this is the "neurobiological understanding of the basic emotional operating systems of the mammalian brain, and the various conscious and non-conscious internal states they generate" (Panksepp, 1998, p5^[52]).

Joseph LeDoux: Two pathways of affective-emotional processing

In *The Emotional Brain* (1996^[44]), LeDoux established the notion of the Low and the High roads, in order to show, among other things, that emotional responses can occur without the involvement of cognitive processing systems of the brain. According to LeDoux (1996^[44]):

When a certain region of the brain is damaged, animals or humans lose the capacity to appraise the emotional significance of certain stimuli without any loss in the capacity to perceive the same stimuli as objects. The emotional meaning of a stimulus can begin to be appraised by the brain before the perceptual systems have fully processed the stimulus. The brain mechanisms through which memories of the emotional significance of stimuli are registered, stored, and retrieved are different from the mechanisms through which cognitive memories of the same stimuli are processed. (LeDoux,1996, p69^[44]).

One of the arguments made by LeDoux (1996^[44]) is that emotional appraisal may have more rapid effect in the determination of behavioural responses than perceptual and cognitive processing:

The systems that perform emotional appraisals are directly connected with systems involved in the control of emotional responses. Once an appraisal is made by these systems, responses occur automatically. In contrast, systems involved in cognitive processing are not so tightly coupled with responses control systems. The linkage of appraisal mechanisms with response control systems means that when the appraisal mechanisms detect a significant event, the programming and often the execution of a set of appropriate responses will occur. (LeDoux,1996, 69-70^[44]).

Prior to cognitive activity, the amygdala detects and modulates responses to natural dangers (like predators), and it binds contingencies between novel threats and the stimuli that predict their occurrence (Dalgleish, 2004^[18]; LeDoux, 1998^[45]). Based on the knowledge that external stimuli reach the amygdala by means of direct pathways from the thalamus, as well as through an indirect route that, from the thalamus, crosses the cortex before converging to the amygdala, LeDoux establishes the notion of the low and the high roads (LeDoux, 1996^[44]; 1998^[45]; 2000^[47]). The low road is the short and more rapid path that modulates our ability to respond promptly to those stimuli, which we have learned to associate with aversive outcomes prior to their cognitive assessment. The high road is instead the connective pathway between the corpus geniculatum, cortical tissue, and amygdala. This pathway integrates the emotional response with the more detailed analysis of the distinctive features of stimuli, and it shapes our awareness of contingency between specific stimuli and responses.

The amygdala operates as a central threat detector in the brain, responding to relevant stimuli and triggering a cascade of events – both through the high and low roads – that mediate emotional and behavioural responses to them. It projects to a variety of brain stem areas, each of which controls particular responses (LeDoux, 1996^[44]). In cases of lesions in the central gray matter, the freezing response to fear is impaired, without alteration in autonomic (changes in blood pressure) and endocrine responses (release of stress hormones). Lesions to the lateral hypothalamus determine instead the reduction of autonomic responses (blood pressure), but not the freezing or autonomic responses (LeDoux, 1996, p160^[44]). Finally, startle reflex and emotion modulation are impaired after a right amygdala lesion (LeDoux, 1996, p160^[44]).

Experimental research has shown that the amygdala plays a pivotal role especially in the modulation of fear responses (Bechara *et al.*, 1995^[9]; Davidson,

1995^[23]; Kapp *et al.*, 1992^[41]; LeDoux, 1996^[44]; 1998^[45]; 2000^[47]). Indeed, many neuroimaging studies have demonstrated that the human amygdala is a critical component of the neural substrates of emotional experience, and that this structure has a central role in the mediation of fear, anxiety, and negative affectivity.

A neuroscientific approach to the interactions of cognition and emotion

Although cognition and emotions are research topics originally rooted into different disciplines (i.e. neuroscience and clinical psychology), the evidence accumulated through years of empirical work unequivocally shows that their mechanisms interact closely one with another. We have already suggested in previous work (Augustenborg, 2010^[4]; Pereira Jr. and Furlan, 2010^[59]; Pereira Jr. and Almada, 2011^[58]) the role of feelings and emotions in the mediation of stimuli significance and in the modulation of behaviour. In fact, the Endogenous Feedback Network (EFN) model (Augustenborg, 2010^[4]) defends that they contribute to both stimuli-response integration, and to processional speed. Furthermore, the proposed framework plausibly accounts for the occurrence of emotions also in absence of a corresponding stimuli. In this section, we will consider in greater details how such functions are indeed supported by empirical research, and how interaction between cognition and emotions are endorsed by our growing knowledge of brain connectivity.

Cognitive and affective processes appear to interact (Panksepp, 2003^[54]), although to a substantial degree they correspond to distinct neurobiological events, in terms of anatomical, neurochemical, and functional criteria. According to Panksepp, "the arousal of feeling states helps to channel activities of the cognitive apparatus and thereby facilitates behavioral choices" (1998, p39^[52]). Grav et al. (2002^[36]), among others, have elaborated on models that describe how emotions and cognition are integrated. They assume that the two systems are distinct, but at the same time interact to become functional and adaptive (Gray et al., 2002^[36]; Gray, 2004^[35]). Their interactions involve a large circuit including several limbic and cortical areas. For instance, studies using functional brain imaging have shown that induction of emotional states correlates with activity in lateral prefrontal cortex (Braver, Cohen and Barch, 2002^[14]) and many others have shown the role of orbitofrontal cortex in emotion and emotion-related learning (O'Doherty et al., 2001^[63]). The latter study indicates that both lateral and medial orbitofrontal cortical areas play a substantial role in the brain regions responsible for reward and punishment. This research corroborates the idea according to which the lateral area of the orbitofrontal cortex is associated with an aversive outcome, while the medial area of the orbitofrontal cortex is associated with reward. According to O'Doherty et al. (2001[63]), evidence from lesion studies suggests that the orbitofrontal cortex, but not other regions of prefrontal cortex, is essential for performance on an emotion-related reversal learning task. Beer et al. (2006^[3]) also advocate the idea that orbitofrontal cortex has a significant role in emotion-cognition interactions.

Some emotions have selective effects on cognitive control, and may influence cognitive mechanisms that support action control and goal-directed behaviour (Gray, 2001^[34]). Many aspects of human mental life, including empathy, beliefs, attitudes, the self, altruism, creativity, decision making, and moral reasoning, are hence believed to reflect a "true marriage of cognitive and affective abilities" (Gray, 2004, p48^[35]). In fact, feelings and emotions play crucial functions both in the selection of stimuli and in our choice of eventual responses. Such roles indicate a close interaction between cortical and subcortical areas, respectively, involved in cognitive and affective (automatic) processes.

Recognised as one of the brain structures primarily linked to emotions, the amygdala appears to cover a significant role in the mediation of such interactions, as the above reviewed work of Joseph LeDoux has made evident. The amygdala is situated in the medial temporal lobe, anterior to the hippocampal structure, and it is connected to visual cortex, visual thalamus, dorsolateral prefrontal cortex as well as to subcortical structures. Damage to the amygdala determines patients' inability to produce learned fear responses and deficits in long-term memory (Bechara et al., 1995^[10]). In instructed fear paradigms, for example, the participants are informed about the negative valence and the contingency of a stimulus. While in healthy subjects awareness of the negative valence of a stimulus is sufficient to activate the amygdala in magnitude similar to the arousal that an unexpected, aversive stimulus would have determined; patients with amygdala lesions fail to show any physiological expression of fear^b (Phelps, 2002^[61]). However, as outlined by Bechara et al. (1995^[10]), such patients preserve both awareness of stimulus contingency and the understanding of its valence, that is, they are able to verbally account for the potential danger of the stimulus. It has to be noted however that the amygdala is *per se* not responsible for the expression of fear, as it basically possesses no neurons able to process the meaning of stimuli (LeDoux, 1996^[44]). Instead, information from cortical sensory areas directly affects the sensory thalamus, from where the input reaches the amygdala (Damasio, 1994^[20]). Consequently, activation of the amygdala triggers physiological responses via connective pathways from the central nucleus of the amygdala toward the brainstem (where they activate the sympathetic nervous system), and toward the hypothalamus (which in turn affects the hormonal secretions of the pituitary gland), (Kapp and Cain, 2001^[42]; Kapp *et al.* 1992^[41]). Although this has not yet reached the stage of explicit naming and accessible recognition (so far no cognitive mechanism has been involved), the information is sufficient to shape a rudimentary assessment of the stimulus' valence, which can then motivate toward a specific response.

In a study performed by Anderson and Pelphs (2002^[3]), no differences in the magnitude and frequency of self-reported positive or negative affect were found between control subjects and patients with amygdala damage. This

^bEvidence suggests that inhibition of physiological responses correlates with damage in the left amygdala, but not in the right region of this structure (Funayama *et al.*, 2001³⁰).

research was divided into two studies, and both concluded that the structure of affective states was not altered by amygdala damage. In this sense, Anderson and Pelphs (2002^[3]) substantiated the notion according to which the amygdala is not necessary for the generation of the phenomenal affective states, even though the human amygdala may be recruited in the constitution of affective states in the intact brain. The core of Anderson and Pelphs' idea is that human affective experiences depend on internal processes, even in the absence of stimuli and contexts related to threats and rewards.

This controversy about the centrality of the amygdala for affective/ emotional processing can be bypassed by a model of brain affective/emotional information processing based on a broader circuit, as in the case of the integrative and modulating role attributed to the astroglial network by Pereira Jr and Furlan (2010^[59]), and Pereira Jr., Furlan and Pereira (2011^[60]). This framework can accommodate the findings and theoretical views of LeDoux, without commitment to a central position of the amygdala in emotional processing.

In accordance with the presence of two pathways connecting the amygdala, both directly to the thalamus and also to higher processing areas (LeDoux, 1996^[44]), emotional responses do not require perceptual consciousness. Besides being conveyed towards the amygdala, information from the thalamus is simultaneously sent to cortical areas where the stimulus is thoroughly assessed (e.g., per category, meaning, contextual relevance etc.), leading eventually to the generation of an intentional response. It is only at this stage that conceptual knowledge will emerge and – via descending pathways toward the amygdala - determine whether the physiological arousal has to be maintained (that is, stimulus is recognised as a threat), or the organism may relax (that is, stimulus is in fact harmless).

In sum, pathways from subcortical structures toward cortical areas can trigger both behavioural responses (e.g., fleet) and cognitive mechanisms (e.g., attention), while pathways from cortical areas toward the brain inner structures can either inhibit or increment the emotional reactions. Therefore, such reciprocal interactions between our cognitive and emotional mechanisms highlight one of the functions of emotions: that is, to prepare the organism toward an adaptive response which, by not depending from the time-consuming constraints of a cognitive evaluation, can occur rapidly. Our ability to detect fear expressed by unconsciously (masked) perceived faces (Adolph, 2002^[1]) supports an adaptive role of emotions as early detectors of stimuli bearing possible negative consequences for the organism.

Thus, emotions appear significantly involved in shaping the content of our cognition, since they can affect the chances that given stimuli and events are granted increased attentional resources compared to others. This function is clearly demonstrated by studies employing the attentional blink paradigm.

These experiments are based on the knowledge that visual stimuli following too closely the presentation of a target has decreased chances of being detected than those which appear after a longer time interval. However, a number of studies (e.g., Schwabe et al., 2011^[66]; Anderson, 2005^[2]) have shown that stimuli bearing emotional significance are likely to be detected even if they are presented in the refractory window that closely follows the appearance of the preceding target. Similar experiments involving brain-damaged patients have shown that amygdala lesions determine the disappearance of such emotional advantage. Accordingly, studies carried on by Öhman et al., 2001^[50] have shown that masked threatening stimuli attract attention more rapidly than neutral ones. This is also supported by evidence collected by Vuilleumier et al., 2004^[69] showing that the amygdala - via connective pathways to visual areas - is involved in the enhanced activation of visual processing areas during the presentation of emotional stimuli^c. The role of emotions as attention-markers is further confirmed by evidence that patients suffering from specific neurological conditions (e.g., visual extinction, neglect, and blindsight) show amelioration of deficits when they are presented with emotionally significant stimuli (see Hamm et al., 2003^[39]; Grandjean et al., 2008^[33]; Grabowska et al., 2011^[32]).

A shift of attention towards one stimulus above others is also implicit in decision-making processes. As Gray *et al.*, 2005^[37] have pointedly argued, the benefit of possessing a system able to process multiple options and to simultaneously assess various behavioural responses is counterbalanced by an increased risk of conflicts between different possible choices. The bias shaped by emotions toward a given option can in this context contribute to solve the so-called "control-dilemmas" that may emerge between our cognitive knowledge and our emotional preference for a specific choice. Thus summarising, while cognition may affect our emotional responses by means of inhibitory control, our emotions may affect cognition by means of tipping the scale towards specific decisions. Emotions can additionally affect our cognitive style as indicated by evidence showing that negative affect (*moods*) stimulate systematic processing, while positive affect appears to lead to more heuristic attitudes in decision-making (Bolte, Goschke, and Kuhl, 2003^[13]).

As previously mentioned, damage to the amygdala determines also impairments in long-term memory. This structure, which itself is not responsible for the encoding and storing of memories, affects instead the quality of our memories, and it contributes to selection of stimuli and events most relevant to encoding. In situations of reduced attentional resources for example, the emotional valence of a specific stimulus increases its chances of being attended to, and therefore remembered. Consequently, the emotional tag placed by the amygdala on given stimuli also improves our faculty to learn from past events. In fact, McGaugh (2000^[48]) has shown that the amygdala modulates our ability

^cStudies have confirmed for example that the speed of processing of emotional facial expressions is faster than other features of the stimulus (Halgren *et al.*, 2000³⁸; Kawasaki *et al.*, 2001⁴³).

to remember by affecting the hippocampal complex which is responsible for the initial encoding of episodic and declarative memory. The stress hormones released during emotional arousal trigger a mechanism that improves the consolidation and storage of hippocampus-dependent memories. Such interaction has been demonstrated by studies in which the inhibition of stress hormones, by administration of beta-blockers, had determined the attenuation of emotional memories' recollection (van Stegeren, 2008^[68]).

By means of attentional modulation, our emotions can boost the likelihood of assigning increased processional resources toward some stimuli above others. Emotions can also facilitate both the encoding and retrieval of specific memories and representations, determine the triggering of behavioural responses, and also affect our decision-making processes. By the same token, attention, memory, accessible knowledge and our intentional behaviour can affect emotions both in terms of intensity and valence. In sum, the feelings of our experiences are shaped by the meanings we have learned to ascribe to specific stimuli and events: Such meaning is emotionally and cognitively encoded in a unitary data-cluster^d bearing the subjective "what-it-is-*likeness*" of every experience.

Implications for a theory of consciousness: The endogenous feedback network model

The alliance between cognition and emotions bears crucial implications for any theory of consciousness that imposes limited capacities to our unconscious processes. Our sense organs are an open window toward our environment: at any one time, sounds, visual and perceptual stimuli, smells and flavours impinge our senses and, while we might be able to limit their occurrence (e.g., by closing our eyes, blocking our ears), the magnitude and variety of perceptions often exceed our contextual needs and the processional capacities of our brain. Nevertheless, it is crucial for us to be able to discern between relevant and irrelevant stimuli, to draw pertinent information from our environment, and to allow such knowledge to reflect on our responses and decisions. How can we carry on such selections, become aware of specific stimuli above others, and at the same time optimally administrate our resources?

It is unlikely that, in order to assess the value of all the information to which we have access, we must carry on an extensive cognitive evaluation of each given stimulus. Global Workspace theories of consciousness (e.g., Baars, 1988^[5]; Dehaene and Naccache, 2001^[25]) have proposed models in which stimuli gain processional resources on the bases of their contextual relevance. In the context of visual perception, it is therefore suggested that the object's physical features, its meaning and the subjective relevance attributed to it, play a crucial role in determining whether the stimulus is granted attentional resources or ignored. By

^dDamasio's model of time-locked multiregional retroactivation (1989²¹) can well represent the way in which different processes can ally to produce integrated representations.

means of an eventual allocation of attention, we may then become conscious of the specific stimulus above others, and we may consequently be able to better assess its value, to mnemonically store its meaning, and to strategically and intentionally retrieve such information in future circumstances. Although these models take into consideration the weight that subjective values and pre-existing information may have on the selection and interpretation of specific stimuli, they assume a role of minor relevance to the phenomenality of perceptions and to the capacities of our unconscious processes. It is in this context that affective neuroscience takes on the crucial role of a mediator by creating a bridge between our cognitive processes and the phenomenal elements that both accompany and affect them [Figure 1].

Affective and cognitive processes should be given equal emphasis when modelling the dynamics of conscious experience. The interaction with the rest of the body and with the environment should also be taken into account.

Engel and Singer (2001^[27]) had suggested that temporal synchronisation of unconscious neuronal coalitions leads to dynamic binding, and therefore to the emergence into consciousness of specific representation above others. Global Workspace Theory (Baars, 1998^[5]) has also proposed that consciousness emerges as the result of unconscious integration of data from a distributed neural network. What is common to both suggestions is their assumption that consciousness shapes knowledge, and it does so by binding distributed information into meaningful concepts. Nevertheless, the evidence we have discussed earlier in this section shows that emotions participate actively in the processing of information by modulating a broad variety of cognitive mechanisms (e.g., attention, meaning-making). We have furthermore considered the many instances in which empirical studies have demonstrated that emotions, although not consciously perceived, can determine

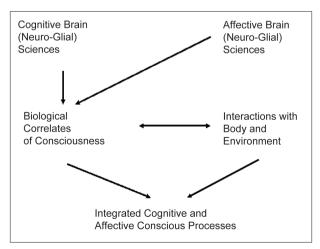


Figure 1: Epistemological interdisciplinary requirements for a science of consciousness

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cognitive styles, intentional behavioural responses, memory formation (by means of attention enhancement), as well as intentional mnemonic retrieval. In other words, the information borne by *feelings* (i.e. emotions deprived of cognitive evaluation) appears to contribute significantly to the content and the quality of our cognitive processes. It can therefore be argued that information can cluster into meaningful events even though these might not be precisely reportable. Such information may then be manipulated both by emotional and cognitive processes, it can be modified by associative learning, and be deployed in intentional behavioural responses. As accessible (attended) and inaccessible (non-attended) processes appear to significantly affect one another, it should appear clear that a convincing theory of consciousness must therefore offer an equally valid theory of degrees of consciousness and unconsciousness (see Carrara-Augustenborg and Pereira Jr., 2012^[17]).

The Endogenous Feedback Network (EFN) theory shapes a framework able to account for both attended and unattended perceptual mechanisms, as well as for degrees of consciousness between the two. It acknowledges that a significant amount of information integration unfolds below our awareness' thresholds and, importantly, that such information can be *flexibly* and *strategically* deployed within a broad range of cognitive processes. The EFN conceptualises consciousness as the global broadcast of the neural changes triggered by stimuli sensorial detection and processing. In such sense, consciousness reflects a constant flow of information that unfolds independently from attentional mechanisms, and that also includes the computations carried by the neural pathways modulating affective responses.

Within the frames of the EFN, the term consciousness is employed in adherence with its etymological root (lat. cum scientia: "with knowledge of"), and it is taken to indicate the presence of knowledge within the organism. The eventual allocation of attention toward specific segments of such information flow may then allow specific contents of the broadcast to emerge into the accessible and reportable state that characterises awarenesss^e. At the functional level, the role of the conscious broadcast is to promptly mediate the stimulus' significance in order to allow an appropriate response also prior to the occurrence of an eventual cognitive assessment. In this light, phenomenal consciousness reflects the feeling derived from the detection of a percept and - in the instance of a negative stimulus - it would correlate with the activation of the amygdala following the exposure to the emotionally significant input. It is however relevant to note that - as suggested by the EFN - behavioural and emotional responses may occur also in absence on external stimuli. Thoughts, mnemonic retrieval, and internal sensations (e.g., hunger, anxiety) may in fact trigger a chain of neural computations able to reverberate and consequently be broadcast along the endogenous feedback network.

^eSee Carrara-Augustenborg (2012¹⁶) for an in depth discussion regarding the distinction between consciousness, unconsciousness and awareness.

As discussed earlier in this section, our experience of a given emotion is an act of recollection which involves both cortical and subcortical structures. Exposure to a stimulus can activate the pertinent emotional and cognitive data-cluster which can then prepare the organism toward the response associated with the specific stimulus. In sum, feelings may reflect mental "short-cuts" which rapidly bind the stimulus assessment to specific responses and/or meanings independently from a complete (and time-consuming) cognitive appraisal. This suggestion is supported at the anatomical level by the short connective route between thalamus and amygdala. Such direct pathway may determine in fact a rapid response, which only later may be inhibited or supported by the outcomes of the cognitive processing mediated by the longer pathway between thalamus and amygdala via sensory and associative cortical areas.

The distinction between *feelings* (core affect lacking cognitive appraisal) and *emotions* (feelings we have learned to explicitly recognise and describe) correlates with our proposed distinction between *consciousness* (information that elicits a feeling, but lacking cognitive appraisal) and *awareness* (conscious segments which we can explicitly access). If we accept that feelings can affect a significant range of cognitive mechanisms, and that the information they bear can shape coherent percepts even prior to their formalisation into *concepts*^f (i.e., emotions), we might then also accept that broadcast knowledge may be coherently deployed without necessarily having been translated into accessible *concepts* (i.e., awareness).

If we then seem able to make significant use of both feelings and consciousness independently from the explicit acknowledgement of either one, what are the respective functions of emotions and awareness? As other theories have also previously suggested, our awareness of specific stimuli above others allows us the possibility to isolate the former from a potentially crowded background of perceptions. By means of directed attention, we are able to appraise the specific representation, devoting to its assessment our complete cognitive toolbox. Additionally, the ability to overtly recognise specific emotions might have great adaptive value since it would allow us to communicate such states to others, and conversely to experience empathy by grasping how others might perceive (and react to) specific stimuli and events^g. In other words, emotions may represent the organism's feedback with regard to both own and others subjective experience of specific behaviours and decisions.

As previously mentioned, the role of consciousness is instead to broadcast the occurrence of neural activity within and between specialised areas prior to the emergence of awareness. This constant flow of computations allows rapid endogenous updates of the status of the organism since its informational content

^fBy *concept* is intended an information-cluster which we have learned to explicitly recognise, categorise and eventually describe.

^gThe role of emotions is the development of Theory of Mind is also supported by evidence that individuals affected by autism present impairments in experiencing fear-learned startle responses (Wilbarger *et al.* 2009⁶⁶).

is communicated also prior to the emergence of the cognitive and conceptual appraisal of the percept.

Concluding Remarks [Figure 2: Flowchart of Paper]

We propose a comprehensive model of consciousness within which affects, feelings, and emotions play a crucial role in stimuli-response integration. We have suggested that the neural changes produced by sensorial detection and processing of stimuli and events merge into a constant informational broadcast. By mediating the integration of data in real-time, such global network shapes a flow of distributed information processing across the brain able to facilitate behavioural responses, and to optimise the allocation of mental resources (e.g., by eventually affecting attentional mechanisms^h). Within such framework, feelings represent non-cognitive markers able to link the neural changes that accompany specific representations to their mnemonically stored data-clusters. The formalisation of such feelings into broadly nuanced emotions determines finally our faculty to explicitly recognise significant contingencies and experiences, and it boosts our ability to remember and to learn on the basis of previous experiences.

In conclusion, the EFN model appears to accommodate both the views proposed by Panksepp and LeDoux, and the approach suggested by Damasio and Bechara. While in the classical approach to the relation of emotion and cognition (Stuss and Benson, 1986^[67]) the frontal lobes are assigned the role of coordinators - in maintaining affective states and their emotional expressions under cognitive control - the EFN model suggests a more distributed processing network, allowing relatively independent broadcastings of feeling and cognitively processed information, instantiating different degrees of consciousness in the presence and absence of external stimulation. In this sense, the EFN framework offers angles compatible with the model proposed by Pereira Jr. and Furlan (2010^[59]), Pereira Jr., Furlan and Pereira, (2011^[60]), which accounts for the variable degrees of interaction between cognitive and affective states.

Take home message

The conceptual revolution brought about by affective neuroscience led to an emphasis on experimental studies of affective states and processes which were not accessible to conscious attention. These states and processes were then called "unconscious emotion". However, many of these states/processes elicit *conscious feelings*. In the perspective of our proposed theory of consciousness, the expression "unconscious emotion" refers to conscious feelings, which are components of episodes of "affective consciousness" (according to the proposal of Panksepp, 2005a^[56]). Feelings are events of the endogenous feedback network,

^hIn anatomical terms, this interaction is mediated by signals from ventral to dorsal region of the central nucleus of the amygdala which in turn modulates attention (De Gelder, 2005²⁴).

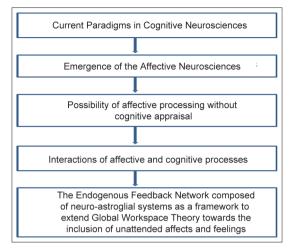


Figure 2: Flowchart of paper

when the information content of a stimulus elicits a reactive process (e.g., an evoked electric potential), which feeds back on the network's processing units, leading to the formation of a conscious episode that may be (or not be) expressed in terms of emotions and respective covert/overt behaviours.

Conflict of interest

None declared.

Declaration

This is our original, unpublished work, not under consideration for publication elsewhere.

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Questions that this Paper Raises

- 1. What does Affective Neuroscience mean for a Theory of Consciousness?
- 2. What are the differences between core affects, feelings, and emotions?
- 3. What are the brain circuits responsible for affective and cognitive processing? How do they run in parallel and at the same time reciprocally interact?
- 4. What are the main contributions of Panksepp and LeDoux in the emerging field of Affective Neuroscience?
- 5. How does the flux of consciousness extend beyond the focus of attention?

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